INTEGRATED PRINCIPLES OF ZOOLOGY

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ELEVENTH EDITION

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Washington and Lee University

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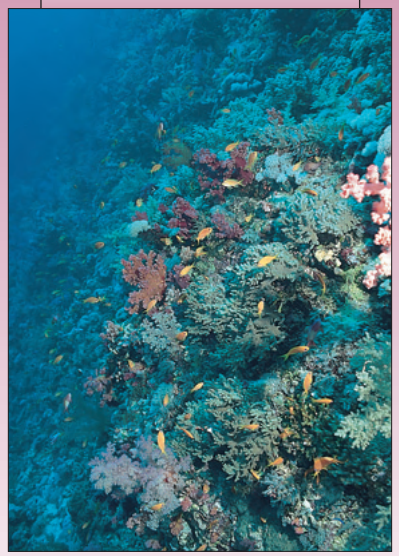
CONTENTS IN BRIEF

CONTENTS

PART THREE



THE DIVERSITY OF ANIMAL LIFE

◀ | ▶ | e-Text Main Menu | Textbook Table of Contents

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Over the years, Dr. Hickman has led many field trips to the Galápagos Islands. His current research is on intertidal zonation and marine invertebrate systematics in the Galápagos. He has published two field guides in the Galápagos Marine Life Series for the identification of echinoderms and marine molluscs. His interests include scuba diving, woodworking, and participating in chamber music ensembles.

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PREFACE

PREAMBLE

How does one direct the revision of a classic? As the Editor faced with the responsibility of instructing authors to improve further an incredibly successful and comprehensive text, I thought the answer to be a special focus on "contemporary." The eleventh edition is a bridge to the twenty-first century in teaching general zoology. It combines classical coverage of animal biology with new research, new phylogenies, and new technologies.

Students using this text will be exposed to the most current coverage of zoology in addition to being the first to have integrated multimedia as part of their studies. ***Integrated Principles of Zoology*** is supported by a tutorial CD-ROM, the Essential Study Partner; an Online Learning Center Web site with additional readings, animations, and quizzing; and a Visual Resource Library CD-ROM that contains 1,000 line drawings and photos to enhance lecture presentations.

Along with the authors, our editorial team strives to produce the finest educational resources to support your instructional and educational objectives. I invite you to read, enjoy, and respond to a classic of the twenty-first century!

Margaret J. Kemp
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Integrated Principles of Zoology is a college text adaptable to any introductory course in zoology. This eleventh edition, as with previous editions, describes the diversity of animal life and the fascinating adaptations that enable animals to inhabit nearly all conceivable ecological niches. We retain in this revision the basic organization of the tenth edition and its distinctive features, especially emphasis on the principles of evolution and zoological science. Also retained are several pedagogical features that have made previous editions easily accessible to students: opening chapter dialogues drawn from the chapter's theme; chapter summaries and review questions to aid student comprehension and study; accurate and visually appealing illustrations; in-text derivations of generic names; chapter notes and essays that enhance the text by offering interesting sidelights to the narrative; and an extensive glossary providing pronunciation, derivation, and definition of terms used in the text.

New to the Eleventh Edition

Many of the changes in this edition were guided by the suggestions of more than 60 zoology instructors who read and commented on sections of the tenth edition. In addition, the vertebrate chapters of Part Three, and several chapters on functional systems (Part Four) were revised by invited Contributors, all experienced zoologists who were solicited for their interest and expertise in the subject matter of specific chapters. In general, all chapters were revised to make the text current while eliminating excessive detail, and to place more emphasis on experimentation and comparative studies in zoology.

Chapter Organization

- Separate treatments of the origin of life and chemistry of life are condensed into a single chapter (Chapter 2), thus streamlining the presentation by discussing basic chemistry in the context of the origin of life.
- The order of chapters in Part Two is altered to offer a better study sequence for students, providing a grounding in genetics and evolutionary theory before undertaking the chapters on reproduction and development. There are numerous places in the development chapter in which an understanding of genetics is crucial.
- A completely new chapter on immunology (Chapter 37) was developed, covering both vertebrate and invertebrate immunology and embracing many new discoveries in this fast-moving field.

New Pedagogy

- Throughout the text we updated references, revised or replaced many illustrations, and rewrote many of the Review Questions to provoke thought and reduce emphasis on rote memorization.

◀ | ▶ | e-Text Main Menu | Textbook Table of Contents

- Suggested Internet topics are added at the end of each chapter; hyperlinks are available on this text's Online Learning Center web site at www.mhhe.com/zoology.
- The end paper on Origin of Life and Geologic Time Table has been replaced with a revised version in full color.

The principal revisions are explained below.

Part One: Introduction to the Living Animal

- Chapters 2 (Chemistry) and 3 (Origin of Life) now form an integrated review of the kinds of organic molecules found in living systems and their origins in the earth's primitive reducing atmosphere. A review of basic chemistry (atoms, elements, and molecules; bonding theory; acids, bases, salts, and buffers) is available for reference; it will be found at our Online Learning Center web site www.mhhe.com/zoology).
- For Chapter 3, on cells as units of life, we revised the discussion of cell structure and cell junctions, and reorganized the sequence of certain topics. Several illustrations in this and the following chapter on cellular metabolism were redrawn for this edition.

Part Two: Continuity and Evolution of Animal Life

- Chapter 5, Principles of Genetics, features a revised section on molecular genetics, adding a new coverage of genomics and a new subsection on molecular systematics. The increasing ease with which genes can be sequenced and compared to sequences of the same gene in other taxa has led to a great many revisions of phylogenies based on sequence analysis. Such findings have made necessary many changes in the diversity chapters in Part Three of this book.
- Chapter 7, The Reproductive Process, was revised to clarify relationships among bisexual reproduction, hermaphroditism, and parthenogenesis. A new section on sex determination summarizes the most recent understanding of the male determining gene and masculinizing hormones, and discovery of the sex reversing X region on the X chromosome and its role in promoting ovary formation. The final section on endocrine events that orchestrate reproduction was rewritten and updated.
- Chapter 8, Principles of Development, was extensively revised in both text and line art. The order in which material on cleavage is presented was reorganized to clarify relationships among principal topics of yolk amount and distribution, cleavage type, cleavage pattern, and subtopics of direct and indirect development, mosaic versus regulative development, and differences between protostomes and deuterostomes. Cleavage of centrolecithal eggs was added. The section on gastrulation now compares the process in sea stars, reptiles, birds, and mammals. Among other sections revised and updated were those on cytoplasmic specification and homeotic genes.

Part Three: The Diversity of Animal Life

- Chapter 9 provides a concise presentation on animal architecture as an introduction to animal diversity, which is the core of most zoology courses. Several sections of this chapter were revised: complexity and body size, muscular tissue, animal body plans, body cavities, and terminology used in specifying aspects of symmetry.
- Chapter 10, Classification and Phylogeny of Animals, explains the principles of animal taxonomy and how they are applied by the competing schools of evolutionary taxonomy and cladistics. Because classification pervades every course in zoology, students should understand that systematics provides the evolutionary basis for zoological study. Changes include revision of systematics of great apes to use a cladistic classification, and updating of the material on classification of the Bilateria to incorporate results of new molecular phylogenetic studies.
- The title of Chapter 11 was changed from "The Animal-like Protista" to "Protozoan Groups." Although both Protozoa and Protista no longer are considered valid taxa, we continue to use the terms "protozoa" and "protozoan" informally to distinguish these animal-like phyla. Among sections revised in the protozoan chapter are pseudopodial movement, mechanism of contractile vacuole action, and the final sections on phylogeny and classification.
- For Chapter 12 (Mesozoa and Parazoa) we revised the sections on origin and phylogeny of Metazoa, and deleted reference to class Sclerospongiae, which is no longer recognized as a valid taxon.
- We made several changes in Chapters 14 and 15 on acoelomate and pseudocoelomate animals, including reorganization of the material on class Turbellaria, and revision of the phylogeny sections for both chapters. There is evidence now that acoels (order Acoela) are not flatworms but form the sister group for all other Bilateria. All remaining acoelomates are now placed in the newly erected protostome superphylum Lophotrochozoa.
- Each of the pseudocoelomate phyla is assigned to either Lophotrochozoa or to the alternative superphylum Ecdysozoa. Phylogeny sections for mollusc, annelid, and arthropod chapters also were revised to embrace new

information from sequence analysis, which places Mollusca and Annelida in superphylum Lophotrochozoa, and Arthropoda in superphylum Ecdysozoa. We point out, however, that analysis upon which the Lophotrochozoa/Ecdysozoa hypothesis is based fails to support monophyly of Mollusca and Annelida. Nevertheless, few if any zoologists believe molluscs and annelids are not monophyletic groups.

- In Chapter 20, on terrestrial mandibulates, we introduce the term parasitoid and emphasize the importance of parasitoids in controlling populations of other insects. Among other changes in this chapter we strengthened coverage of pheromones, including use of pheromone baits in insect traps and importance of such use in monitoring insects of economic importance.
- Lophophorate animals (Chapter 22) are now assigned to Protostomia, forming an important group in superphylum Lophotrochozoa. If lophophorates are protostomes as most recent evidence suggests, the trimerous coelomic arrangement must have evolved independently in protostomes and deuterostomes.
- Chapter 25 (chordates) received minor revision, including reworking sections on ancestry and evolution, chordate fossil discoveries, and position of amphioxus in speculations on chordate ancestry.
- Chapter 26 on fishes was extensively revised. With Osteichthyes no longer considered a valid taxon, Actinopterygii and Sarcopterygii are elevated to class; this change is accompanied by a discussion of the origin and radiation of ray-finned fishes, radiation of the neopterygians, and morphological trends that permitted great diversification of the teleosts. Introductory sections on ancestry, relationships, and biology of fishes were rewritten to clarify relationships among major fish groups. Revisions in the section on sharks include discussions of sensory systems, shark attacks, and reproduction. Several changes were made in the art program, including corrections in synapomorphies in the cladogram of fishes.
- The title of Chapter 28 was changed to Reptilian Groups to emphasize paraphyly in class Reptilia. Topics revised in this chapter include lung breathing in turtles, viviparity, and characteristics that distinguish reptiles from amphibians.
- In the bird chapter (Chapter 29) we added a note on recent fossil bird discoveries, and revised discussions of skeletal weight comparisons in birds and mammals, bird kidney function, and sun-azimuth orientation of bird migration. We reorganized the treatment of forms of bird wings for flight and added a new illustration to show hovering flight in hummingbirds.
- Chapter 30, Mammals, includes an updated discussion of the first hominids to summarize recent fossil finds, and a revised illustration of hominid skulls. Other changes: adoption of a cladistic classification for primates, and revision of discussions of horns and antlers, glands, feeding specializations, body weight and food consumption, and reproductive patterns.

Part Four: Activity of Life

- The revisions for Chapter 31, Support, Protection, and Movement, include discussions of skin cancer from sunlight, mechanisms of ciliary movement, energy for muscle contraction, fast and slow fibers, and description of dermal derivative in vertebrates.
- Chapter 32, Homeostasis, was updated throughout. Treatments revised include hyperosmotic regulation in invertebrates, hypoosmotic regulation in fishes, shark kidney function, mechanism of contractile vacuole function, and glomerular filtration.
- A major improvement in flow and unity of Chapter 33, Internal Fluids and Respiration, was transfer of defense mechanisms and immunity to a separate chapter (Chapter 37).
- Chapter 34, Digestion and Nutrition, includes a discussion on nutritional requirements to embrace new understanding of relationships among the hunger center, brown fat, the protein thermogenin, and the recently discovered hormone leptin. We also updated statistics on world meat consumption, malnutrition, and world population. The discussion on gastrointestinal hormones, previously included in the endocrine chapter, was moved to this chapter.
- The chapter on nervous coordination (Chapter 35) was revised throughout. The most important revisions appear in sections dealing with nature of the nerve impulse, synapses, evolution of invertebrate nervous systems, reflex acts and reflex arcs, autonomic nervous systems, odor reception, and color vision.
- Chapter 36, Chemical Coordination, features an updated section on second messenger system, and new sections that describe the role of growth hormone as a diabetogenic hormone, and action of the most recently discovered hormone, leptin, in regulating eating behavior and energy balance.
- Chapter 37, Immunity, is *new* and covers the topics of susceptibility and resistance, innate defense mechanisms, acquired immune response in vertebrates, blood group antigens, and immunity in invertebrates. The section on acquired immune response in vertebrates includes descriptions of self–nonself discrimination (MHC proteins), recognition molecules (antibodies and T-cell receptors), cytokines, humoral response (T_H2 arm), and cell-mediated response (T_H1 arm).
- Chapter 38 concludes this unit with a discussion of animal

behavior. It features an expanded explanation of the ritualization of behavior, and new sections on diversity of mating systems, altruistic behavior and kin selection, and animal cognition. The latter describing the remarkable studies of the Gardners with the chimpanzee Washoe, and Pepperberg's work with an African grey parrot.

Part Five: The Animal and Its Environment

- Chapter 39, The Biosphere and Animal Distribution, includes an updated discussion of the proposed effect of carbon dioxide on the earth's climate. It also provides an expanded explanation of the earth's heat engine, with accompanying new art, and added mean annual temperature and rainfall values to all biome descriptions.
- Chapter 40, Animal Ecology, was completely rewritten to provide much greater emphasis on populational and community ecology. It features expanded explanations of niche, characteristics of population (age structure, growth rates, survivorship), population regulation, and interactions among populations in communities.

Teaching and Learning Aids

To help students in **vocabulary development**, as in previous editions we have boldfaced key words, and provided the derivations of technical and zoological terms, and generic names of animals where they first appear in the text. In this way students gradually become familiar with the more common roots that comprise many technical terms. An extensive glossary of almost 1,100 terms provides pronunciation, derivation, and definition of each term. Many new terms were added to the glossary or rewritten for this edition.

A distinctive feature of this text is a **chapter prologue** for each chapter that draws out some theme or fact relating to the subject of the chapter. Some present biological, particularly evolutionary, principles; others (especially those in the survey sections) illuminate distinguishing characteristics of the group treated in the chapter. Each is intended to present an important concept drawn from the chapter in an interesting manner that will facilitate learning by students, as well as engage their interest and pique their curiosity.

Chapter notes, which appear throughout the book, augment the text material and offer interesting sidelights without interrupting the narrative. We prepared many new notes for this edition and revised several of the existing notes.

To assist students in chapter review, each chapter ends with a **concise summary,** a list of **review questions,** and **annotated selected references.** The review questions enable the student to self-test retention and understanding of the more important chapter material.

The **historical appendix,** unique to this textbook, lists key discoveries in zoology, and separately describes books and publications that have greatly influenced the development of zoology. Many readers have found this appendix an invaluable reference to be consulted long after their formal training in zoology. The historical appendix will be found on this textbook's Online Learning Center web site at www.mhhe.com/zoology.

Again, William C. Ober and Claire W. Garrison have enhanced 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 seven 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.

Supplements

The **Instructor's Manual and Test Item File** provides annotated chapter outlines, chapter-specific changes for this edition, lecture enrichment suggestions, commentaries and lesson plans, questions for advanced classes, and a listing of resource references for each chapter. Also included is a listing of transparencies and slides available with the book, and a comprehensive test bank offering 35 to 50 objective questions per chapter. We trust this will be of particular value to first-time users of the text, although experienced teachers may also find much of value.

The **Laboratory Manual** by Cleveland P. Hickman, Jr., Frances M. Hickman, and Lee B. Kats, *Laboratory Studies in Integrated Zoology*, has been revised to include new exercises on molecular techniques. This manual can be adapted conveniently for two semester, one semester, or term courses by judicious selection of exercises.

Test questions contained in the Instructor's Manual and Test File are also available as a **Computerized Test Bank,** a test-generation system for IBM and Macintosh computers. Using this system, instructors can create tests or quizzes quickly and easily. Questions can be sorted by type or level of difficulty, and instructors also can add their own material to the bank of questions provided.

A set of 150 full-color **transparency acetates** of important textual illustrations are available with this edition of *Integrated Principles of Zoology*. Labeling is clear, dark, and bold for easy reading.

A set of 148 animal diversity slides, photographed by the authors and Bill Ober on their various excursions, are offered in this unique textbook supplement. Both invertebrates and vertebrates are represented.

Descriptions, including specific names of each animal and brief overview of the animal's ecology and/or behavior, accompany the slides.

A **Zoology Visual Resource Library CD-ROM,** containing 1,000 line drawings and photos, is now available to instructors to enhance lecture presentations (see page xxiv for more details).

A tutorial CD-ROM, the **Essential Study Partner,** will be available soon to aid students in their study of zoology (see page xxi for more details).

An **Online Learning Center web site** is available with this edition, and contains additional readings, animations, quizzing, key terms flashcards, cladogram exercises, and much more (see page xix for specific information). Check it out at www.mhhe.com/zoology.

By the end of 2000, this text will also be available in a CD-ROM format, complete with hyperlinks to the Online Learning Center, an interactive glossary, and animations (see page xxii for more details).

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Chapter 35 Nervous Coordination
Chapter 36 Chemical Coordination
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Although we make every effort to bring to you an error-free text, errors of many kinds inevitably find their way into a textbook of this scope and complexity. We will be grateful to readers who have comments or suggestions concerning content to send their remarks to Donna Nemmers, Developmental Editor, 2460 Kerper Boulevard, Dubuque, IA 52001. Donna may also be contacted by e-mail: donna_nemmers@mcgraw-hill.com, or through this textbook's web site: www.mhhe.com/zoology.

Cleveland P. Hickman, Jr.
Larry S. Roberts
Allan Larson

The Online Learning Center

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This text-specific web site allows students and instructors from all over the world to communicate. Instructors can create a more interactive course with the integration of this site, and students will find tools such as practice quizzing, key term flashcards, and animations that will help them improve their grades and learn that zoology can be fun.

Student Resoures

Chapter Synopsis
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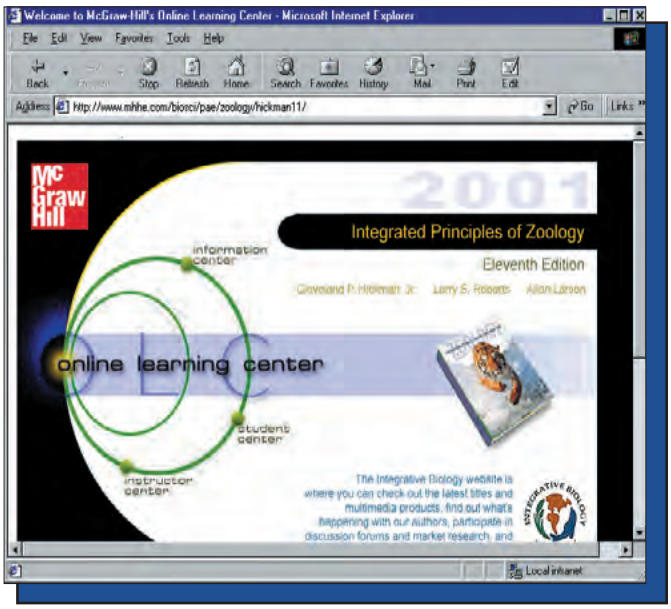
"Development of Zoology" timeline
"Basic Structure of Matter" appendix



Instructor Resources

Instructor's Manual
- Chapter outlines
- Eleventh edition changes
- Lecture enrichment
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- Advanced class questions
- Source materials

Links to related web sites to expand on particular topics
List of Visual Resource Library (VRL) images
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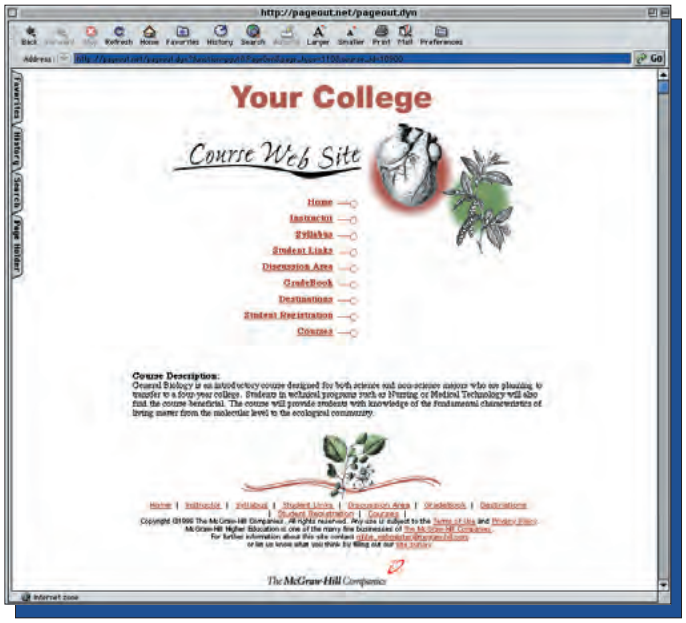

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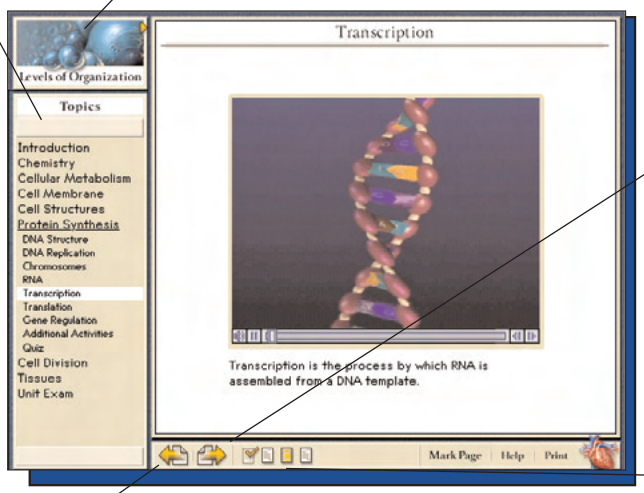

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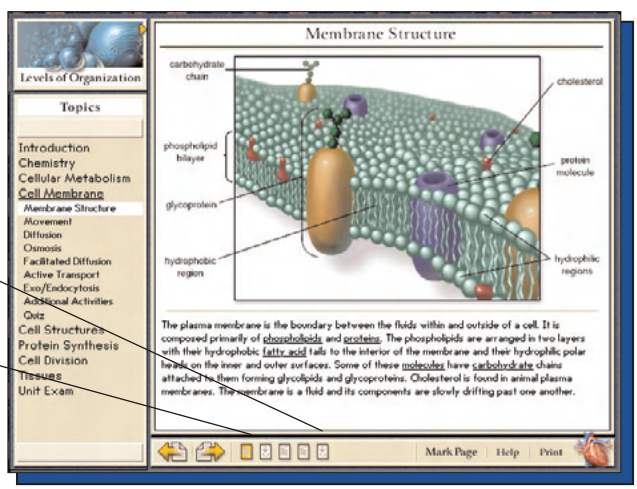

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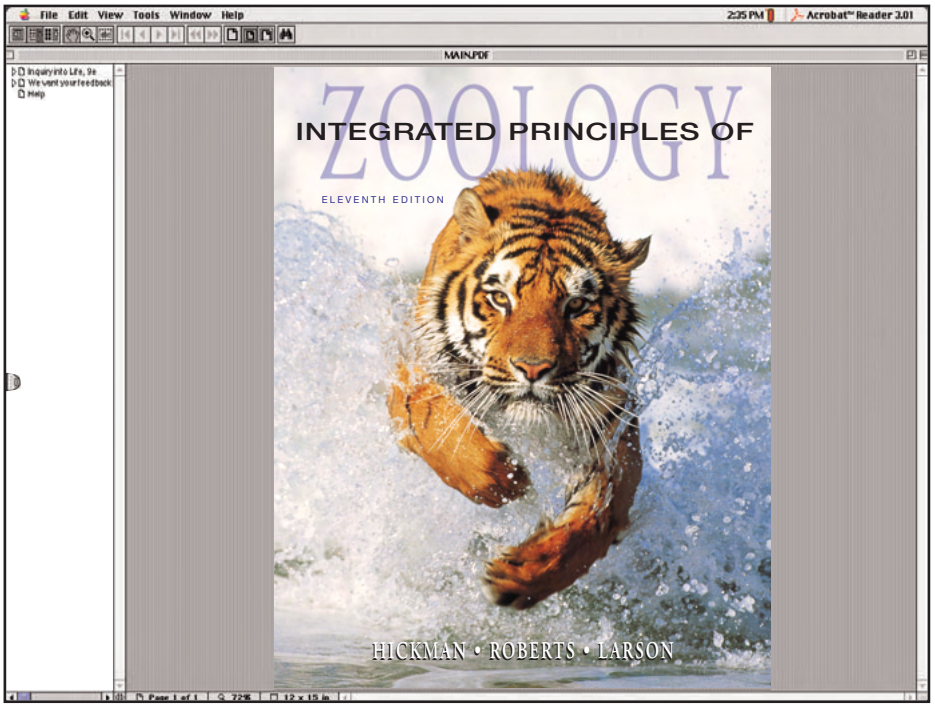

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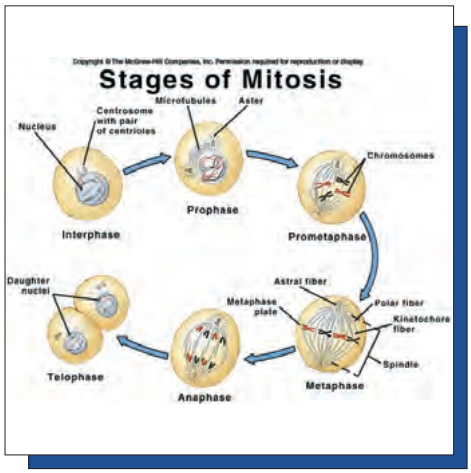

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PART ONE

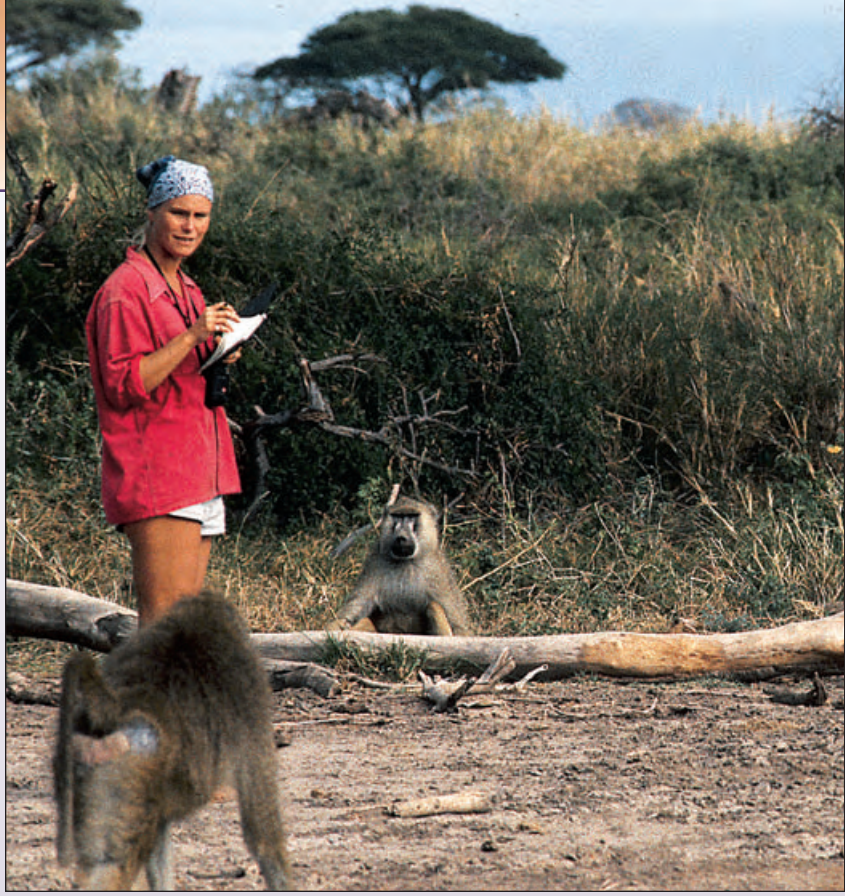
Introduction to the Living Animal

A green frog, *Rana clamitans*, in a Michigan pond.

CHAPTER

1

Life: Biological Principles and the Science of Zoology



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

The Uses of Principles

We gain knowledge of the animal world not in a passive or haphazard manner but by actively applying important guiding principles to our investigations. Just as the exploration of outer space is both guided and limited by available technologies, exploration of the animal world depends critically on our questions, methods, and principles. The body of knowledge that we call zoology makes sense only when the principles that we use to construct it are clear.

The principles of modern zoology have a long history and many sources. Some principles derive from the laws of physics and chemistry, which all living systems obey. Others derive from the scientific method, which tells us that our hypotheses regarding the animal world are useless unless they guide us to gather data that potentially can refute them. Many important principles derive 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 all of life shares a common evolutionary origin, principles learned from the study of one group often may be applied to other groups as well. By tracing the origins of our operating principles, we see that zoologists are not an island unto themselves but form an integrated part of the scientific community.

We begin our study of zoology not by focusing narrowly within the animal world, but by searching broadly 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 inquiry into the animal world. The mythologies of nearly every human culture document 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 throughout all branches of science. We start by documenting the diversity of animal life and organizing 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 (Figure 1-1). We strive through this work to understand how animal diversity originated and how animals perform the basic processes of life that permit them to thrive in many diverse environments.

This chapter introduces the fundamental properties of animal life, the methodological principles on which their study is based, 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 guides our study of heredity and variation in animals. These theories unify our knowledge of the animal world.

Fundamental Properties of Life

Does Life Have Defining Properties?

We begin with the difficult question, What is life? Although many attempts have been made to define life, simple definitions are doomed to failure. When we try to give life a simple definition, we look for fixed properties maintained throughout life's history. However, the properties that life exhibits today (pp. 3–10) are very different from those present at its origin. The history of life shows perpetual change, which we call *evolution*. As the genealogy of life progressed and branched from the earliest living form to the millions of species living today, new properties evolved and passed from parents to their offspring. Through this process, living systems have generated many rare and spectacular features that have no counterparts in the nonliving world. Unexpected properties emerge on many different lineages in life's evolutionary history, producing the great organismal diversity observed today.

We might try to define life on the basis of universal properties evident at its origin. Replication of molecules, for example, can be traced to life's origin and represents one of life's universal properties. Defining life based on properties present at its origin faces the major problem that these are the properties most likely to be shared by some nonliving forms. To study the origin of life, we must ask how organic molecules acquired the ability for precise replication. But where do we draw the line between those replicative processes that characterize life and those that are merely general chemical features of the matter from which life arose? Replication of complex crystalline structures in nonliving chemical assemblages might be confused, for example, with the replicative molecular properties associated with life. If we define life using only the most advanced properties that characterize the highly evolved living systems observed today, the nonliving world would not intrude on our definition, but we would eliminate the early forms of life from which all others descended and which give life its historical unity.

Ultimately our definition of life must be based on the common history of life on earth. Life's history of descent with modification gives it an identity and continuity that separates it from the nonliving world. We can trace this common history backward through time from the diverse forms observed today and in the fossil record to their common ancestor that arose in the atmosphere of the primitive earth (see Chapter 2). All organisms forming part of this long history of hereditary descent from life's common ancestor are included in our concept of life.

We do not force life into a simple definition, but we can readily identify the living world through its history of common evolutionary descent and separate it from the nonliving. Many remarkable properties have arisen during life's history and are observed in various combinations among living forms. These properties, discussed in the next section, clearly identify their possessors as part of the unified historical entity called life. All such features occur in the most highly evolved forms of life, such as those that compose the animal kingdom. Because they are so important for maintenance and functioning of living forms that possess them, these properties should persist through life's future evolutionary history.

General Properties of Living Systems

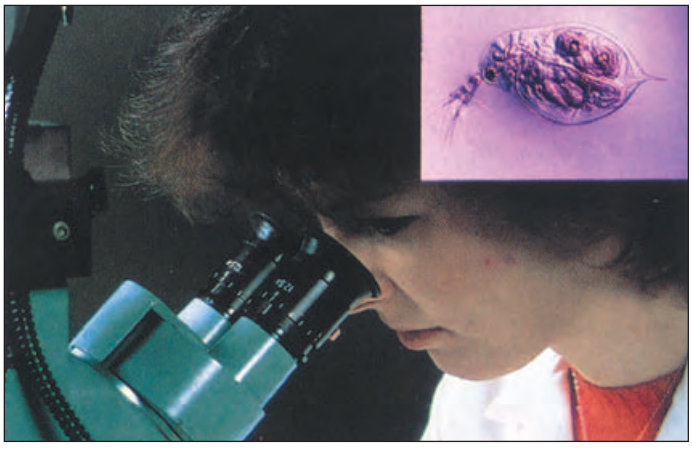
The most outstanding general features that have arisen during life's history include chemical uniqueness; complexity and hierarchical organization; reproduction (heredity and variation); possession of a genetic program; metabolism; development; and environmental interaction.

1. **Chemical uniqueness.** *Living systems demonstrate a unique and complex molecular organization.* The history of life has featured the assembly of large molecules, known as macromolecules, that are far more complex than the small molecules that constitute nonliving matter. These macromolecules are composed of the same kinds of atoms and chemical bonds that occur in nonliving matter and they obey all fundamental laws of chemistry; it is only the complex organizational structure of these macromolecules that makes them unique. 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 functions in living systems.

A

B

C



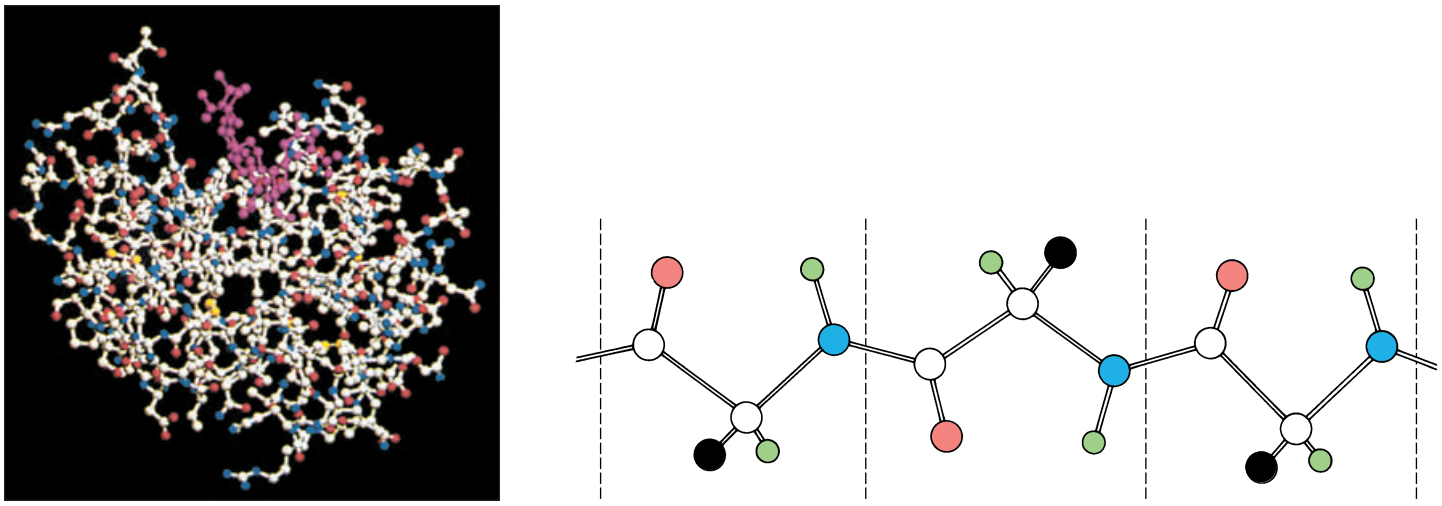
D

Figure 1-1

A few of the many dimensions of zoological research: **A,** Observing moray eels in Maui, Hawaii; **B,** Working with tranquilized polar bears; **C,** Banding mallard ducks; **D,** observing *Daphnia pulex* (×150) microscopically.

The general structures of these macromolecules evolved and stabilized early in the history of life. With some modifications, these same general structures are found in every form of life that we observe today. Proteins, for example, contain about 20 specific kinds of amino acid subunits linked together by peptide bonds in a linear sequence (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 2-11). 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 the protein molecule is subject to enormous variation. This variation underlies much of the diversity that we observe among different kinds of living forms. The nucleic acids, carbohydrates, and lipids likewise contain characteristic bonds that link variable subunits (Chapter 2). This organization gives living systems both a biochemical unity and a great potential for 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 the nonliving world. In living systems, we find a hierarchy of levels that includes, in ascending order of complexity, macromolecules, cells, organisms, populations, and species (Figure 1-3). Each level builds on the level below it and has its own internal structure, which is also often hierarchical. Within the cell, for example,



A B

Figure 1-2

A computer simulation of the three-dimensional structure of the lysozyme protein **(A),** which is used by animals to destroy bacteria. The protein is a linear string of molecular subunits called amino acids, connected as shown in **B,** that 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.** The purple molecule in **A** is a structure from the bacterial cell wall that is broken by lysozyme.

macromolecules are compounded 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 Chapters 3 and 4). The organismal level also has a hierarchical substructure; cells are combined into tissues, which are combined into organs, which likewise are combined into organ systems (see Chapter 9).

Cells (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 viewed as the basic units of living systems (Chapter 3). We can isolate cells from an organism and cause them to grow and multiply under laboratory conditions in the presence of nutrients alone. This semiautonomous replication is not possible for any individual molecules or subcellular components,

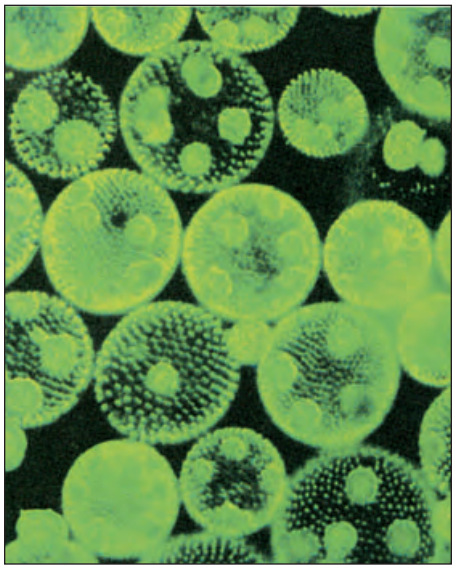


Figure 1-3

Volvox globator (see pp. 224–225) is a multicellular phytoflagellate 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.

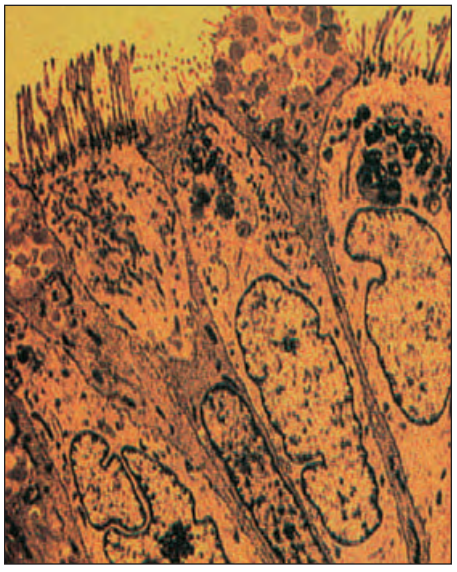


Figure 1-4

Electron micrograph of ciliated epithelial cells and mucus-secreting cells (see pp. 185–188). Cells are the basic building blocks of living organisms.

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	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	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

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 characteristic of this hierarchy is that the properties of any given level cannot be obtained from even 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 observed in bees, occur at the populational level; it would not be possible to infer properties of this social system by knowing only properties of individual bees.

The appearance of new characteristics at a given level of organization is called **emergence,** and these characteristics are known as **emergent properties.** These properties arise from interactions that occur among the component parts of a system. For this reason, we must study all levels directly, and subdivisions of the field of biology (molecular biology; cell biology; organismal anatomy, physiology and genetics; population biology) reflect this fact (Table 1-1). We find that 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, it would be impossible for a population of organisms that lack hearing to develop a spoken language. Nonetheless, properties of parts of a living system do not rigidly determine the properties of the whole. Many different spoken languages have 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 products of evolution. Before multicellular organisms evolved, there was no distinction between the organismal and cellular levels, and it is still absent from single-celled organisms (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 a process of reproduction. Although life certainly originated from nonliving matter at least once (Chapter 2), this

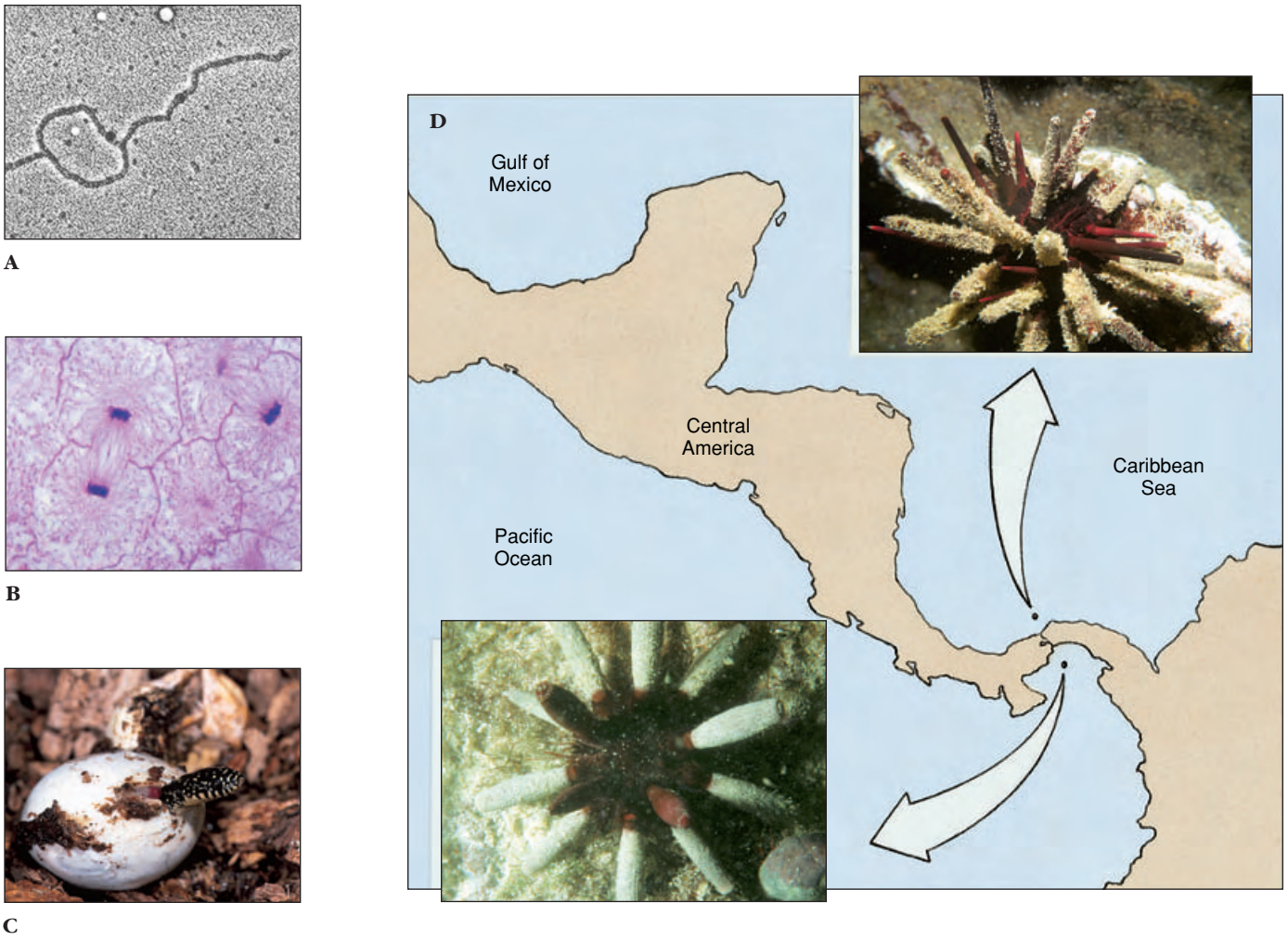


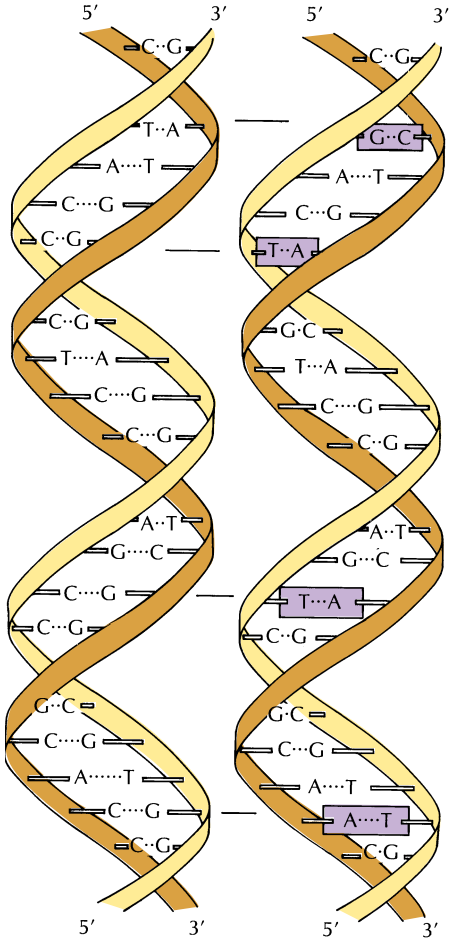
Figure 1-5

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 the sea urchin (*Eucidaris*) after geographic separation of Caribbean (*E. tribuloides*) and Pacific (*E. thouarsi*) populations by the formation of a land bridge.

required enormously long periods of time and conditions very different from those of the modern biosphere. At each level of the biological hierarchy, living forms reproduce to generate others like themselves (Figure 1-5). Genes are replicated to produce new genes. Cells divide to produce new cells. Organisms reproduce, **sexually** or **asexually,** to produce new organisms (Chapter 5). Populations can become fragmented to give rise to new populations, and species can give rise to new species through a process known as speciation. Reproduction at any level of the hierarchy 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 features 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) observed at the organismal level. Variation is the production of *differences* among the traits of different individuals. In the reproductive process, the properties of descendants resemble those of their parents to varying degrees but are usually not identical to them. Replication of deoxyribonucleic acid (DNA) occurs with high fidelity, but errors occur at repeatable rates. Cell division is an exceptionally precise process, especially with regard to the nuclear material, but chromosomal changes occur

A



B

Figure 1-6

James Watson and Francis Crick with a model of the DNA double helix **(A).** Genetic information is coded in the nucleotide base sequence inside the DNA molecule. 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 encode alternative traits, such as different eye colors.

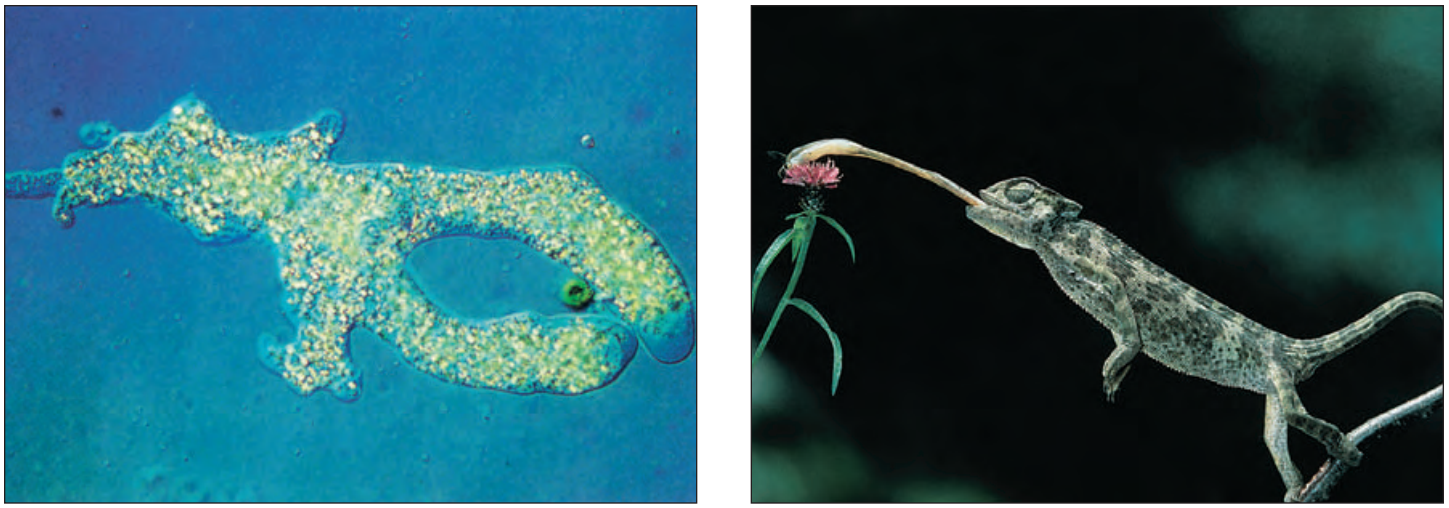
nonetheless at measurable rates. Organismal reproduction likewise demonstrates both heredity and variation, the latter being obvious especially in sexually reproducing forms. The production of new populations and species also demonstrates conservation of some properties and changes of others. Two closely related frog species may have similar mating calls but differ in the rhythm of repeated sounds.

We will see later in this book that the interaction of heredity and variation in the reproductive process is the basis for organic evolution (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* (Figure 1-6). The structures of the protein molecules needed for organismal development and functioning are encoded in **nucleic acids** (Chapter 5). For animals and most other organisms, the genetic information is contained in **DNA.** 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 represents 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 known as the **genetic code.**

The genetic code was established early in the evolutionary history of life, and the same code is present 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 in which the altered protein structures are still compatible with their cellular functions would such a change have a chance to 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 nuclear DNA, the likelihood of getting a change in the code that does not disrupt cellular functions is greater there than in the nucleus.

5. **Metabolism.** *Living organisms maintain themselves by obtaining nutrients from their environments* (Figure 1-7). The nutrients are broken down to obtain chemical energy and molecular components for use in building and maintaining the living system (Chapter 4). We call these essential chemical processes **metabolism.** They include digestion, production of energy (respiration), and synthesis of molecules and structures. Metabolism is often viewed as an interaction of destructive (catabolic) and constructive (anabolic) reactions. The most fundamental



A B

Figure 1-7
Feeding processes illustrated by **(A)** an ameba surrounding food and **(B)** a chameleon capturing insect prey with its projectile tongue.

anabolic and catabolic chemical processes used by living systems arose early in the evolutionary history of life and are shared by all living forms. These include synthesis of carbohydrates, lipids, nucleic acids, and proteins and their constituent parts and the 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 that are found throughout the animal kingdom. Cellular respiration occurs, for example, in the mitochondria. The cellular and nuclear membranes regulate metabolism by controlling the movement of molecules across the cellular and nuclear boundaries, respectively. The study of the performance of complex metabolic functions is known as **physiology.** We will 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 the basic physiological functions of life (Chapters 11 through 37).

A B

Figure 1-8
Pupal and adult stages of an insect life cycle: **A,** Adult monarch butterfly emerging from its pupal case; **B,** Fully formed adult monarch butterfly.

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 the egg by sperm) to its final adult form (Chapter 8). Development usually features changes in size and shape, and the differentiation of structures within the 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. In some multicellular forms, different stages of their life

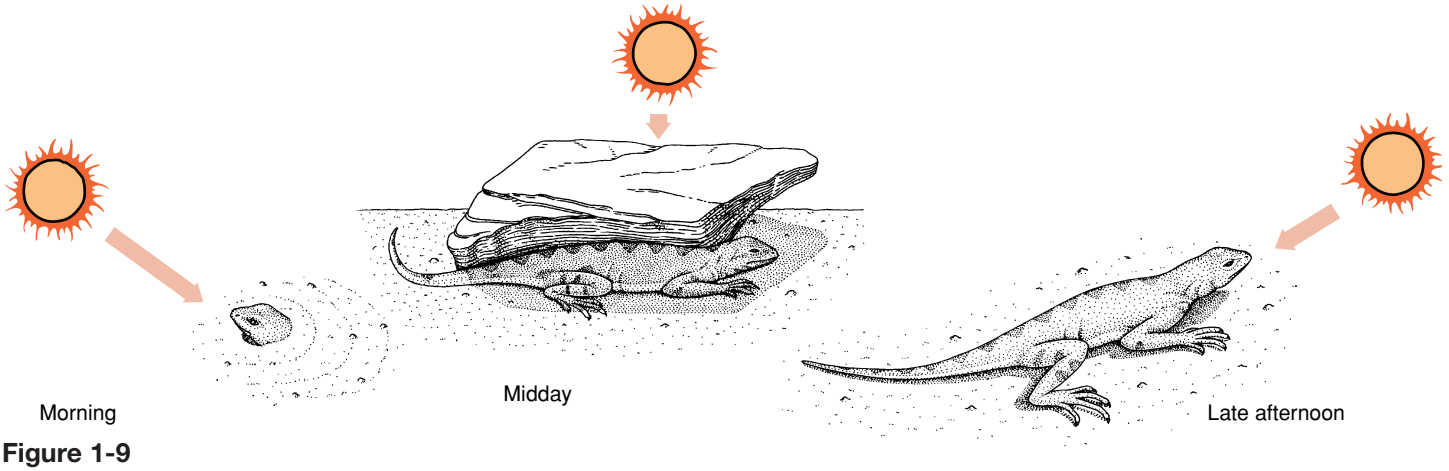


Figure 1-9
A lizard regulates its body temperature by choosing different locations (microhabitats) at different times of day.

cycle are so dissimilar that they are hardly recognizable as part of the same species. Embryos are distinctly different from juvenile and adult forms into which they will develop. Even the postembryonic development of some organisms includes stages that are 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 (Figure 1-8). Among animals, the early stages of development are often more similar among organisms of related species than are later developmental stages. In our survey of animal diversity, we will describe all stages of observed life histories, but we will concentrate on adult stages in which diversity both within and between different animal groups tends to be greatest.

7. **Environmental interaction.** *All animals interact with their environments.* The study of organismal interaction with the environment is known as **ecology.** Of special interest are the factors that affect the geographic distribution and abundance of animals (Chapters 39 and 40). The science of ecology permits us to understand how an organism can perceive environmental stimuli and respond in appropriate ways by adjusting its metabolism and physiology (Figure 1-9). All organisms respond to stimuli in their environment, and this property is 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 may be quite complex, such as a bird responding to a complicated series of signals in a mating ritual (see Chapter 38). Life and the environment are inseparable. We cannot isolate the evolutionary history of a lineage of organisms from the environments in which it occurred.

Life Obeys Physical Laws

To untrained observers, these seven properties of life may appear to violate the basic laws of physics. Vitalism, the idea that life is endowed with 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 operate and evolve within the constraints of the basic laws of physics and chemistry. The laws governing energy and its transformations (thermodynamics) are particularly important for understanding life (Chapter 4). The **first law of thermodynamics** is the law of conservation of energy. Energy is neither created nor destroyed, but it 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 in the form of light and heat. Sunlight is captured by green plants and cyanobacteria and transformed by photosynthesis into chemical bonds. The energy in chemical bonds is a form of potential energy that can be 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 the animals that eat the plants, and these animals may in turn provide energy for other animals that eat them.

The **second law of thermodynamics** states that physical systems tend to proceed toward a state of greater disorder, or **entropy.** The energy obtained and stored by plants is subsequently released by a variety of mechanisms and finally dissipated as heat. The high degree of molecular organization found in living cells is attained and maintained 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. The process of evolution whereby organismal complexity can increase over time may appear at first to violate the second law of thermodynamics, but it does not. Organismal complexity is achieved and maintained only by the constant use and dissipation of energy flowing into the biosphere from the

sun. The survival, growth, and reproduction of animals requires energy that comes from breaking complex food molecules into simple organic waste products. The processes by which animals acquire energy through nutrition and respiration command the attention of the many physiological sciences.

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 known as **eukaryotes,** organisms whose cells contain membrane-enclosed nuclei. This larger limb includes the plants and fungi. Perhaps the most distinctive characteristic of the animals as a group is their means of nutrition, which consists of eating other organisms. This basic way of life has led to the evolution of many diverse systems for locomotion and for capturing and processing a wide array of food items.

Animals can be distinguished also by the absence of properties that have evolved in other eukaryotes. Plants, for example, have evolved the ability to use light energy to produce organic compounds (photosynthesis), and they have evolved rigid cell walls that surround their cell membranes; photosynthesis and cell walls are absent from animals. Fungi have evolved the ability to acquire nutrition by absorption of small organic molecules from their environment, and they have a body plan consisting of tubular filaments called *hyphae;* structures of this kind are absent from the animal kingdom.

Some organisms combine the properties of animals and plants. For example, *Euglena* (Figure 1-10) is a motile, single-celled organism that resembles plants in being photosynthetic, but it 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 are sometimes grouped into the kingdom Protista, although this kingdom is an arbitrary grouping of unrelated lineages that violates taxonomic principles (see Chapter 10).

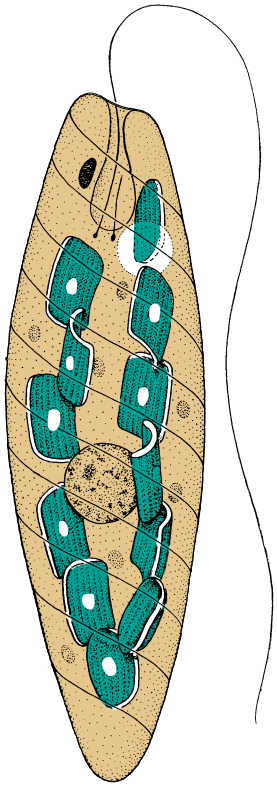


Figure 1-10
Some organisms, such as the flagellate *Euglena* (shown here) and *Volvox* (see Figure 1-3), combine properties that are normally associated with both animals (motility) and plants (photosynthetic ability).

The fundamental structural and developmental features evolved by the animal kingdom are presented in detail in Chapters 8 and 9.

Principles of Science

Nature of Science

We stated in the first sentence of this chapter that zoology is the scientific study of animals. A basic understanding of zoology therefore requires an understanding of what science is, what it is not, and how knowledge is gained by using the scientific method.

Science is a way of asking questions about the natural world and obtaining precise answers to them. Although science, in the modern sense, has arisen recently in human history (within the last 200 years or so), the tradition of asking questions about the natural world is an ancient one. In this section we examine the methodology that zoology shares with science as a whole. These features distinguish the sciences from those activities that we exclude from the realm of science, such as art and religion.

Despite the enormous impact that science has had on our lives, many people have only a minimal understanding of the real nature 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 actually a religious position advocated by a minority of the American religious community, and it does not qualify as science. The 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 suit was brought by the American Civil Liberties Union on behalf of 23 plaintiffs, including a number of religious leaders and groups representing several denominations, individual parents, and educational associations. The plaintiffs contended that the law was a violation of the First Amendment to the U.S. Constitution, which prohibits "establishment of religion" by the government. This prohibition includes passing a law that would aid one religion or prefer one religion over another. On January 5, 1982, Judge Overton permanently enjoined the State of Arkansas from enforcing Act 590.

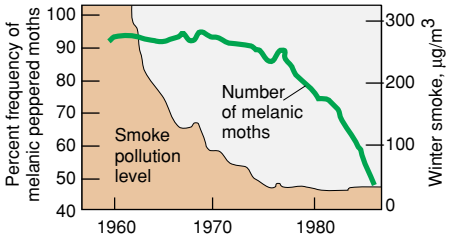
Considerable testimony during the trial dealt with the nature of science. Some witnesses defined science simply, if not very informatively, as "what is accepted by the scientific community" and "what scientists do." However, on the basis of other testimony by scientists, Judge Overton was able to state explicitly these essential characteristics of science:

1. It is guided by natural law.
2. It has to be explanatory by reference to natural law.
3. It is testable against the observable world.
4. Its conclusions are tentative, that is, are not necessarily the final word.
5. It is falsifiable.

The pursuit of scientific knowledge must be guided by the physical and chemical laws that govern the state of existence. Scientific knowledge must explain what is observed by reference to natural law without requiring the intervention of a supernatural being or force. We must be able to observe events in the real world, directly or indirectly, to test hypotheses about nature. If we draw a conclusion relative to some event, we must be ready always to discard or to modify our conclusion if further observations contradict it. As Judge Overton stated, "While anybody is free to approach a scientific inquiry in any fashion they choose, they cannot properly describe the methodology used as scientific if they start with a conclusion and refuse to change it regardless of the evidence developed during the course of the investigation." Science is neutral on the question of religion, and the results of science do not favor one religious position over another.

A

B



C

Figure 1-11

Light and melanic forms of the peppered moth, *Biston betularia* on, **A,** a lichen-covered tree in unpolluted countryside and, **B,** a soot-covered tree near industrial Birmingham, England. These color variants have a simple genetic basis. **C,** Recent decline in the frequency of the melanic form of the peppered moth with falling air pollution in industrial areas of England. The frequency of the melanic form still exceeded 90% in 1960, when smoke and sulfur dioxide emissions were still high. Later, as emissions fell and light-colored lichens began to grow again on the tree trunks, the melanic form became more conspicuous to predators. By 1986, only 50% of the moths were still of the melanic form, the rest having been replaced by the light form.

Scientific Method

These essential criteria of science form the basis for an approach known as the **hypothetico-deductive method.** The first step of this method is the generation of hypotheses or potential answers to the question being asked. These hypotheses are usually based on prior observations of nature, or they are derived from theories based on such observations. Scientific hypotheses often constitute general statements about nature that may explain a large number of diverse observations. Darwin's hypothesis of natural selection, for example, explains the observations that many different species have properties that adapt them to their environments. On the basis of the hypothesis, the scientist must make a prediction about future observations. The scientist must say, "If my hypothesis is a valid explanation of past observations, then future observations ought to have certain characteristics." The best hypotheses are those that make many predictions which, if found erroneous, will lead to rejection, or falsification, of the hypothesis.

The hypothesis of natural selection was invoked to explain variation observed in British moth populations (Figure 1-11). In industrial areas of England having heavy air pollution, many populations of moths contain primarily darkly pigmented (melanic) individuals, whereas moth populations inhabiting clean forests show a much higher frequency of lightly pigmented individuals. The hypothesis suggests that moths can survive most effectively by matching their surroundings, thereby remaining invisible to birds that seek to eat them. Experimental studies have shown that, consistent with this hypothesis, birds are able to locate and then to eat moths that do not match their surroundings, but that birds in the same area frequently fail to find moths that match their surroundings. Another testable prediction of the hypothesis of natural selection is that when polluted areas are cleaned, the moth populations should demonstrate an increase in the frequency of lightly pigmented individuals. Observations of such populations confirmed the result predicted by natural selection.

If a hypothesis is very powerful in explaining a wide variety of related phenomena, it attains the status of a theory. Natural selection is a good example. Our example of the use of natural selection to explain observed pigmentation patterns in moth populations is only one of many phenomena to which natural selection applies. Natural selection provides a potential explanation for the occurrence of many different traits distributed among

virtually all animal species. Each of these instances constitutes a specific hypothesis generated from the theory of natural selection. Note, however, that falsification of a specific hypothesis does not necessarily lead to rejection of the theory as a whole. Natural selection may fail to explain the origins of human behavior, for example, but it provides an excellent explanation for many structural modifications of the pentadactyl (five-fingered) vertebrate limb for diverse functions. Scientists test many subsidiary hypotheses of their major theories to ask whether their theories are generally applicable. The most useful theories are those that can explain the largest array of different natural phenomena.

We emphasize that the meaning of the word "theory," when used by scientists, is not "speculation" as it is in ordinary English usage. Failure to make this distinction has been prominent in creationist challenges to evolution. The creationists have spoken of evolution as "only a theory," as if it were little better than a guess. In fact, the theory of evolution is supported by such massive evidence that most biologists view repudiation of evolution as tantamount to repudiation of reason. Nonetheless, evolution, along with all other theories in science, is not proven in a mathematical sense, but it is testable, tentative, and falsifiable. Powerful theories that guide extensive research are called **paradigms.** The history of science has shown that even major paradigms are subject to refutation and replacement when they fail to account for our observations of the natural world. They are then replaced by new paradigms in a process known as a **scientific revolution.** For example, prior to the 1800s, animal species were studied as if they were specially created entities whose essential properties remained unchanged through time. Darwin's theories led to a scientific revolution that replaced these views with the evolutionary paradigm. The evolutionary paradigm has guided biological research for more than 130 years, and to date there is no scientific evidence that falsifies it; it continues to guide active inquiry into the natural world, and it is generally accepted as the cornerstone of biology.

*Mayr, E. 1982. *The Growth of Biological Thought.* Cambridge, Harvard University Press, pp. 67–71.

Experimental versus Evolutionary Sciences

The many questions that people have asked about the animal world since the time of Aristotle can be grouped into two major categories.* The first category seeks to understand the **proximate** or **immediate causes** that underlie the functioning of biological systems at a particular time and place. These include the problems of explaining how animals perform their metabolic, physiological, and behavioral functions at the molecular, cellular, organismal, and even populational levels. For example, how is genetic information expressed to guide the synthesis of proteins? What causes cells to divide to produce new cells? How does population density affect the physiology and behavior of organisms?

The biological sciences that address proximate causes are known as **experimental sciences,** and they proceed using the experimental method. This method consists of three steps: (1) predicting how a system being studied will respond to a disturbance, (2) making the disturbance, and then (3) comparing the observed results with the predicted ones. Experimental conditions are repeated to eliminate chance occurrences that might produce erroneous conclusions. **Controls**—repetitions of the experimental procedure that lack the disturbance—are established to protect against any unperceived factors that may bias the outcome of the experiment. The processes by which animals maintain a body temperature under different environmental conditions, digest their food, migrate to new habitats, or store energy are some additional examples of physiological phenomena that are studied by experiment (Chapters 31 through 38). Subfields of biology that constitute experimental sciences include molecular biology, cell biology, endocrinology, developmental biology, and community ecology.

In contrast to questions concerning the proximate causes of biological systems are questions of the **ultimate causes** that have produced these systems and their distinctive characteristics through evolutionary time. For example, what are the evolutionary factors that caused some birds to acquire complex patterns of seasonal migration between temperate and tropical areas? Why do different species of animals have different numbers of chromosomes in their cells? Why do some animal species maintain complex social systems, whereas the animals of other species are largely solitary?

The biological sciences that address questions of ultimate cause are known as **evolutionary sciences,** and they proceed largely using the **comparative method** rather than experimentation. Characteristics of molecular biology, cell biology, organismal structure, development, and ecology are compared among related species to identify their patterns of variation. The patterns of similarity and dissimilarity are then used to test hypotheses of relatedness, and thereby to reconstruct the evolutionary tree that relates the species being studied. The evolutionary tree is then used to examine hypotheses of the evolutionary origins of the diverse molecular, cellular, organismal, and populational properties observed in the animal world. Clearly, the evolutionary sciences rely on results of the experimental sciences as a starting point. Evolutionary sciences include comparative biochemistry, molecular evolution, comparative cell biology, comparative anatomy, comparative physiology, and phylogenetic systematics.

Theories of Evolution and Heredity

We turn now to a specific consideration of the two major paradigms that guide zoological research today: Darwin's theory of evolution and the chromosomal theory of inheritance.

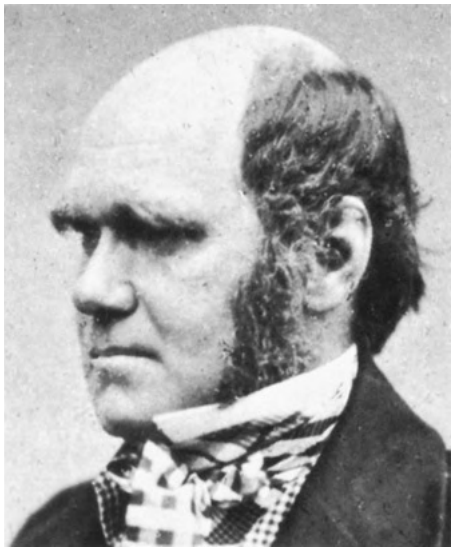


Figure 1-12
Modern evolutionary theory is strongly identified with Charles Robert Darwin who, with Alfred Russel Wallace, provided the first credible explanation of evolution. This photograph of Darwin was taken in 1854 when he was 45 years old. His most famous book, *On the Origin of Species,* appeared five years later.

Darwin's Theory of Evolution

Darwin's theory of evolution is now over 130 years old (Chapter 6). Darwin articulated the complete theory when he published his famous book *On the Origin of Species by Means of Natural Selection* in England in 1859 (Figure 1-12). Biologists today are frequently asked, "What is Darwinism?" and "Do biologists still accept Darwin's theory of evolution?" These questions cannot be given simple answers, because Darwinism encompasses several different, although mutually compatible, theories. Professor Ernst Mayr of Harvard University has argued that Darwinism should be viewed as five major theories.* These five theories have somewhat different origins and different fates and cannot be discussed accurately as if they were only a single statement. The theories are (1) perpetual change, (2) common descent, (3) multiplication of species, (4) gradualism, and (5) natural selection. The first three theories are generally accepted as having universal application throughout the living world. The theories of gradualism and natural selection are controversial among evolutionists, although both are strongly advocated by a large portion of the evolutionary community and are important components of the Darwinian evolutionary paradigm. Gradualism and natural selection are clearly part of the evolutionary process, but their explanatory power might not be as widespread as Darwin intended. Legitimate controversies regarding gradualism and natural selection often are misrepresented by creationists as challenges to the first three theories presented above, although the validity of those first three theories is strongly supported by all relevant observations.

1. **Perpetual change.** This is the basic theory of evolution on which the others are based. It states that the living world is neither constant nor perpetually cycling, but is always changing. The properties of organisms undergo transformation across generations throughout time. This theory originated in antiquity but did not gain widespread acceptance until Darwin advocated it in the context of his other four theories. "Perpetual change" is documented by the fossil record, which clearly refutes creationists' claims for a recent origin of all living forms. Because it has withstood repeated testing and is supported by an overwhelming number of observations, we now regard "perpetual change" as a scientific fact.
2. **Common descent.** The second Darwinian theory, "common descent," states that all forms of life descended from a common ancestor through a branching of lineages (Figure 1-13). The opposing argument, that the different forms of life arose independently and descended to the present in linear, unbranched genealogies, has been refuted by comparative studies of organismal form, cell structure, and macromolecular structures (including those of the genetic material, DNA). All of these studies confirm the theory that life's history has the structure of a branching evolutionary tree, known as a **phylogeny.** Species that share relatively recent common ancestry have more similar features at all levels than do species that have only an ancient common ancestry. Much current research is guided by Darwin's theory of common descent toward reconstructing life's phylogeny using the patterns of similarity and dissimilarity observed among species. The resulting phylogeny serves as the basis for our taxonomic classification of animals (Chapter 10).
3. **Multiplication of species.** Darwin's third theory states that the evolutionary process produces

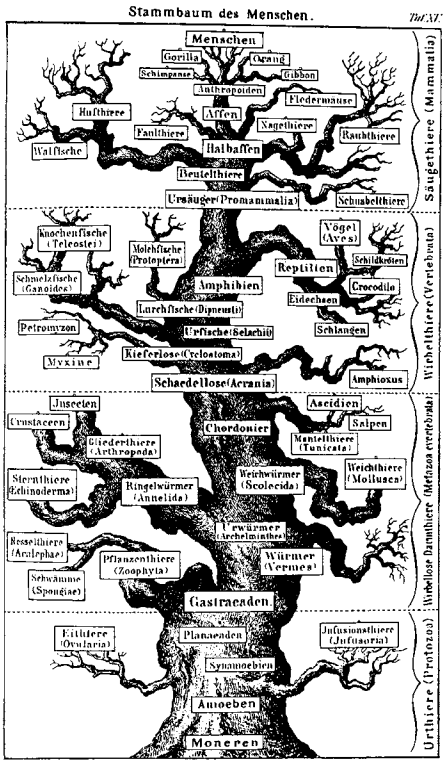


Figure 1-13
An early tree of life drawn in 1874 by the German biologist, Ernst Haeckel, who was strongly influenced by Darwin's theory of common descent. Many of the phylogenetic hypotheses shown in this tree, including the unilateral progression of evolution toward humans (= Menschen, *top*), have since been refuted.

*Mayr, E. 1985. Chapter 25 in D. Kohn, ed. *The Darwinian Heritage.* Princeton, Princeton University Press.

new species by the splitting and transformation of older ones. Species are now generally viewed as reproductively distinct populations of organisms that usually but not always differ from each other in organismal form. Once species are fully formed, interbreeding among members of different species does not occur. Evolutionists generally agree that the splitting and transformation of lineages produces new species, although there is still much controversy concerning the details of this process (Chapter 6) and the precise meaning of the term "species" (Chapter 10). The study of the historical processes that generate new species guides much active scientific research.

4. **Gradualism.** Gradualism states that the large differences in anatomical traits that characterize different species originate through the accumulation of many small incremental changes over very long periods of time. This theory is important because genetic changes having very large effects on organismal form are usually harmful to the organism. It is possible, however, that some genetic variants that have large effects on the organism are nonetheless sufficiently beneficial to be favored by natural selection. Therefore, although gradual evolution is known to occur, it may not explain the origin of all structural differences that we observe among species (Figure 1-14). Scientists are still actively studying this question.
5. **Natural selection.** Natural selection, Darwin's most famous theory, rests on three propositions. First, there is variation among organisms (within populations) for anatomical, behavioral, and physiological traits. Second, the variation is at least partly heritable so that offspring tend to resemble their parents. Third, organisms with different variant forms leave different numbers of offspring to future generations. Variants that permit their possessors most effectively to exploit their environments will preferentially survive and be transmitted to future generations. Over many generations, favorable new traits will spread throughout the population. Accumulation of such changes leads, over long periods of time, to the production of new organismal features and new species. Natural selection is therefore a creative process that generates novel features from the small individual variations that occur among organisms within a population.

Natural selection explains why organisms are constructed to meet the demands of their environments, a phenomenon called **adaptation** (Figure 1-15). Adaptation is the expected result of a process that accumulates the most favorable variants occurring in a population throughout long periods of evolutionary time. Adaptation was viewed previously as strong evidence against evolution, and Darwin's theory of natural selection

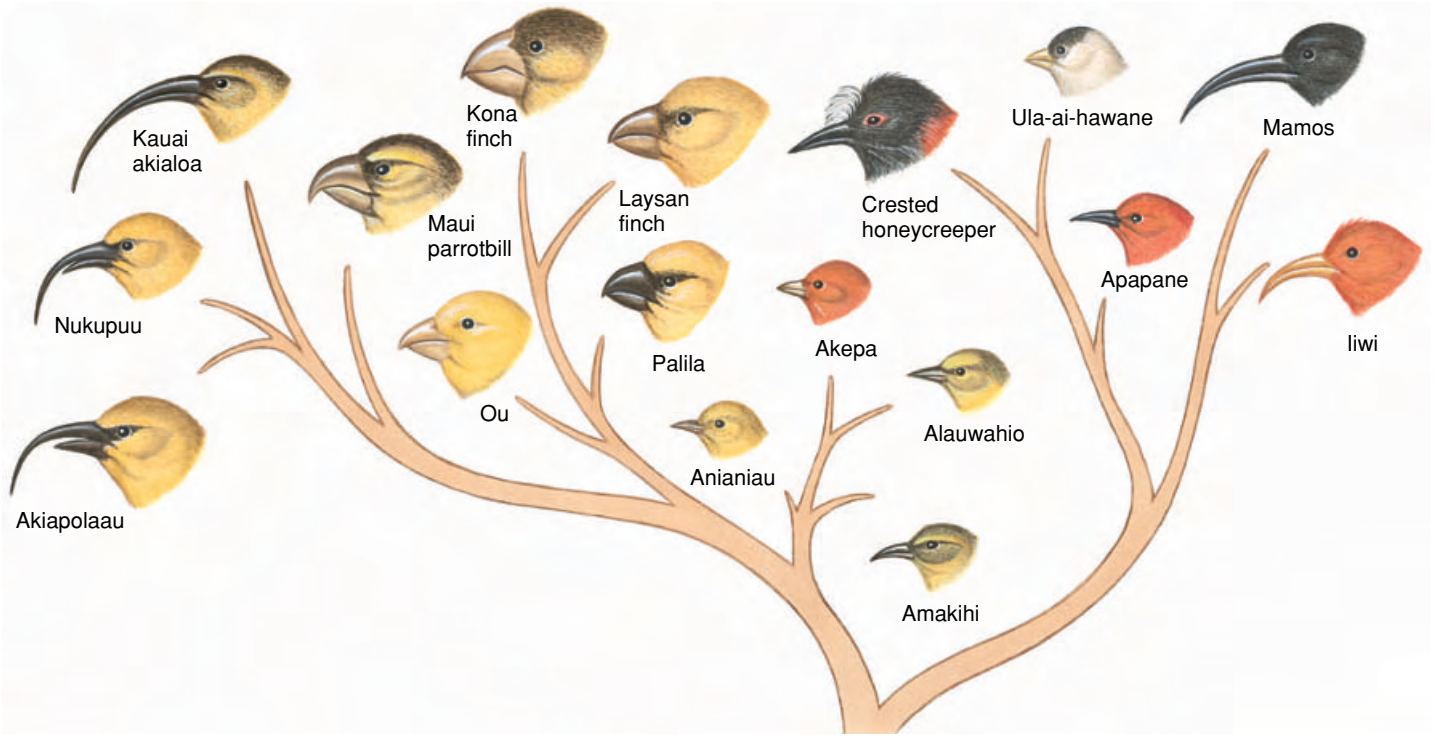


Figure 1-14
Gradualism provides a plausible explanation for the origin of different bill shapes in the Hawaiian honeycreepers shown here. This theory has been challenged, however, as an explanation of the evolution of such structures as vertebrate scales, feathers, and hair from a common ancestral structure. The geneticist Richard Goldschmidt viewed the latter forms as unbridgeable by any gradual transformation series.

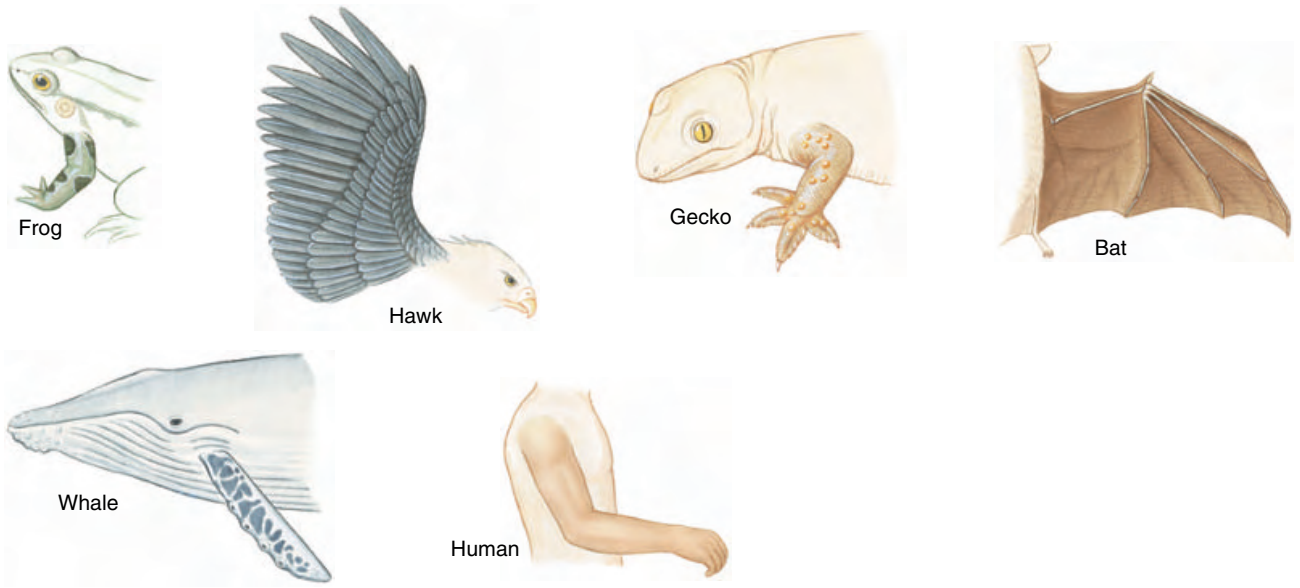


Figure 1-15
According to Darwinian evolutionary theory, the different forms of these vertebrate forelimbs were molded by natural selection to adapt them for different functions. We will see in later chapters that, despite these adaptive differences, these limbs share basic structural similarities.

was therefore important for convincing people that a natural process, capable of being studied scientifically, could produce new species. The demonstration that natural processes could produce adaptation was important to the eventual acceptance of all five Darwinian theories.

Darwin's theory of natural selection faced a major obstacle when it was first proposed: it lacked a theory of heredity. People assumed incorrectly that heredity was a blending process, and that any favorable new variant appearing in a population therefore would be lost. The new variant arises initially in a single organism, and that organism therefore must mate with one lacking the favorable new trait. Under blending inheritance, the organism's offspring would then have only a diluted form of the favorable trait. These offspring likewise would mate with others that lack the favorable trait. With its effects diluted by half each generation, the trait eventually would cease to exist. Natural selection would be completely ineffective in this situation.

Darwin was never able to counter this criticism successfully. It did not occur to Darwin that hereditary factors could be discrete and nonblending and that a new genetic variant therefore could persist unaltered from one generation to the next. This principle is known as **particulate inheritance.** It was established after 1900 with the discovery of Gregor Mendel's genetic experiments, and it was eventually incorporated into what we now call the **chromosomal theory of inheritance.** We use the term **neo-Darwinism** to describe Darwin's theories as modified by incorporating this theory of inheritance.

Mendelian Heredity and the Chromosomal Theory of Inheritance

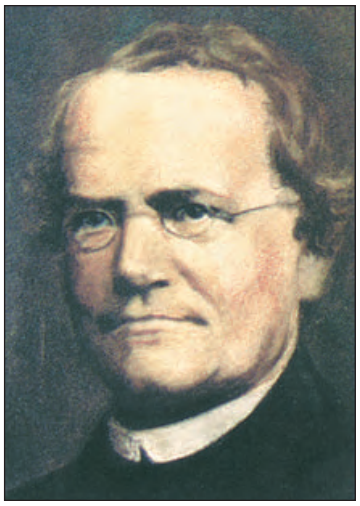
The chromosomal theory of inheritance is the foundation for current studies of genetics and evolution in animals (Chapters 5 and 6). This theory comes from the consolidation of research done in the fields of genetics, which was founded by the experimental work of Gregor Mendel (Figure 1-16), and cell biology.

Genetic Approach

The genetic approach consists of mating or "crossing" populations of organisms that are true-breeding for contrasting traits, and then following the hereditary transmission of those traits through subsequent generations. "True-breeding" means that a population maintains across generations only one of the contrasting states of a particular feature when propagated in isolation from other populations.

Gregor Mendel studied the transmission of seven variable features in garden peas, crossing populations that were true-breeding for alternative traits (for example, tall versus short plants). In the first generation (called the F_1 generation, for "filial"), only one of the alternative parental traits was observed; there was no indication of blending of the parental traits. In the example, the offspring (called F_1 hybrids) formed by crossing the tall and short plants were tall, regardless of whether the tall trait was inherited from the male or the female parent. These F_1 hybrids were allowed to self-pollinate, and both parental traits were found among their offspring (called the F_2 generation), although the trait observed in the F_1 hybrids (tall plants in this example) was three times more common than the other trait. Again, there was no indication of blending of the parental traits (Figure 1-17).

Mendel's experiments showed that the effects of a genetic factor can be masked in a hybrid individual, but that these factors were not physically altered during the transmission process. He



A

B

Figure 1-16

A, Gregor Johann Mendel. **B,** The monastery in Brno, Czech Republic, now a museum, where Mendel carried out his experiments with garden peas.

postulated that variable traits are specified by paired hereditary factors, which we now call "genes." When **gametes** (eggs or sperm) are produced, the two genes controlling a particular feature are segregated from each other and each gamete receives only one of them. Fertilization restores the paired condition. If an organism possesses different forms of the paired genes for a feature, only one of them is expressed in its appearance, but both genes nonetheless will be transmitted unaltered in equal numbers to the gametes produced. Transmission of these genes is particulate, not blending. Mendel observed that the inheritance of one pair of traits is independent of the inheritance of other paired traits. We now know, however, that not all pairs of traits are inherited independently of each other. Numerous studies, particularly of the fruit fly, *Drosophila melanogaster,* have shown that the principles of inheritance discovered initially in plants apply also to animals.

Contributions of Cell Biology

Improvements in microscopes during the 1800s permitted cytologists to study the production of gametes by direct observation of reproductive

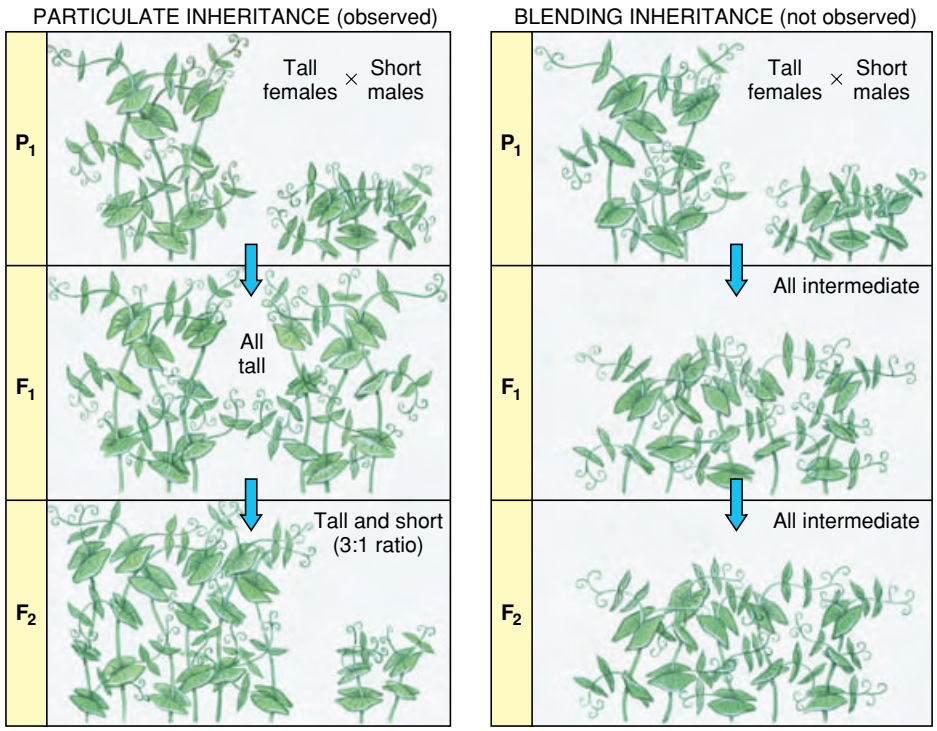


Figure 1-17

Different predictions of particulate versus blending inheritance regarding the outcome of Mendel's crosses of tall and short plants. The prediction of particulate inheritance is upheld and the prediction of blending inheritance is falsified by the results of the experiments. The reciprocal experiments (crossing short female parents with tall male parents) produced similar results. (P_1 = parental generation; F_1 = first filial generation; F_2 = second filial generation.)

The Animal Rights Controversy

In recent years, the debate surrounding the use of animals to serve human needs has intensified. Most controversial of all is the issue of animal use in biomedical and behavioral research and in the testing of commercial products.

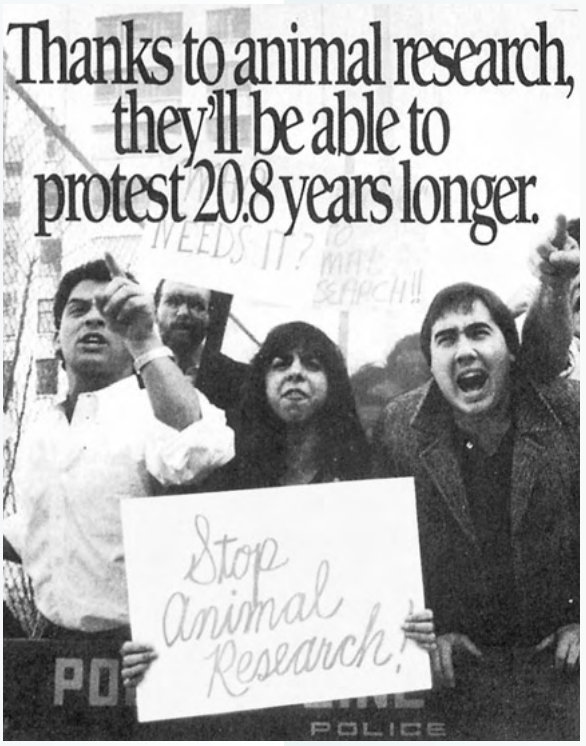
A few years ago, Congress passed a series of amendments to the Federal Animal Welfare Act, a body of laws covering animal care in laboratories and other facilities. These amendments have become known as the three R's: **Reduction** in the number of animals needed for research; **Refinement** of techniques that might cause stress or suffering; **Replacement** of live animals with simulations or cell cultures whenever possible. As a result, the total number of animals used each year in research and in testing of commercial products has declined. Developments in cellular and molecular biology also have contributed to a decreased use of animals for research and testing. The animal rights movement, composed largely of vocal antivivisectionists, has created an awareness of the needs of animals used in research and has stimulated researchers to discover cheaper, more efficient, and more humane alternatives.

However, computers and culturing of cells can simulate the effects on organismal systems of, for instance, drugs, only when the basic principles involved are well known. When the principles themselves are being scrutinized and tested, computer modeling is not sufficient. A recent report by the National Research Council concedes that although the search for alternatives to the use of animals in research and testing will continue, "the chance that alternatives will completely replace animals in the foreseeable future is nil." Realistic immediate goals, however, are reduction in number of animals used, replacement of mammals with other vertebrates, and refinement of experimental procedures to reduce discomfort of the animals being tested.

Medical and veterinary progress depends on research using animals. Every drug and every vaccine developed to improve the human condition has been tested first on animals. Research using animals has enabled medical science to eliminate smallpox and polio, and to immunize against diseases previously common and often deadly, including diphtheria, mumps, and rubella. It also has helped to create treatments for cancer, diabetes, heart disease, and manic-depressive psychoses, and to develop surgical procedures including heart surgery, blood transfusions, and cataract removal. AIDS research is wholly dependent on studies using animals. The similarity of simian AIDS, identified in rhesus monkeys, to human AIDS has permitted the disease in monkeys to serve as a model for the human disease. Recent work indicates that cats, too, may prove to be useful models for the development of an AIDS vaccine. Skin grafting experiments, first done with cattle and later with other animals, opened a new era in immunological research with vast ramifications for treatment of disease in humans and other animals.

Research using animals also has benefited *other animals* through the development of veterinary cures. The vaccines for feline leukemia and canine parvovirus were first introduced to other cats and dogs. Many other vaccinations for serious diseases of animals were developed through research on animals: for example, rabies, distemper, anthrax, hepatitis, and tetanus. No endangered species is used in general research (except to protect that species from total extinction). Thus, research using animals has provided enormous benefits to humans and other animals. Still, much remains to be learned about treatment of diseases such as cancer, AIDS, diabetes, and heart disease, and research with animals will be required for this purpose.

Despite the remarkable benefits produced by research on animals, advocates of animal rights often present an inaccurate and emotionally distorted picture of this research. The ultimate goal of most animal rights activists, who have focused specifically on the use of animals in science rather than on the treatment of animals in all contexts, remains the total abolition of all forms of research using animals. The scientific



According to the U.S. Department of Health and Human Services, animal research has helped extend our life expectancy by 20.8 years.

community is deeply concerned about the impact of these attacks on the ability of scientists to conduct important experiments that will benefit people and animals. They argue that if we are justified to use animals for food and fiber and as pets, we are justified in experimentation to benefit human welfare when these studies are conducted humanely and ethically.

The Association for Assessment and Accreditation of Laboratory Animal Care International supports the use of animals to advance medicine and science when nonanimal alternatives are not available and when animals are treated in an ethical and humane way. Accreditation by this organization allows research institutions to demonstrate excellence in their standards of animal care. Nearly all of the major institutions receiving funding from the National Institutes of Health have sought and received this accreditation. See the web site at *http://www.aaalac.org* for more information on accreditation of laboratory animal care.

References on Animal Rights Controversy

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Describes alternatives that are being developed for the costly and time-consuming use of animals in the testing of thousands of chemicals that each year must be evaluated for potential toxicity to humans.

Pringle, L. 1989. The animal rights controversy. San Diego, California, Harcourt Brace Jovanovich, Publishers.
Although no one writing about the animal rights movement can honestly claim to be totally objective and impartial on such an emotionally charged issue, this book comes as close as any to presenting a balanced treatment.

Rowan, A. N. 1984. Of mice, models, and men: a critical evaluation of animal research. Albany, New York, State University of New York Press.
Good review of the issues. Chapter 7 deals with the use of animals in education, and notes that our educational system provides little help in resolving the contradiction of teaching kindness to animals while using animals in experimentation in biology classes.

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Thoughtful and carefully researched study of the animal rights movement, its ideological roots, and the passionate idealism of animal rights activists.

tissues. Interpreting the observations was initially difficult, however. Some prominent biologists hypothesized, for example, that sperm were parasitic worms in the semen (Figure 1-18). This hypothesis was soon falsified, and the true nature of gametes was clarified. As the precursors of gametes prepare to divide in the early stages of gamete production, the nuclear material condenses to reveal discrete, elongate structures called chromosomes. Chromosomes occur in pairs that are usually similar but not identical in appearance and informational content. The number of chromosomal pairs varies among species. One member of each pair is derived from the female parent and the other from the male parent. Paired chromosomes are physically associated and then segregated into different daughter cells during cell division prior to gamete formation (Figure 1-19). Each resulting gamete receives one chromosome from each

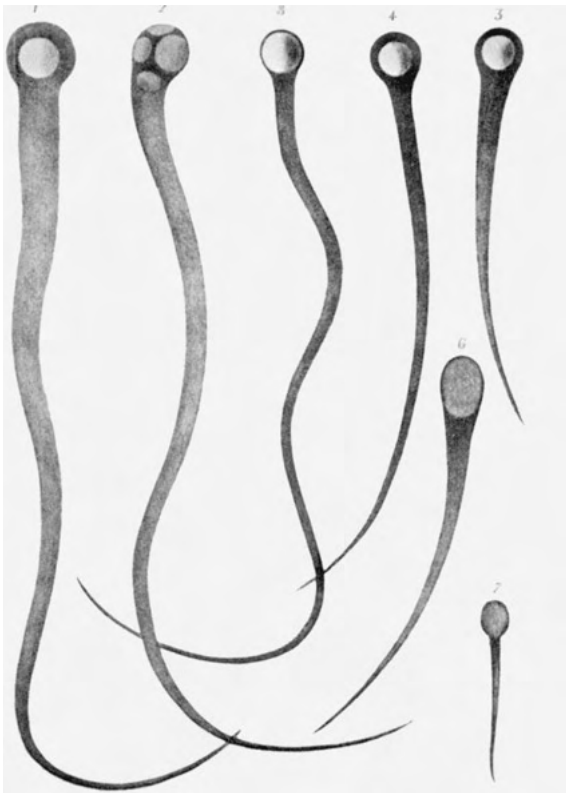

Figure 1-18
An early nineteenth-century micrographic drawing of sperm from (1) guinea pig, (2) white mouse, (3) hedgehog, (4) horse, (5) cat, (6) ram, and (7) dog (Prévost and Dumas, 1821). Some biologists initially interpreted these as parasitic worms in the semen, but on further examination found them to be male gametes.

pair. Different pairs of chromosomes are sorted into gametes independently of each other. Because the behavior of the chromosomal material during gamete formation parallels that postulated for Mendel's genes, Sutton and Boveri in 1903 through 1904 hypothesized that chromosomes were the physical bearers of the genetic material. This hypothesis met with extreme skepticism when first proposed. A long series of tests designed to falsify it nonetheless showed that its predictions were upheld. The chromosomal theory of inheritance is now well established.

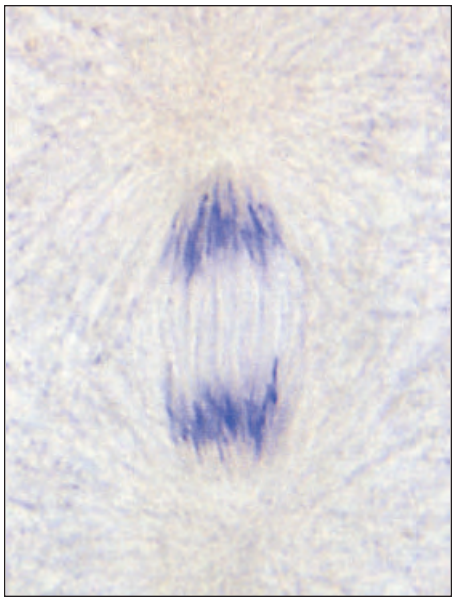

Figure 1-19
Paired chromosomes being separated before nuclear division in the process of forming gametes.

Summary

Zoology is the scientific study of animals, and it is part of biology, the scientific study of life. Animals and life in general can be identified by attributes that they have acquired over their long evolutionary histories. The most outstanding attributes of life include chemical uniqueness, complexity and hierarchical organization, reproduction, possession of a genetic program, metabolism, development, and interaction with the environment. Biological systems comprise a hierarchy of integrative levels (molecular, cellular, organismal, populational, and species levels), each of which demonstrates a number of specific emergent properties.

Science is characterized by the acquisition of knowledge by constructing and then testing hypotheses through observations of the natural world. Science is guided by natural law, and its hypotheses are testable, tentative, and falsifiable. Zoological sciences can be subdivided into two categories, the experimental sciences and the evolutionary sciences. The experimental sciences use the experimental method to ask how animals perform their basic metabolic, developmental, behavioral, and reproductive functions, including investigations of their molecular, cellular, and populational systems. The evolutionary sciences use the comparative method to reconstruct the history of life, and then use that history to understand how diverse species and their molecular, cellular, organismal, and populational properties arose through evolutionary time. Hypotheses that withstand repeated testing and therefore explain many diverse phenomena gain the status of a theory. Powerful theories that guide extensive research are called "paradigms." The major paradigms that guide the study of zoology are Darwin's theory of evolution and the chromosomal theory of inheritance.

The principles given in this chapter illustrate the unity of biological science. All components of biological systems are guided by natural laws and are constrained by those laws. Living organisms can come only from other living organisms, just as new cells can be produced only from preexisting cells. Reproductive processes occur at all levels of the biological hierarchy and demonstrate both heredity and variation. The interaction of heredity and variation at all levels of the biological hierarchy produces evolutionary change and has generated the great diversity of animal life documented throughout this book.

Review Questions

1. Why is life difficult to define?
2. What are the basic chemical differences that distinguish living from nonliving systems?
3. Describe the hierarchical organization of life. How does this organization lead to the emergence of new properties at different levels of biological complexity?
4. What is the relationship between heredity and variation in reproducing biological systems?
5. Describe how the evolution of complex organisms is compatible with the second law of thermodynamics.
6. What are the essential characteristics of science? Describe how evolutionary studies fit these characteristics whereas "scientific creationism" does not.
7. Use studies of natural selection in British moth populations to illustrate the hypothetico-deductive method of science.
8. How do we distinguish the terms hypothesis, theory, paradigm, and scientific fact?
9. How do biologists distinguish experimental and evolutionary sciences?

10. What are Darwin's five theories of evolution (as identified by Ernst Mayr)? Which are accepted as fact and which continue to stir controversy among biologists?
11. What major obstacle confronted Darwin's theory of natural selection when it was first proposed? How was this obstacle overcome?
12. How does neo-Darwinism differ from Darwinism?
13. Describe the respective contributions of the genetic approach and cell biology to formulating the chromosomal theory of inheritance.

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Beyond Bio 101: The Transformation of Undergraduate Biology Education. Much information on job opportunities in biology, graduate schools, and more produced by the Howard Hughes Medical Institute. Links to information on biology as a career, medicine, and more.

American Institute of Biological Sciences (AIBS): Careers in Biology. A Lifetime with Science. A comprehensive description of what a major in biology might lead a student to do.

On-Line Biology Glossary. A glossary that may be useful during this course, from the publishers of your text.

The Tree of Life. Explores the phylogenetic relationships between great numbers of organisms and is continually updated.

National Biological Information Infrastructure. A gateway site to biological information from a myriad of sources, both governmental and private. Links abound.

Virtual Library of Biodiversity, Ecology, and the Environment. A clickable index, with lists of many endangered species, state issues, and legislation related to endangered species.

Electronic Zoo. Information on animals, and much, much more.

Careers in Medicine. Thinking of a career in health care? This terrific site is a must-see for anyone considering medicine. Much thought-provoking information, links, and lists of organizations with more information.

CalPhotos: Animals. An immense database that has information and photos of nearly any animal you could imagine. A good resource for photos to include in research papers.

Links to Many Specific Career Descriptions. At least 200 links to web sites can be found through this site, which is updated frequently. An alphabetical listing of occupations in biology allows the user to see web sites under many of the listings that include detailed descriptions of careers.

The Talk.Origins Archive: The Origin of Species, 1st Edition by Charles Darwin. The entire book online!

National Wildlife and International Wildlife Magazine Articles. Text of current and past articles from both magazines.

Wandtafeln (Wall Charts) of Rudolph Leuckart. Includes images of these remarkable charts that are a unique teaching aid in the study of zoology. Classic old-fashioned art.

OLC Student Center Website

PART FOUR

Activity of Life

Female broad-billed hummingbird sipping nectar.

CHAPTER

31

Support, Protection, and Movement

An ant carries with ease a flower petal that is heavier than the ant's body weight.

Of Grasshoppers and Superman

"A dog," remarked Galileo in the seventeenth century, "could probably carry two or three such dogs upon his back; but I believe that a horse could not carry even one of its own size." Galileo was referring to the principle of scaling, a procedure that allows us to understand the consequences of changing body size. A grasshopper can jump to a height of 50 times the length of its body, yet a man in a standing jump cannot clear an obstacle that is no higher than he is tall. Without an understanding of scaling, this comparison could easily lead us to the erroneous conclusion that there is something very special about the musculatures of insects. To the authors of a nineteenth-century entomology text it seemed that "This wonderful strength of insects is doubtless the result of something peculiar in the structure and arrangement of their muscles, and principally their extraordinary power of contraction." But grasshopper muscles are in fact no more powerful than human muscles because *muscles of small and large animals exert the same force per cross-sectional area*. Grasshoppers leap high in proportion to their size because they are small, not because they possess extraordinary muscles.

The authors of this nineteenth-century text further suggested that it was fortunate that higher animals were withheld the powers of insects, for they would surely have "caused the early desolation of the world." More probably, such powers would have led to their own desolation. For earthly mortals would need more than superhuman muscles were they to leap in the proportions of a grasshopper. They would require superhuman tendons, superhuman ligaments, and superhuman bones to withstand the stresses of mighty contractions, not to mention the crushing strains of landing again on earth at terminal velocity. The feats of Superman would be quite impossible were he built of the structural materials available to earthbound animals, rather than of the wondrous materials available to inhabitants of the mythical planet Krypton. ■

Integument among Various Groups of Animals

The integument is the outer covering of the body, a protective wrapping that includes the skin and all structures derived from or associated with skin, such as hair, setae, scales, feathers, and horns. In most animals it is tough and pliable, providing mechanical protection against abrasion and puncture and forming an effective barrier against invasion of bacteria. It may provide moisture proofing against fluid loss or gain. The skin helps protect the underlying cells against the damaging action of the ultraviolet rays of the sun. In addition to being a protective cover, the skin serves a variety of important regulatory functions. For example, in endothermic animals, it is vitally concerned with temperature regulation, since most of the body's heat is lost through the skin; it contains mechanisms that cool the body when it is too hot and slow heat loss when the body is too cold. The skin contains sensory receptors that provide essential information about the immediate environment. It has excretory functions and in some animals respiratory functions as well. Through skin pigmentation the organism can make itself more or less conspicuous. Skin secretions can make the animal sexually attractive or repugnant or provide olfactory cues that influence behavioral interactions between individuals.

Invertebrate Integument

Many protozoa have only the delicate cell or plasma membranes for external coverings; others, such as *Paramecium*, have developed a protective pellicle. Most multicellular invertebrates, however, have more complex tissue coverings. The principal covering is a single-layered **epidermis.** Some invertebrates have added a secreted noncellular **cuticle** over the epidermis for additional protection.

The molluscan epidermis is delicate and soft and contains mucous glands, some of which secrete the calcium carbonate of the shell. Cephalopod molluscs (squids and octopuses) have developed a more complex integument, consisting of cuticle, simple epidermis, layer of connective tissue, layer of reflecting cells (iridocytes), and thicker layer of connective tissue.

Arthropods have the most complex of invertebrate integuments, providing not only protection but also skeletal support. Development of a firm exoskeleton and jointed appendages suitable for attachment of muscles has been a key feature in the extraordinary diversity of this phylum, the largest of animal groups. Arthropod integument consists of a single-layered **epidermis** (also called more precisely **hypodermis**), which secretes a complex cuticle of two zones (Figure 31-1A). The thicker inner zone, the **procuticle,** is composed of protein and chitin (a polysaccharide) laid down in layers (lamellae) much like veneers of plywood. The outer zone of cuticle, lying on the external surface above the procuticle, is the thin **epicuticle.** The epicuticle is a nonchitinous complex of proteins and lipids that provides a protective moisture-proofing barrier to the integument.

Arthropod cuticle may remain as a tough but soft and flexible layer, as it is in many microcrustaceans and insect larvae. However, it may be hardened by either of two ways. In the decapod crustaceans, for example, crabs and lobsters, the cuticle is stiffened by **calcification,** the deposition of calcium carbonate in the outer layers of the procuticle. In insects hardening occurs when protein molecules bond together with stabilizing cross-linkages within and between adjacent lamellae of the procuticle. The result of this process, called **sclerotization,** is formation of a highly resistant and insoluble protein, **sclerotin.** Arthropod cuticle is one of the toughest materials synthesized by animals; it is strongly resistant to pressure and tearing and can withstand boiling in concentrated alkali, yet it is light, having a specific mass of only 1.3 (1.3 times the weight of water).

When arthropods molt, the epidermal cells first divide by mitosis. Enzymes secreted by the epidermis digest most of the procuticle. The digested materials are then absorbed and consequently are not lost to the body. Then in the space beneath the old cuticle a new epicuticle and procuticle are formed. After the old cuticle is shed, the new cuticle is thickened and calcified or sclerotized.

Vertebrate Integument and Derivatives

The basic plan of the vertebrate integument, as exemplified by frog and human skin (Figure 31-1B and C), includes a thin, outer stratified epithelial layer, the **epidermis,** derived from ectoderm and an inner, thicker layer, the **dermis,** or true skin, which is of mesodermal origin. (Ectoderm and mesoderm are germ layers, described in Figure 8-24, p. 175.)

Although the epidermis is thin and appears simple in structure, it gives rise to most derivatives of the integument, such as hair, feathers, claws, and hooves. The dermis contains blood vessels, collagenous fibers, nerves, pigment cells, fat cells, and connective tissue cells called fibroblasts. These elements support, cushion, and nourish the epidermis, which is devoid of blood vessels.

The epidermis is a stratified squamous epithelium (p. 186) consisting usually of several layers of cells. The basal part is made up of cells that undergo frequent mitosis to renew layers that lie above. As outer layers of cells are displaced upward by new generations of cells beneath, an exceedingly tough, fibrous protein called **keratin** accumulates in the interior of the cells. Gradually, keratin replaces all metabolically active cytoplasm. The cell dies and is eventually shed, lifeless and scalelike. Such is the origin of dandruff as well as a significant fraction of household dust. This process is called **keratinization,** and the cell, thus transformed, is said to be **cornified.** Cornified cells, highly resistant to abrasion and water diffusion, comprise the

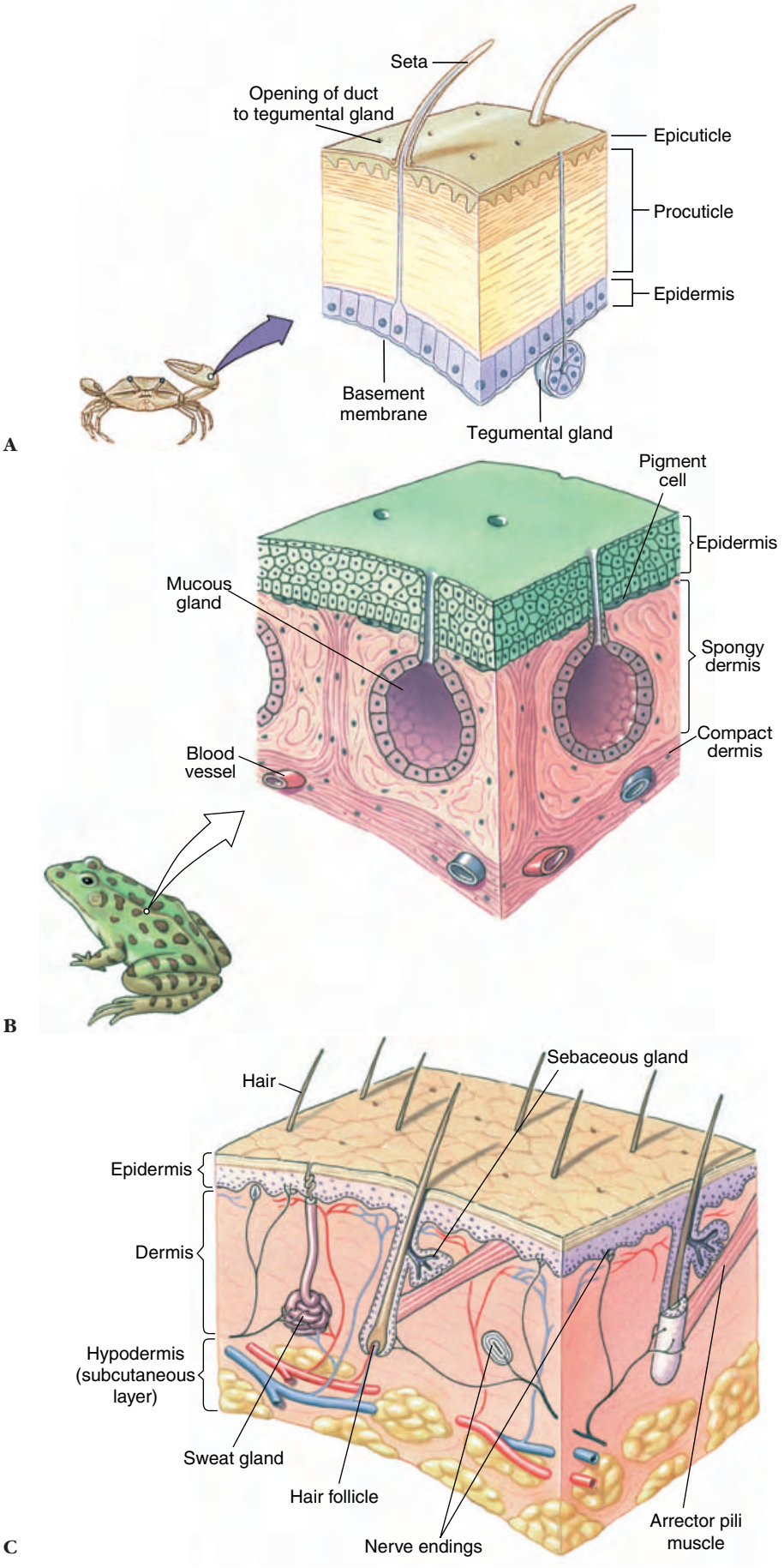


Figure 31-1
Integumentary systems of animals, showing the major layers. **A,** Structure of arthropod (crustacean) body wall showing cuticle and epidermis. **B,** Structure of amphibian (frog) integument. **C,** Structure of human integument.

outermost **stratum corneum.** This epidermal layer becomes especially thick in areas exposed to persistent pressure or wear such as calluses, foot pads of mammals, and the scales of reptiles and birds.

The **dermis,** as already mentioned, mainly serves a supportive role for the epidermis. Nevertheless, true bony structures, where they occur in the integument, are always dermal derivatives. Heavy bony plates were common in ostracoderms and placoderms of the Paleozoic era (Figure 25-17, p. 504) and persist is some living fishes, such as sturgeons (Figure 26-19, p. 522). Scales of contemporary fishes are bony dermal structures that have evolved from the bony armor of the Paleozoic fishes but are much smaller and more flexible. Fish scales are thin bony slivers covered with a mucus-secreting epidermis (Figure 31-2). Most amphibians lack dermal bones in their skin, whereas in reptiles dermal bones provide the armor of crocodilians, the beaded skin appearance of many lizards, and also contribute to the shell of turtles. Dermal bone also gives rise to antlers, as well as the bony core of horns.

Lizards, snakes, turtles, and crocodilians were among the first to exploit the adaptive possibilities of the remarkably tough protein keratin. The reptilian epidermal scale that develops from keratin is a much lighter and more flexible structure than the bony, dermal scale of fishes, yet it provides excellent protection from abrasion and desiccation. Scales may be overlapping structures, as in snakes and some lizards, or develop into plates, as in turtles and crocodilians. In birds, keratin found new uses. Feathers, beaks, and claws, as well as scales, are all epidermal structures composed of dense keratin. Mammals continued to capitalize on keratin's virtues by turning it into hair, hooves, claws, and nails. As a result of its keratin content, hair is by far the

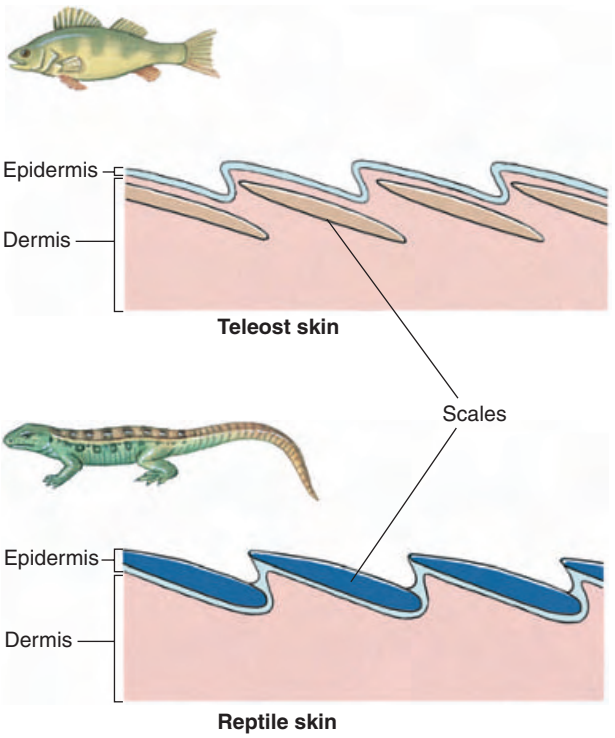


Figure 31-2

Integument of bony fishes and lizards. Bony (teleost) fishes have bony scales from dermis, and lizards have horny scales from epidermis. Thus they are not homologous structures. Dermal scales of fishes are retained throughout life. Since a new growth ring is added to each scale each year, fishery biologists use scales to tell the age of fishes. Epidermal scales of reptiles are shed periodically.

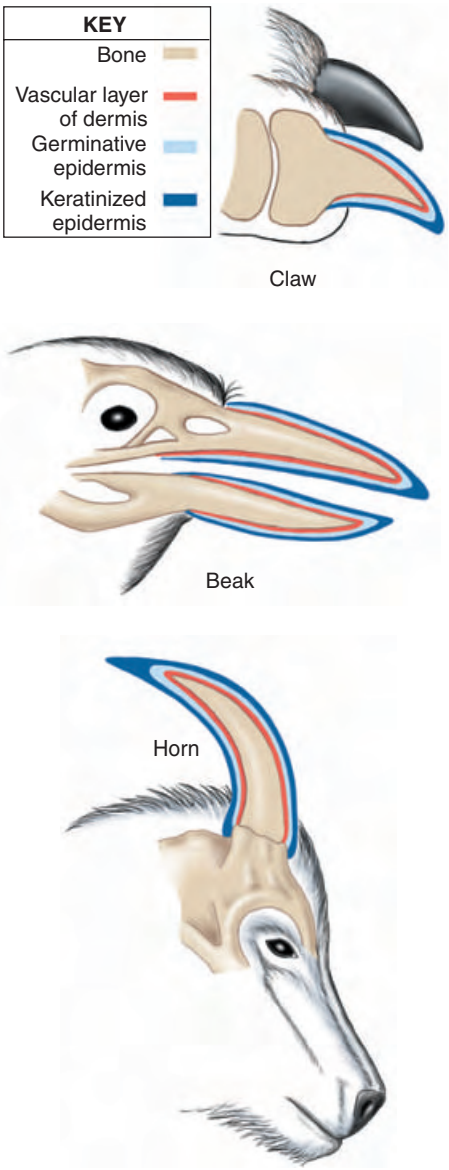


Figure 31-3

Similarity of structure of integumentary derivatives. Claws, beaks, and horns are all built of similar combinations of epidermal (keratinized) and dermal components. A central bony core is covered by a vascularized nutritive layer of the dermis. An outer epithelial layer has a basal germinative component which proliferates to allow these structures to grow continually. The thickened surface epithelium is keratinized or cornified. Note that the relative thickness of each component is not drawn to scale.

strongest material in the body. It has a tensile strength comparable to that of rolled aluminum and is nearly twice as strong, weight for weight, as the strongest bone.

Structures such as claws, beaks, nails, and horns are made up of combinations of epidermal (keratinized) and dermal components. Their basic structure is the same, with a central bony core covered by a vascularized nutritive layer of the dermis, and an outer epithelial layer. This epithelial layer has a germinative component responsible for the continual growth of horns, hooves, claws, and beaks. The outer epithelial layer is keratinized. Overgrowth of these structures is prevented by constant wear and abrasion (Figure 31-3).

Animal Coloration

The colors of animals may be vivid and dramatic when serving as important recognition marks or as warning coloration, or they may be subdued or cryptic when used for camouflage. Integumentary color is usually produced by pigments, but in many insects and in some vertebrates, especially birds, certain colors are produced by the physical structure of the surface tissue, which reflects certain light wavelengths and eliminates others. Colors produced this way are called **structural color,** and they are responsible for the most beautifully iridescent and metallic hues to be found in the animal kingdom. Many butterflies and beetles and a few fishes thus share with birds the distinction of being the earth's most resplendent animals. Certain structural colors of feathers are caused by minute, air-filled spaces or pores that reflect white light (white feathers) or some portion of the spectrum (for example, Tyndall blue coloration produced by scattering of light [see note, p. 588]). Iridescent colors that change hue as the animal's angle shifts with respect to the observer are produced when light is reflected from several layers of thin, transparent film. By phase interference, light waves reinforce, weaken, or eliminate each other to produce some of the purest and most brilliant colors we know.

More common than structural colors in animals are **pigments** (biochromes), an extremely varied group of large molecules that reflect light rays. In crustaceans and ectothermic vertebrates these pigments are contained in large cells with branching processes, called **chromatophores** (Figure 31-4A). The pigment may concentrate in the center of the cell in an aggregate too small to be visible, or it may disperse throughout the cell and its processes, providing maximum display. The chromatophores of cephalopod molluscs are entirely different (Figure 31-4B). Each is a small sac-like cell filled with pigment granules and surrounded by muscle cells that, when contracted, stretch the whole cell out into a pigmented sheet. When the muscles relax, the elastic chromatophore quickly shrinks to a small sphere. With such pigment cells the squids and octopuses can alter their color more rapidly than any other animal.

The most widespread of animal pigments are the **melanins,** a group of black or brown polymers that are responsible for the various earth-colored shades that most animals wear. Yellow and red colors are often caused by **carotenoid** pigments, which are frequently contained within special pigment cells called **xanthophores.** Most vertebrates are incapable of synthesizing their own carotenoid pigments but must obtain them directly or indirectly from plants. Two entirely different classes of pigments called ommochromes and pteridines are usually responsible for the yellow pigments of molluscs and arthropods. Green colors are rare; when they occur, they are usually produced by yellow pigment overlying blue structural color. **Iridophores,** a third type of chromatophore, contain crystals of guanine or some other purine, rather than pigment. They produce a silvery or metallic effect by reflecting light.

By vertebrate standards, mammals are a somber-colored group (p. 615). Most mammals are more or less color blind, a deficiency that is doubtless connected with the lack of bright colors in the group. Exceptions are the brilliantly colored skin patches of some baboons and mandrills. Significantly, primates have color vision and thus can appreciate such eye-catching ornaments. The muted colors of mammals are caused by melanin, which is deposited in growing hair by dermal melanophores.

Injurious Effects of Sunlight

The familiar vulnerability of the human skin to sunburn reminds us of the potentially damaging effects of ultraviolet radiation on protoplasm. Many animals, such as protozoa and flatworms, if exposed to the sun in shallow water are damaged or killed by ultraviolet radiation. Most land animals are protected from such damage by the screening action of special body coverings, for example, the cuticle of arthropods, the scales of reptiles, and the feathers and fur of birds and mammals. Humans, however, are "naked apes" that lack the furry protection of most other mammals. We must depend on thickening of the epidermis **(stratum corneum)** and on epidermal pigmentation for protection. Most ultraviolet radiation is absorbed in the epidermis, but about 10% penetrates the dermis. Damaged cells in both the epidermis and dermis release histamine and other vasodilator substances that cause blood vessel enlargement in the dermis and the characteristic red coloration of sunburn. Light skins suntan through the formation of the pigment **melanin** in the deeper epidermis and by "pigment darkening," that is, the photooxidative blackening of bleached pigment already present in the epidermis. Unfortunately, tanning does not bestow perfect protection. Sunlight still ages the skin prematurely, and tanning itself causes the skin to become dry and leathery. Sunlight also is responsible for approximately 1 million new cases of skin cancer annually in the United States alone, making skin cancer the most common of malignancies among Caucasians. There is now strong evidence that genetic mutations caused by high doses of sunlight received during the pre-adult years are responsible for skin cancers that appear after middle age.

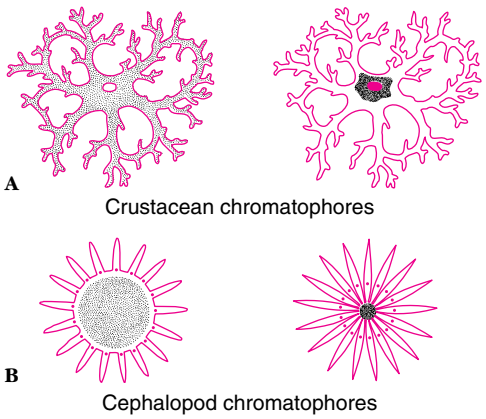


Figure 31-4
Chromatophores. **A,** The crustacean chromatophore showing the pigment dispersed (*left*) and concentrated (*right*). Vertebrate chromatophores are similar. **B,** The cephalopod chromatophore is an elastic capsule surrounded by muscle fibers that, when contracted (*left*), stretch out the capsule to expose the pigment.

Skeletal Systems

Skeletons are supportive systems that provide rigidity to the body, surfaces for muscle attachment, and protection for vulnerable body organs. The familiar bone of the vertebrate skeleton is only one of several kinds of supportive and connective tissues serving various binding and weight-bearing functions, which are described in this discussion.

Hydrostatic Skeletons

Not all skeletons are rigid; many invertebrate groups use their body fluids as an internal hydrostatic skeleton. Muscles in the body wall of the earthworm, for example, have no firm base for attachment but develop muscular force by contracting against the coelomic fluids, which are enclosed within a limited space and are incompressible, much like the hydraulic brake system of an automobile.

Alternate contractions of the circular and longitudinal muscles of the body wall enable the worm to thin and thicken, setting up backward-moving waves of motion that propel the animal forward (Figure 31-5).

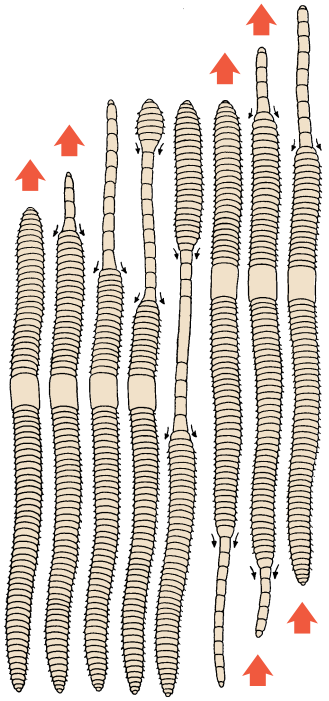


Figure 31-5
How an earthworm moves forward. When circular muscles contract, longitudinal muscles are stretched by internal fluid pressure and the worm elongates. Then, by alternate contraction of longitudinal and circular muscles, a wave of contraction passes from anterior to posterior. Bristlelike setae are extended to anchor the animal and prevent slippage.

Earthworms and other annelids are helped by septa that separate the body into more or less independent compartments (Figure 17-1, p. 358). An obvious advantage is that if a worm is punctured or even cut into pieces, each part can still develop pressure and move. Worms that lack internal compartments, for example, the lugworm *Arenicola* (Figure 17-5, p. 361), are rendered helpless if body fluid is lost through a wound.

There are many examples in the animal kingdom of muscles that not only produce movement but also provide a unique form of skeletal support. The elephant's trunk is an excellent example of a structure that lacks any obvious form of skeletal support, yet is capable of bending, twisting, elongating, and lifting heavy weights (Figure 31-6). The elephant's trunk, tongues of mammals and reptiles, and tentacles of cephalopod molluscs are

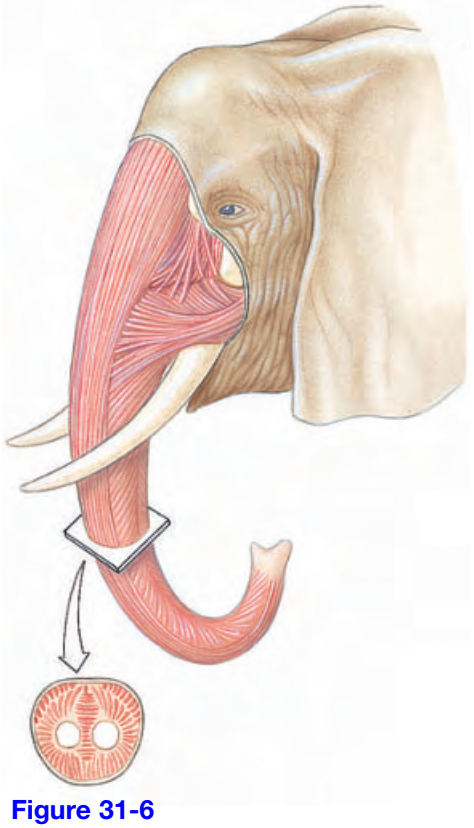


Figure 31-6
Muscular trunk of an elephant, an example of a muscular hydrostat.

examples of **muscular hydrostats.** Like the hydrostatic skeletons of worms, muscular hydrostats work because they are composed of incompressible tissues that remain at constant volume. The remarkably diverse movements of muscular hydrostats depend on muscles arranged in complex patterns.

Rigid Skeletons

Rigid skeletons differ from hydrostatic skeletons in one fundamental way: rigid skeletons consist of rigid elements, usually jointed, to which muscles can attach. Muscles can only contract; to be lengthened they must be extended by the pull of an antagonistic set of muscles. Rigid skeletons provide the anchor points required by opposing sets of muscles, such as flexors and extensors.

Antagonistic muscles are functional opposites that oppose each other's action. For example, the biceps brachii on one side of the upper arm is opposed in its action by the triceps brachii on the opposite side of the arm. By contracting against each other, they balance and smooth rapid movements.

There are two principal types of rigid skeletons: **exoskeleton,** typical of molluscs, arthropods and many other invertebrates; and **endoskeleton,** characteristic of echinoderms and vertebrates. The invertebrate exoskeleton may be mainly protective, but it may also perform a vital role in locomotion. An exoskeleton may take the form of a shell, a spicule, or a calcareous, proteinaceous, or chitinous plate. It may be rigid, as in molluscs, or jointed and movable, as in arthropods. Unlike an endoskeleton, which grows with the animal, an exoskeleton is often a limiting coat of armor that must be periodically molted to make way for an enlarged replacement (molting in crustaceans is described on p. 397). Some invertebrate exoskeletons, such as the shells of snails and bivalves, grow with the animal.

The arthropod-type exoskeleton is perhaps a better arrangement for small animals than a vertebrate-type endoskeleton because a hollow cylindrical tube can support much more weight without collapsing than can a solid cylindrical rod of the same material and weight. Arthropods can thus enjoy both protection and structural support from their exoskeleton. But for larger animals the hollow cylinder would be completely impractical. If made thick enough to support the body weight, it would be too heavy to lift; but if kept thin and light, it would be extremely sensitive to buckling or shattering on impact. Finally, can you imagine the sad plight of an animal the size of an elephant when it shed its exoskeleton to molt?

The vertebrate endoskeleton is formed inside the body and is composed of bone and cartilage, which are forms of dense connective tissue. Bone not only supports and protects but is also the major body reservoir for calcium and phosphorus. In amniote vertebrates red blood cells and certain white blood cells are formed in the bone marrow.

Notochord and Cartilage

The **notochord** (see Figure 25-1, p. 489) is a semirigid supportive axial rod of the protochordates and all vertebrate larvae and embryos. It is composed of large, vacuolated cells and is surrounded by layers of elastic and fibrous sheaths. It is a stiffening device, preserving body shape during locomotion. Except in the jawless vertebrates (lampreys and hagfishes), the notochord is surrounded or replaced by the backbone during embryonic development.

Cartilage is a major skeletal element of some vertebrates. The jawless fishes (for example, lampreys) and the elasmobranchs (sharks, skates, and rays) have purely cartilaginous skeletons, which oddly enough is a derived feature, since their Paleozoic ancestors had bony skeletons. Other vertebrates as adults have principally bony skeletons with some cartilage interspersed. Cartilage is a soft, pliable, characteristically deep-lying tissue. Unlike most connective tissues, which are quite variable in form, cartilage is basically the same wherever it is found. The basic form, **hyaline cartilage,** has a clear, glassy appearance (see Figure 9-6, p. 187). It is composed of cartilage cells **(chondrocytes)** surrounded by firm complex protein gel interlaced with a meshwork of collagenous fibers. Blood vessels are virtually absent—the reason that sports injuries involving cartilage heal poorly. In addition to forming the cartilaginous skeleton of some vertebrates and that of all vertebrate embryos, hyaline cartilage makes up the articulating surfaces of many bone joints of most adult vertebrates and the supporting tracheal, laryngeal, and bronchial rings.

Cartilage similar to hyaline cartilage occurs in some invertebrates, for example the radula of gastropod molluscs and lophophore of brachiopods. The cartilage of cephalopod molluscs is of a special type with long, branching processes that resemble the cells of vertebrate bone.

Bone

Bone is a living tissue that differs from other connective and supportive tissues by having significant deposits of inorganic calcium salts laid down in an extracellular matrix. Its structural organization is such that bone has nearly the tensile strength of cast iron, yet is only one-third as heavy.

Bone is never formed in vacant space but is always laid down by replacement in areas occupied by some form of connective tissue. Most bone develops from cartilage and is called **endochondral** ("within-cartilage") or **replacement bone.** Embryonic cartilage is gradually eroded leaving it extensively honeycombed; bone-forming cells then invade these areas and begin depositing calcium salts around strandlike remnants of the cartilage. A second type of bone is **intramembranous bone,** which develops directly from sheets of embryonic cells. Dermal bone, mentioned earlier, is a type of intramembranous bone. In tetrapod vertebrates intramembranous bone is restricted mainly to bones of the face, cranium and clavicle; the remainder of the skeleton is endochondral bone. Whatever the embryonic origin, once fully formed, endochondral and intramembranous bone look the same.

Fully formed bone, however, may vary in density. **Cancellous** (or spongy) **bone** consists of an open, interlacing framework of bony tissue, oriented to give maximum strength under the normal stresses and strains that the bone receives. All bone develops first as cancellous bone, but some bones, through further deposition of bone salts, become **compact.** Compact bone is dense, appearing solid to the unaided eye. Both cancellous and compact bone are found in the typical long bones of tetrapods (Figure 31-7).

Microscopic Structure of Bone

Compact bone is composed of a calcified bone matrix arranged in concentric rings. The rings contain cavities **(lacunae)** filled with bone cells **(osteocytes),** which are interconnected by many minute passages **(canaliculi).** These passages serve to distribute nutrients throughout the bone. This entire organization of lacunae and canaliculi is arranged into an elongated cylinder called an **osteon** (also called **haversian system**) (Figure 31-7). Bone consists of bundles of osteons cemented together and interconnected with blood vessels and nerves. Because of blood vessels and nerves throughout bone, it is living tissue, although nonliving "ground substance" predominates. As a result of its living state, bone breaks can heal, and bone diseases can be as painful as any other tissue disease.

Following menopause, a woman loses 5% to 6% of her bone mass annually, often leading to the disease osteoporosis and increasing the risk of bone fractures. Dietary supplementation with calcium has been advocated to prevent such losses, but even large doses of calcium alone have little effect in slowing demineralization unless accompanied by therapy with the female sex hormone estrogen (because ovarian production of estrogen drops significantly after menopause). Among animals, only humans, especially females, are troubled with osteoporosis, perhaps a consequence of the long postreproductive life of the human species.

Bone growth is a complex restructuring process, involving both its destruction internally by bone-resorbing cells **(osteoclasts)** and its deposition externally by bone-building cells **(osteoblasts).** Both processes occur simultaneously so that the marrow cavity inside grows larger by bone resorption while new bone is laid down outside by bone deposition. Bone growth responds to several hormones, in particular **parathyroid hormone** from the parathyroid gland, which stimulates bone resorption, and **calcitonin** from the thyroid gland, which inhibits bone resorption. These two hormones, together with a derivative of vitamin D, are responsible for maintaining a constant level of calcium in the blood. The effect of hormones on bone growth and resorption is described in more detail on p. 762.

Bone

Like muscle, bone is subject to "use and disuse." When we exercise our muscles, our bones respond by producing new bone tissue to give added strength. In fact, the

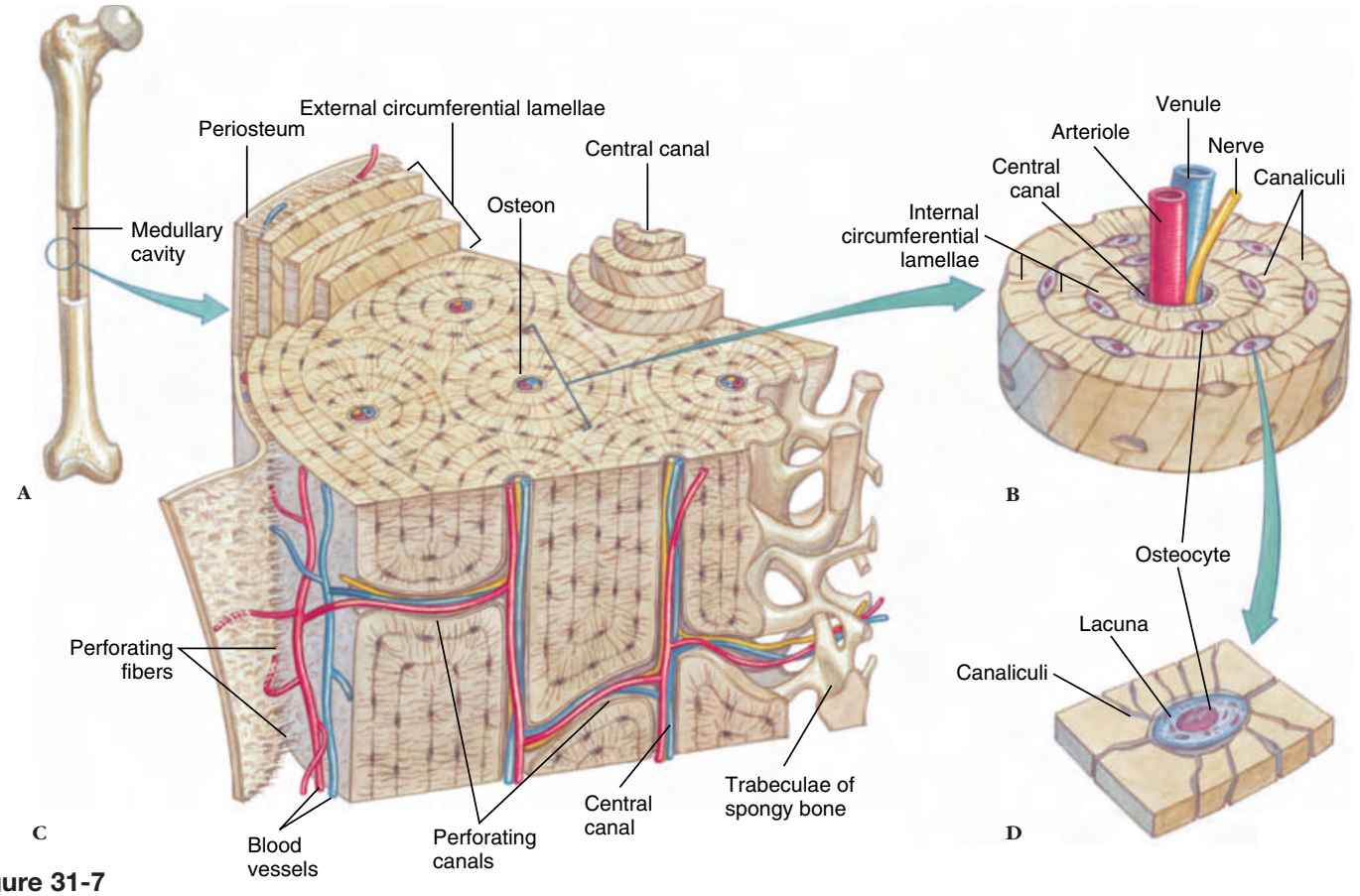


Figure 31-7

Structure of compact bone. **A,** Adult long bone with a cut into the medullary cavity. **B,** Enlarged section showing osteons, the basic histological unit of bone. **C,** Enlarged view of an osteon showing the concentric lamellae and the osteocytes (bone cells) arranged within lacunae. **D,** An osteocyte within a lacuna. Bone cells receive nutrients from the circulatory system via tiny canaliculi that interlace the calcified matrix. Bone cells are known as osteoblasts when they are building bone, but, in mature bone shown here, they become resting osteocytes. Bone is covered with compact connective tissue called periosteum.

bumps and processes to which muscles attach are produced by bone in response to the action of muscle forces. Conversely, when bones are not subject to stress, as in space flight, the body resorbs the mineral, and the bones become weak. Astronauts who spend many months in space must be carried from their capsules upon their return to earth.

Plan of the Vertebrate Skeleton

The vertebrate skeleton is composed of two main divisions: **axial skeleton,** which includes skull, vertebral column, sternum, and ribs, and **appendicular skeleton,** which includes the limbs (or fins or wings) and pectoral and pelvic girdles (Figures 31-8 and 31-9). Not surprisingly, the skeleton has undergone extensive remodeling in the course of vertebrate evolution. The move from water to land forced dramatic changes in body form. With increased cephalization, the further concentration of brain, sense organs, and food-gathering and respiratory apparatus in the head, the skull became the most intricate portion of the skeleton. Some early fishes had as many as 180 skull bones (a source of frustration to paleontologists) but through loss of some bones and fusion of others, skull bones became greatly reduced in number during evolution of the tetrapods. Amphibians and lizards have 50 to 95, and mammals, 35 or fewer. Humans have 29.

The vertebral column is the main stiffening axis of the postcranial skeleton. In fishes it serves much the same function as the notochord from which it is derived; that is, it provides points for muscle attachment and prevents telescoping of the body during muscle contraction. With evolution of amphibious and terrestrial tetrapods, the vertebrate body was no longer buoyed by the aquatic environment. The vertebral column became structurally adapted to withstand new regional stresses transmitted to the column by the two pairs of appendages. In amniote tetrapods (reptiles, birds, and mammals), the vertebrae are differentiated into **cervical** (neck), **thoracic** (chest), **lumbar** (back), **sacral** (pelvic), and **caudal** (tail) vertebrae. In birds and also in humans the caudal vertebrae are reduced in number and size, and the sacral vertebrae are fused. The number of vertebrae varies among the different vertebrates. Pythons seems to lead the list with more than 400. In humans (Figure 31-9) there are 33 in a young child, but in adults 5 are fused to form the **sacrum** and 4 to form the **coccyx.** Besides the sacrum and coccyx, humans have 7 cervical, 12 thoracic, and 5 lumbar vertebrae. The number of cervical vertebrae (7) is constant in nearly all mammals,

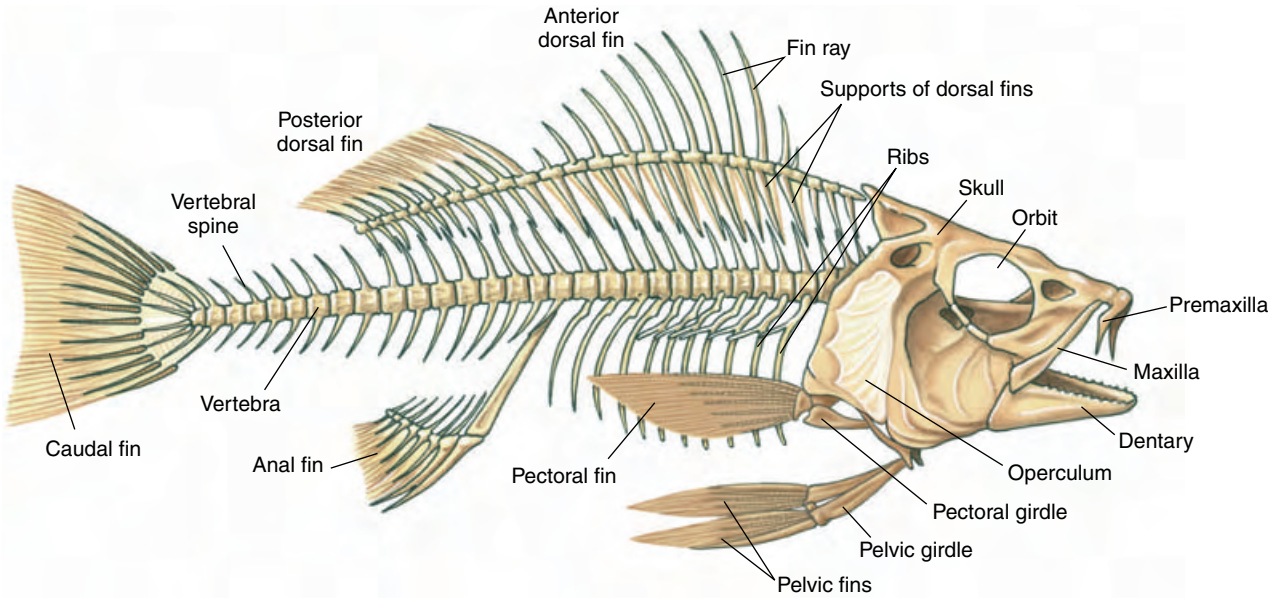


Figure 31-8
Skeleton of a perch.

whether the neck is short as in dolphins, or long as in giraffes.

The first two cervical vertebrae, **atlas** and **axis,** are modified to support the skull and permit pivotal movements. The atlas bears the globe of the head much as the mythological Atlas bore the earth on his shoulders. The axis, the second vertebra, permits the head to turn from side to side.

Ribs are long or short skeletal structures that articulate medially with vertebrae and extend into the body wall. Fishes have a pair of ribs for every vertebra (Figure 31-8); they serve as stiffening elements in the connective tissue septa that separate the muscle segments and thus improve the effectiveness of muscle contractions. Many fishes have both dorsal and ventral ribs, and some have numerous riblike intermuscular bones as well—all of which increase the difficulty and reduce the pleasure of eating certain kinds of fish. Other vertebrates have a reduced number of ribs, and some, such as the familiar leopard frog, have no ribs at all. In mammals the ribs together form the thoracic basket, which supports the chest wall and prevents collapse of the lungs. Mammals such as sloths have 24 pairs of ribs, whereas horses posses 18 pairs. Primates other than humans have 13 pairs of ribs; humans have 12 pairs, although approximately 1 person in 20 has a thirteenth pair.

Most vertebrates, fishes included, have paired appendages. All fishes except agnathans have thin pectoral and pelvic fins that are supported by the pectoral and pelvic girdles, respectively (Figure 31-8). Tetrapods (except caecilians, snakes, and limbless lizards) have two pairs of **pentadactyl** (five-toed) limbs, also supported by girdles. The pentadactyl limb is similar in all tetrapods, alive and extinct; even when highly modified for various modes of life, the elements are rather easily homologized (the evolution of the pentadactyl limb is illustrated in Figure 27-1, p. 541).

Modifications of the basic pentadactyl limb for life in different environments involve distal elements much more frequently than proximal, and it is far more common for bones to be lost or fused than for new ones to be added. Horses and their relatives evolved a foot structure for fleetness by elongation of the third toe. In effect, a horse stands on its third fingernail (hoof), much like a ballet dancer standing on the tips of the toes. The bird wing is a good example of distal modification. The bird embryo bears 13 distinct wrist and hand bones (carpals and metacarpals), which are reduced to three digits in the adult. Most finger bones (phalanges) are lost, leaving four bones in three digits (see p. 589). The proximal bones (humerus, radius, and ulna), however, are only slightly modified in the bird wing.

In nearly all tetrapods the pelvic girdle is firmly attached to the axial skeleton, since the greatest locomotory forces transmitted to the body come from the hindlimbs. The pectoral girdle, however, is much more loosely attached to the axial skeleton, providing the forelimbs with greater freedom for manipulative movements.

Effect of Body Size on Bone Stress

As Galileo realized in 1638, the ability of animals' limbs to support a load decreases as animals increase in size (chapter opening essay, p. 642). Imagine two animals, one twice as long as the other, that are proportionally identical. That is, the larger animal is twice as long, twice as wide, and twice as tall as the smaller. The volume (and the weight) of the larger animal will be eight times the volume of the smaller ($2 \times 2 \times 2 = 8$). However, the strength of the larger animal's legs will be only four times the strength of the

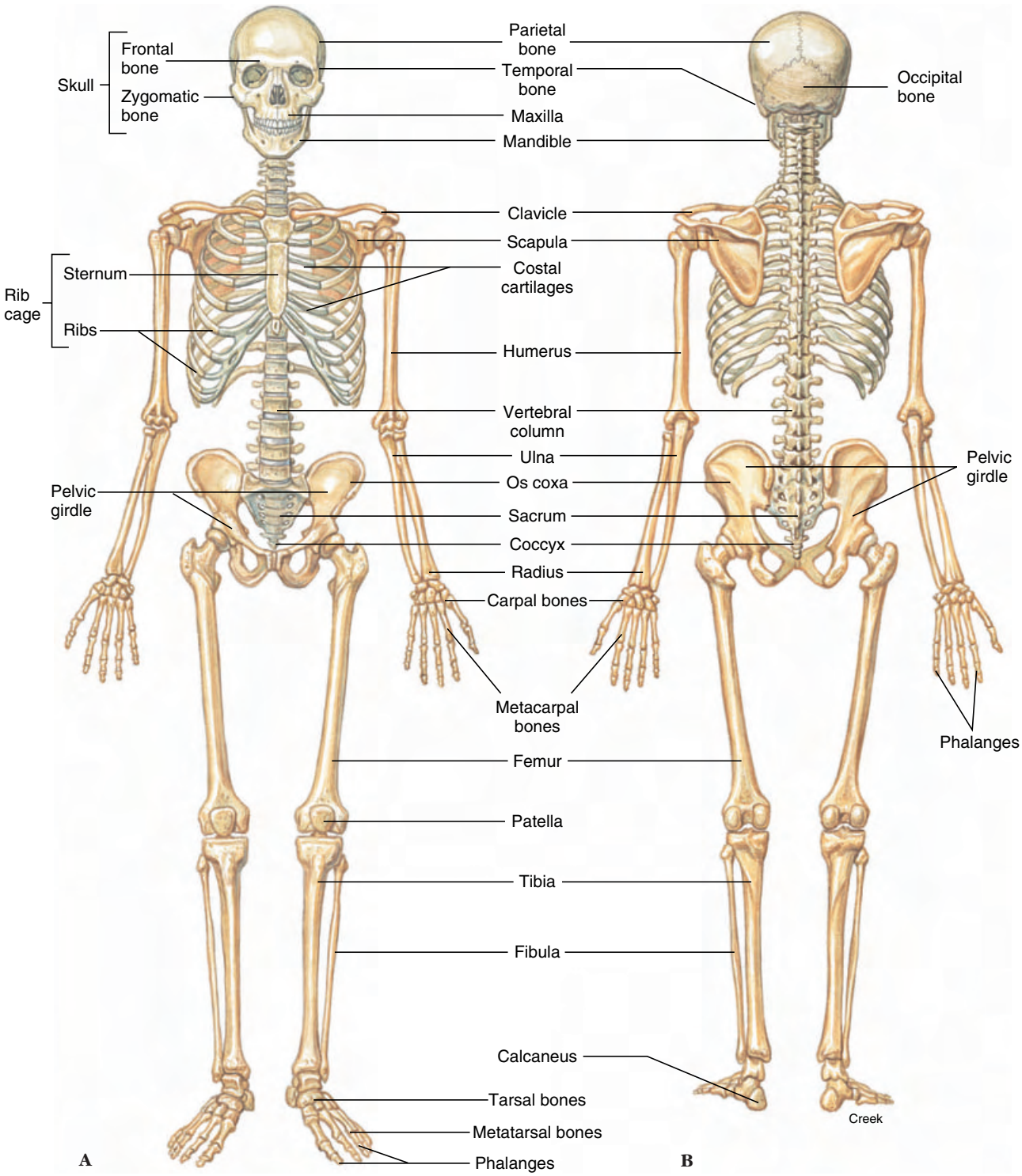


Figure 31-9

Human skeleton. **A,** Ventral view. **B,** Dorsal view. In comparison with other mammals, the human skeleton is a patchwork of primitive and specialized parts. Erect posture, brought about by specialized changes in legs and pelvis, enabled the primitive arrangement of arms and hands (arboreal adaptation of human ancestors) to be used for manipulation of tools. Development of the skull and brain followed as a consequence of the premium natural selection put on dexterity and ability to appraise the environment.

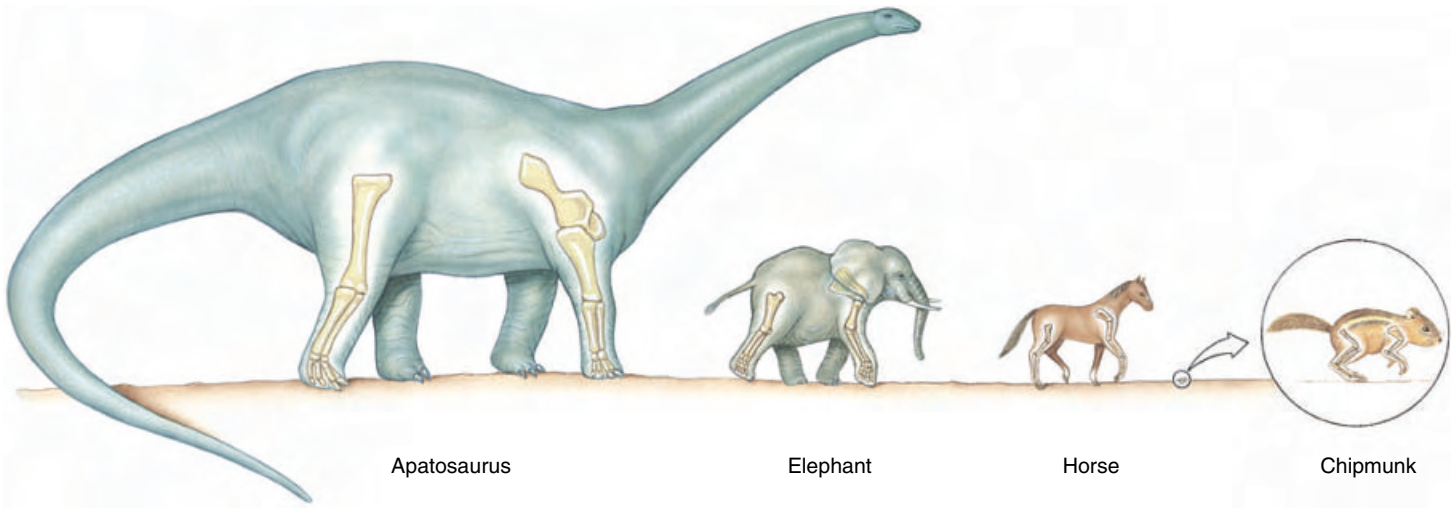


Figure 31-10
Comparison of postures in small and large mammals, showing the effect of scale. Because of its more upright posture, bone stresses in the horse are similar to those in the chipmunk. In mammals larger than horses (above about 300 kg), greatly increased stresses require that bones become exceedingly robust and that the animal lose agility.

smaller, because bone, tendon, and muscle strength are proportional to cross-sectional area. So, as Galileo noted, eight times the weight would have to be carried by only four times the strength. Because the maximum strength of mammalian bone is rather uniform per unit of cross-sectional area, how can animals become larger without placing unbearable stresses on long limb bones? One obvious solution is to make bones stouter and therefore stronger. However, throughout much of their size range, bone shape in different sized mammals does not change much. Instead, mammals have adapted limb posture so that stresses are shifted to align with the long axis of the bones, rather than transversely. Small animals the size of a chipmunk run in a crouched limb posture, whereas a large mammal such as a horse, has adopted an upright posture (Figure 31-10). Bones and muscles are capable of carrying far more weight when aligned more closely with the ground reaction force, as they are in a horse's leg. In this way, peak bone stresses during strenuous activity are no greater for a galloping horse than for a running chipmunk or dog.

For animals larger than horses, further mechanical advantage by changing limb posture is not possible because the limbs are fully upright. Instead, the long bones of an elephant weighing 2.5 metric tons, and those of the enormous dinosaur *Apatosaurus*, weighing an estimated 34 metric tons, are (were) extremely thick and robust (Figure 31-10), providing the safety factor these massive animals require(d). However, top running speeds of the largest terrestrial mammals decline with increasing size. Nevertheless, recent calculations of bone stresses in dinosaurs suggest that even the largest were capable of considerable agility (Alexander, 1991).

Animal Movement

Movement is an important characteristic of animals. Animal movement occurs in many forms in animal tissues, ranging from barely discernible streaming of cytoplasm to extensive movements of powerful striated muscles. Most animal movement depends on a single fundamental mechanism: **contractile proteins,** which can change their form to elongate or contract. This contractile machinery is always composed of ultrafine fibrils—fine filaments, striated fibrils, or tubular fibrils (microtubules)—arranged to contract when powered by **ATP.** By far the most important protein contractile system is the **actomyosin system,** composed of two proteins, **actin** and **myosin.** This is an almost universal biomechanical system found from protozoa to vertebrates; it performs a long list of diverse functional roles. Cilia and flagella, however, are composed of different proteins, and thus are exceptions to the rule. In this discussion we examine the three principal kinds of animal movement: ameboid, ciliary, and muscular.

Ameboid Movement

Ameboid movement is a form of movement especially characteristic of amebas and other unicellular forms; it is also found in many wandering cells of metazoans, such as white blood cells, embryonic mesenchyme, and numerous other mobile cells that move through the tissue spaces. Ameboid cells change their shape by sending out and withdrawing **pseudopodia** (false feet) from any point on the cell surface. Beneath the plasmalemma lies a nongranular layer, the gel-like **ectoplasm,** which encloses the more liquid **endoplasm** (see Figure 11-4, p. 218).

Research with a variety of ameboid cells, including the pathogen-fighting phagocytes present in blood, has produced a consensus model to explain pseudopodial extension and ameboid crawling. Optical studies of an ameba in movement suggest the outer layer of

ectoplasm surrounds a rather fluid core of endoplasm. Movement depends on actin and other regulatory proteins. According to one hypothesis (Stossel, 1994), as the pseudopod extends, hydrostatic pressure forces actin subunits into the pseudopod where they assemble into a network to form a gel state. At the trailing edge of the gel, where the network disassembles, freed actin interacts with myosin to create a contractile force that pulls the cell along behind the extending pseudopod. Locomotion is assisted by membrane-adhesion proteins that attach temporarily to the substrate to provide traction, enabling the cell to crawl steadily forward.

Ciliary and Flagellar Movement

Cilia are minute, hairlike, motile processes that extend from the surfaces of the cells of many animals. They are a particularly distinctive feature of ciliate protistans, but except for nematodes in which motile cilia are absent and arthropods in which they are rare, cilia are found in all major groups of animals. Cilia perform many roles either in moving small organisms such as unicellular ciliates, flagellates, and ctenophores (Figure 31-12B) through their aquatic environment or in propelling fluids and materials across epithelial surfaces of larger animals.

Cilia are of remarkably uniform diameter (0.2 to 0.5 μm) wherever they are found. The electron microscope has shown that each cilium contains a peripheral circle of nine double microtubules arranged around two single microtubules in the center (Figure 31-11). (Several exceptions to the 9 + 2 arrangement have been noted; for example, sperm tails of flatworms have but one central microtubule, and sperm tails of a mayfly have no central microtubule.) Each microtubule is composed of a spiral array of protein subunits called **tubulin.** The microtubule doublets around the periphery are connected to each other and to the central pair of microtubules by a complex system of connective elements. Also extending from each doublet is a pair of arms composed of the protein **dynein.** The dynein arms, which act as cross bridges between the doublets, operate to produce a sliding force between the microtubules.

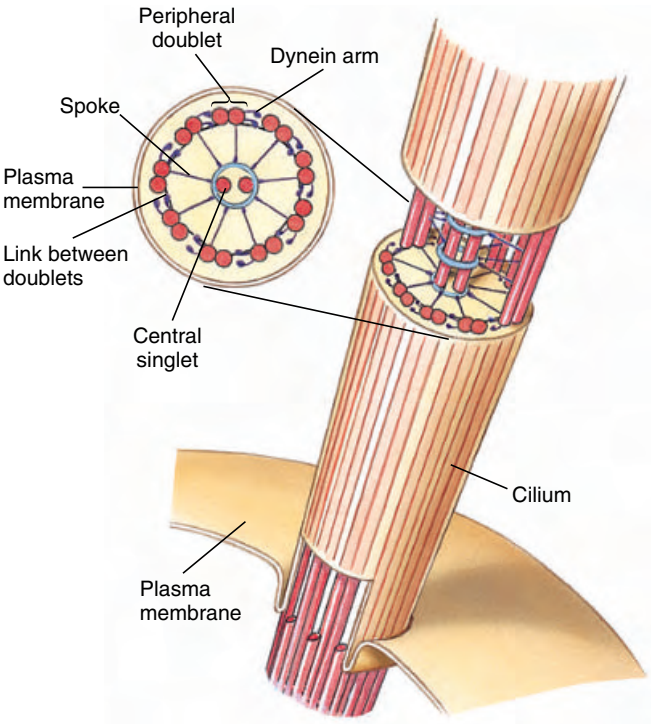


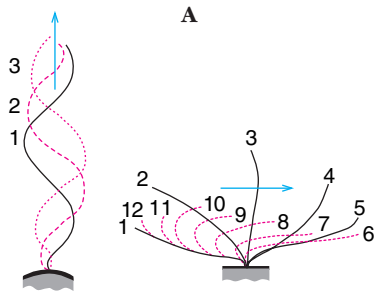
Figure 31-11
Cross section of a cilium showing the microtubules and connecting elements of the 9 + 2 arrangement typical of both cilia and flagella.

A **flagellum** is a whiplike structure longer than a cilium and usually present singly or in small numbers at one end of a cell. They are found in members of flagellate protistans, in animal spermatozoa, and in sponges. The main difference between a cilium and a flagellum is in their beating pattern rather than in their structure, since both look alike internally. A flagellum beats symmetrically with snakelike undulations so that water is propelled parallel to the long axis of the flagellum. A cilium, in contrast, beats asymmetrically with a fast power stroke in one direction followed by a slow recovery during which the cilium bends as it returns to its original position (Figure 31-12A). Water is propelled parallel to the ciliated surface (Figure 31-12B).

Although the mechanism of ciliary movement is not completely understood, it is known that microtubules behave as "sliding filaments" that move past one another much like the sliding filaments of vertebrate skeletal muscle described in the next discussion (sliding microtubule hypothesis, p. 656). During ciliary flexion, the dynein arms link to adjacent microtubules, then swivel and release in repeated cycles, causing microtubules on the concave side to slide outward past microtubules on the convex side. This process increases curvature of the cilium. During the recovery stroke microtubules on the opposite side slide outward to bring the cilium back to its starting position.

Muscular Movement

Contractile tissue is most highly developed in muscle cells called **fibers.** Although muscle fibers themselves can do work only by contraction and cannot actively lengthen, they can be arranged in so many different



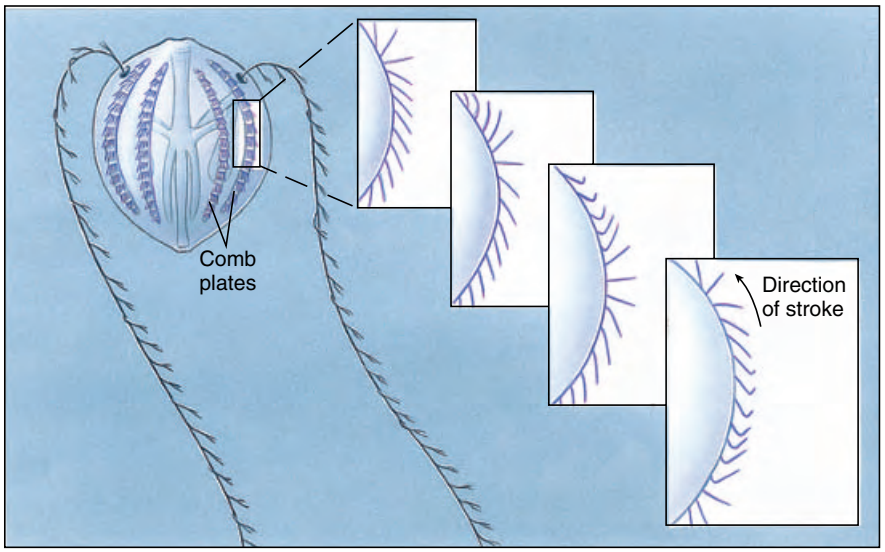


Figure 31-12
A, Flagellum beats in wavelike undulations, propelling water parallel to the main axis of itself. Cilium propels water in direction parallel to the cell surface. **B,** Movement of cilia in comb plates of a ctenophore. Note how the waves of beating comb plates pass down a comb row, opposite the direction of the power stroke of individual cilia. The movement of one comb plate lifts the plate below it and so triggers the next lower plate and so on.

configurations and combinations that almost any movement is possible.

Types of Vertebrate Muscle

Vertebrate muscle is broadly classified on the basis of the appearance of muscle cells (fibers) when viewed with a light microscope. **Skeletal muscle** appears transversely striped **(striated),** with alternating dark and light bands (Figure 31-13). **Cardiac muscle** also possesses striations like skeletal muscle but is uninucleate and with branching cells. A third type of vertebrate muscle is **smooth** (or visceral) **muscle** which lacks the characteristic alternating bands of the striated type.

Skeletal muscle is typically organized into sturdy, compact bundles or bands (Figure 31-13A). It is called skeletal muscle because it is attached to skeletal elements and is responsible for movements of the trunk, appendages, respiratory organs, eyes, mouthparts, and other structure. Skeletal muscle **fibers** are extremely long, cylindrical, multinucleate cells that may reach from one end of the muscle to the other. They are packed into bundles called **fascicles** (L. *fasciculus*, small bundle), which are enclosed by tough connective tissue. The fascicles are in turn grouped into a discrete **muscle** surrounded by a thick connective tissue layer. Most skeletal muscles taper at their ends, where they connect to bones by tendons. Other muscles, such as the ventral abdominal muscles, are flattened sheets.

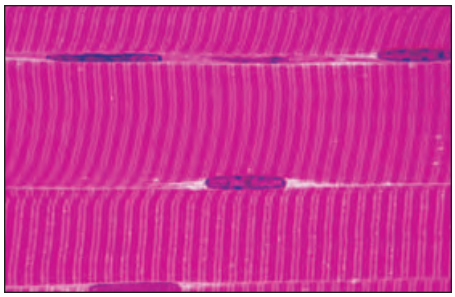
In most fishes, amphibians, and to some extent lizards and snakes, there is a segmented organization of muscles alternating with the vertebrae. The skeletal muscles of other vertebrates, by splitting, fusion, and shifting, have developed into specialized muscles best suited for manipulating jointed appendages that have evolved for locomotion on land. Skeletal muscle contracts powerfully and quickly but fatigues more rapidly than does smooth muscle. Skeletal muscle is sometimes called **voluntary muscle** because it is stimulated by motor fibers and is under conscious cerebral control.

Smooth muscle lacks the striations typical of skeletal muscle (Figure 31-13B). The cells are long, tapering strands, each containing a single nucleus. Smooth muscle cells are organized into sheets of muscle circling the walls of the alimentary canal, blood vessels, respiratory passages, and urinary and genital ducts. Smooth muscle is typically slow acting and can maintain prolonged contractions with very little energy expenditure. It is under the control of the autonomic nervous system; thus, unlike skeletal muscle, its contractions are involuntary and unconscious. The principal functions of smooth muscles are to push material in a tube, such as the intestine, along its way by active contractions or to regulate the diameter of a tube, such as a blood vessel, by sustained contraction.

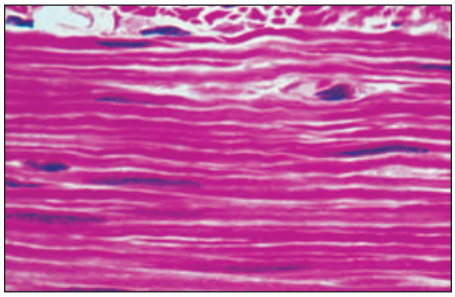
Cardiac muscle, the seemingly tireless muscle of the vertebrate heart, combines certain characteristics of both skeletal and smooth muscle (Figure 31-13C). It is fast acting and striated like skeletal muscle, but contraction is under involuntary autonomic control like smooth muscle. Actually the autonomic nerves serving the heart can only speed up or slow down the rate of contraction; the heartbeat originates within specialized cardiac muscle, and the heart continues to beat even after all autonomic nerves are severed (heart excitation is described on p. 692). Cardiac muscle is composed of closely opposed, but separate, uninucleate cell fibers.

Types of Invertebrate Muscle

Smooth and striated muscles are also characteristic of invertebrate animals, but there are many variations of both types and even instances in which structural and functional features of vertebrate smooth and striated muscle are combined. Striated muscle appears in invertebrate groups as diverse as cnidarians and arthropods. The thickest muscle fibers known, approximately 3 mm in diameter and 6 cm long, are those of giant barnacles



A



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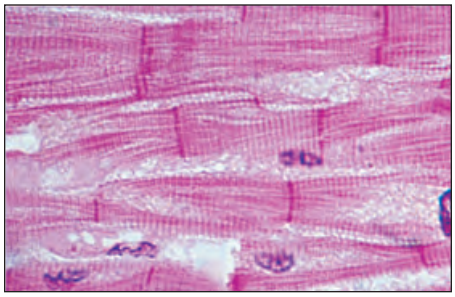

C

Figure 31-13

Photomicrographs of types of vertebrate muscle. **A,** Skeletal muscle (human) showing several striated fibers (cells) lying side by side. Note the peripheral nuclei. **B,** Smooth muscle (human) showing absence of striations. Note elongate nuclei in the long fibers. **C,** Cardiac muscle (monkey). Note the vertical bars, called intercalated discs, joining separate fibers end to end.

and of Alaska king crabs living along the Pacific coast of North America. Such large muscle cells lend themselves well to physiological studies and are understandably popular with muscle physiologists.

In the limited space available to treat the great diversity of muscle structure and function in the invertebrate assemblage, we have selected for discussion two functional extremes: the specialized adductor muscles of molluscs and the fast flight muscles of insects.

Bivalve molluscan muscles contain fibers of two types. One kind is striated muscle that can contract rapidly, enabling the bivalve to snap shut its valves when disturbed. Scallops use these "fast" muscle fibers to swim in their awkward manner (see Figure 16-24B, p. 340). The second muscle type is smooth muscle, capable of slow, long-lasting contractions. Using these fibers, a bivalve can keep its valves tightly shut for hours or even days. Such adductor muscles use little metabolic energy and receive remarkably few nerve impulses to maintain the activated state. The contracted state has been likened to a "catch mechanism" involving some kind of stable cross-linkage between contractile proteins within the fiber. However, despite considerable research, there is still much uncertainty about how this adductor mechanism works.

Insect flight muscles are virtually the functional antithesis of the slow, holding muscles of bivalves. The wings of some small flies operate at frequencies greater than 1000 beats per second. The so-called **fibrillar muscle,** which contracts at these frequencies—far greater than even the most active of vertebrate muscles—shows unique characteristics. It has very limited extensibility; that is, the wing leverage system is arranged so that the muscles shorten only slightly during each downbeat of the wings. Furthermore, muscles and wings operate as a rapidly oscillating system in an elastic thorax (see Figure 20-12, p. 419). Since the muscles rebound elastically and are activated by stretch during flight, they receive impulses only periodically rather than one impulse per contraction; one reinforcement impulse for every 20 or 30 contractions is enough to keep the system active. Insect flight muscles are described in more detail in Chapter 20 (pp. 415–418).

Structure of Striated Muscle

As mentioned earlier, striated muscle is so named because of periodic bands, plainly visible under the light microscope, that pass across the widths of muscle cells. Each cell, or **fiber,** is a multinucleated tube containing numerous **myofibrils,** packed together and invested by the cell membrane, the **sarcolemma** (Figure 31-14). The myofibril contains two types of **myofilaments:** thick filaments composed of the protein **myosin,** and thin filaments, composed of the protein **actin.** These are the actual contractile proteins of the muscle. Thin filaments are held together by a dense structure called the Z line. The functional unit of the myofibril, the **sarcomere,** extends between successive Z lines. These anatomical relationships are diagramed in Figure 31-14.

Human muscle tissue develops before birth, and a newborn child's complement of skeletal muscle fibers is all that he or she will ever have. But while an adult male weight lifter and a young boy have a similar number of muscle fibers, the weight lifter may be several times the boy's strength because repeated high-intensity, short-duration exercise has induced the synthesis of additional actin and myosin filaments. Each fiber has hypertrophied, becoming larger and stronger. Endurance exercise such as long-distance running produces a very different response. Fibers do not become greatly stronger but develop more mitochondria and myoglobin and become adapted for a high rate of oxidative phosphorylation. These changes, together with the development of more capillaries serving the fibers, lead to increased capacity for long-duration activity.

Each thick filament is made up of myosin molecules packed together in an elongate bundle (Figure 31-15). Each myosin molecule is composed of two polypeptide chains, each having a club-shaped head. Lined up as they are in a bundle to form a thick filament, the double heads of each myosin molecule face outward from the center of the filament. These heads act as molecular cross bridges that interact with the thin filaments during contraction.

Thin filaments are more complex because they are composed of three different proteins. The backbone of the

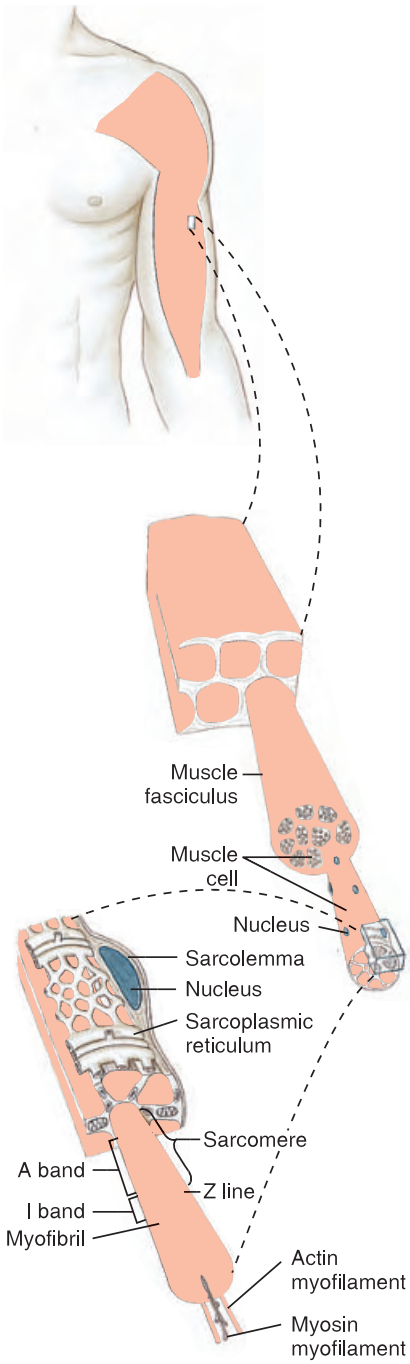

Figure 31-14
Organization of skeletal muscle from gross to molecular level. A skeletal muscle (*top*) is composed of thousands of multinucleated muscle fibers (*center*), each containing thousands of myofibrils (*bottom*). Each myofibril contains numerous thick (myosin) and thin (actin) filaments that interact to slide past each other during contraction to shorten the muscle. The sarcoplasmic reticulum is a network of tubules surrounding the myofibrils that serves as a communication system for carrying a depolarization to the filaments within the muscle fiber.

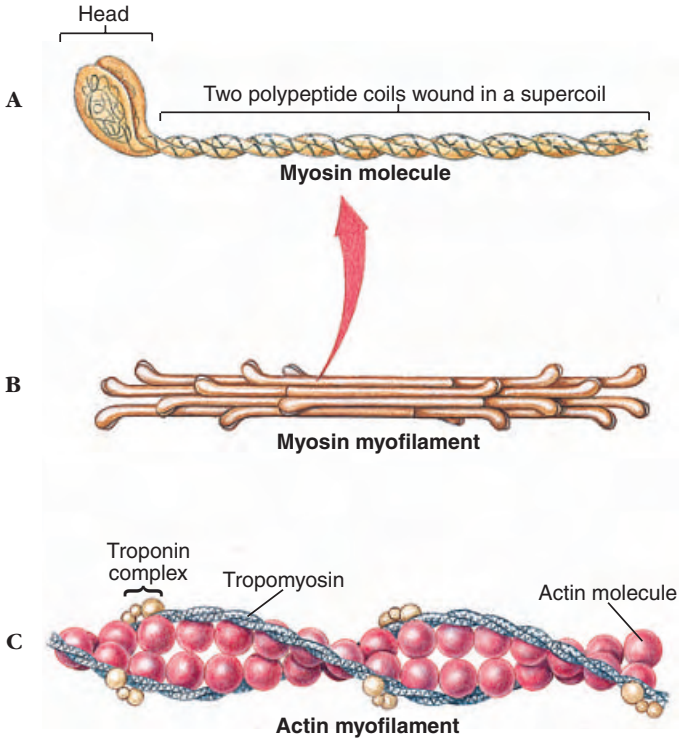

Figure 31-15
Molecular structure of thick and thin myofilaments of skeletal muscle. **A,** The myosin molecule is composed of two polypeptides coiled together and expanded at their ends into a globular head. **B,** The thick myofilament is composed of a bundle of myosin molecules with the globular heads extended outward. **C,** The thin myofilament consists of a double strand of actin surrounded by two tropomyosin strands. A globular protein complex, troponin, occurs in pairs at every seventh actin unit. Troponin is a calcium-dependent switch that controls the interaction between actin and myosin.

thin filament is a double strand of the protein actin, twisted into a double helix. Surrounding the actin filament are two thin strands of another protein, **tropomyosin,** that lie near the grooves between the actin strands. Each tropomyosin strand is itself a double helix as shown in Figure 31-15C.

The third protein of the thin filament is **troponin,** a complex of three globular proteins located at intervals along the filament. Troponin is a calcium-dependent switch that acts as the control point in the contraction process.

Sliding Filament Model of Muscle Contraction

In the 1950s the English physiologists A. F. Huxley and H. E. Huxley independently proposed the **sliding filament model** to explain striated muscle contraction. According to this model, the thick and thin filaments become linked together by molecular cross bridges, which act as levers to pull the filaments past each other. During contraction, cross bridges on the thick filaments swing rapidly back and forth, alternately attaching to and releasing from special receptor sites on the thin filaments, and drawing thin filaments past thick in a kind of ratchet action. As contraction continues, the Z lines are pulled closer together (Fig-ure 31-16). Thus the sarcomere shortens. Because all sarcomere units shorten together, the muscle contracts. Relaxation is a passive process. When cross bridges between the thick and thin filaments release, the sarcomeres are free to lengthen. This requires some force, which is usually supplied by antagonistic muscles or the force of gravity.

Control of Contraction

Muscle contracts in response to nerve stimulation. If the nerve supply to a

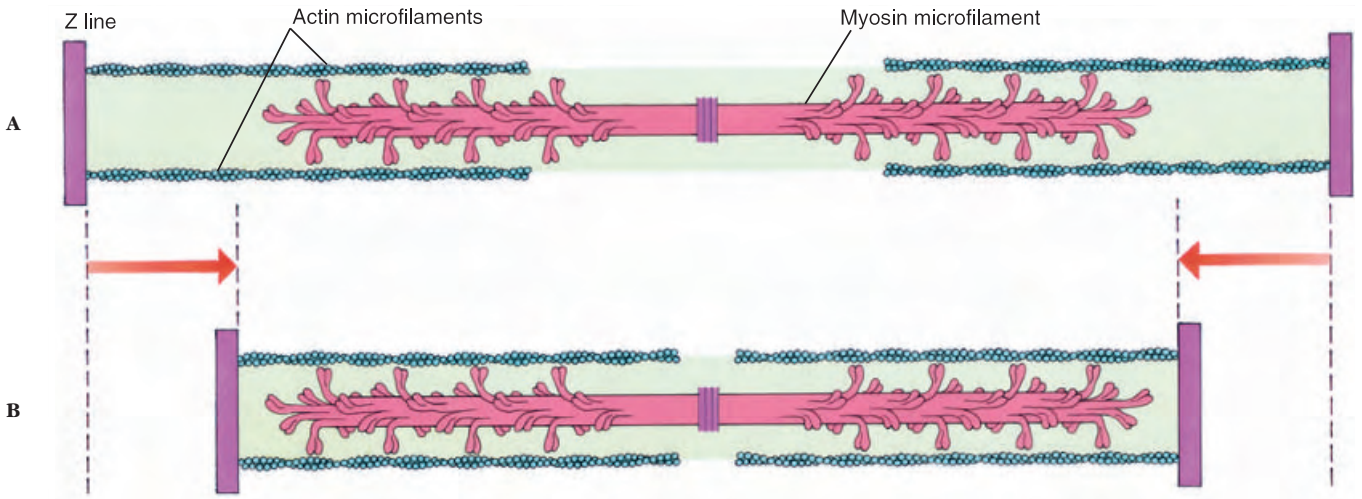

Figure 31-16
Sliding myofilament model, showing how thick and thin myofilaments interact during contraction. **A,** Muscle relaxed. **B,** Muscle contracted.

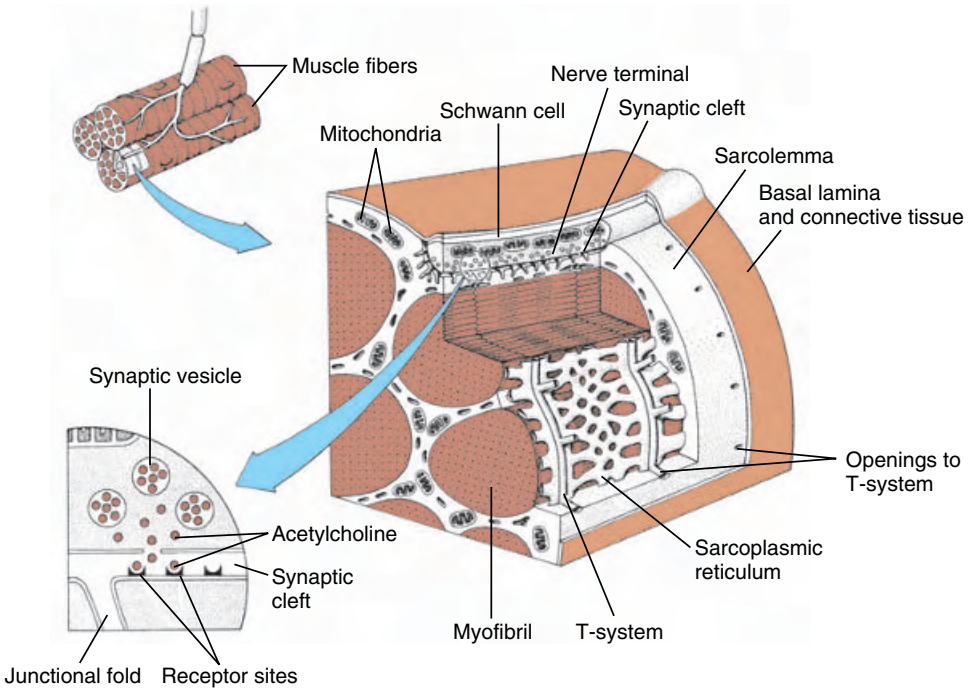

Figure 31-17
Section of vertebrate skeletal muscle showing nerve-muscle synapse (myoneural junction), sarcoplasmic reticulum, and connecting transverse tubules (T-tubule system). Arrival of a nerve impulse at the synapse triggers the release of acetylcholine into synaptic cleft (*inset at left*). The binding of transmitter molecules to receptors generates membrane depolarization. This spreads across the sarcolemma, into the T-tubule system, and to the sarcoplasmic reticulum where the sudden release of calcium sets in motion the contractile machinery of the myofibril.

muscle is severed, the muscle **atrophies,** or wastes away. Skeletal muscle fibers are innervated by motor neurons whose cell bodies are located in the spinal cord. Each cell body gives rise to a motor axon that leaves the spinal cord to travel by way of a peripheral nerve trunk to a muscle where it branches repeatedly into many terminal branches. Each terminal branch innervates a single muscle fiber. Depending on the type of muscle, a single motor axon may innervate as few as three or four muscle fibers (where very precise control is needed, such as the muscles that control eye movement) or as many as 2000 muscle fibers (where precise control is not required, such as large leg muscles). The motor neuron and all muscle fibers it innervates is called a **motor unit.** The motor unit is the functional unit of skeletal muscle. When a motor neuron fires, the action potential passes to all fibers of the motor unit and each is stimulated to contract simultaneously. Total force exerted by a muscle depends on the number of motor units activated. Precise control of movement is achieved by varying the number of motor units activated at any one time. A smooth and steady increase in muscle tension is produced by increasing the number of motor units brought into play; this is called motor unit **recruitment.**

The Myoneural Junction

The place where a motor axon terminates on a muscle fiber is called the **myoneural junction** (Figure 31-17). At the junction is a tiny gap, or **synaptic cleft,** that thinly separates a nerve fiber and muscle fiber. In the vicinity of the junction, the neuron stores a chemical, **acetylcholine,** in minute vesicles known as **synaptic vesicles.** Acetylcholine is released when a nerve impulse reaches a synapse. This substance is a chemical mediator that diffuses across the narrow junction and acts on the muscle fiber membrane to

generate an electrical depolarization. The depolarization spreads rapidly through the muscle fiber, causing it to contract. Thus the synapse is a special chemical bridge that couples together the electrical activities of nerve and muscle fibers.

Built into vertebrate skeletal muscle is an elaborate conduction system that serves to carry the depolarization from the myoneural junction to the densely packed filaments within the fiber. Along the surface of the sarcolemma are numerous invaginations that project as a system of tubules into the muscle fiber. This is called the **T-system** (Figure 31-17). The T-system is continuous with the **sarcoplasmic reticulum,** a system of fluid-filled channels that runs parallel to the myofilaments. The system is ideally arranged for speeding the electrical depolarization from the myoneural junction to the myofilaments within the fiber.

Excitation-Contraction Coupling

How does electrical depolarization activate the contractile machinery? In resting, unstimulated muscle, shortening does not occur because thin tropomyosin strands surrounding the actin myofilaments lie in a position that prevents the myosin heads from attaching to actin. When muscle is stimulated and the electrical depolarization arrives at the sarcoplasmic reticulum surrounding the fibrils, calcium ions are released (Figure 31-17). Some calcium binds to the control protein troponin. Troponin immediately undergoes changes in shape that allow tropomyosin to move out of its blocking position, exposing active sites on the actin myofilaments. The myosin heads then bind to these sites, forming cross bridges between adjacent thick and thin myofilaments. This sets in motion an **attach-pull-release cycle** that occurs in a series of steps as shown in Figure 31-18. Release of bond energy from ATP activates the myosin head, which swings 45 degrees, at the same time releasing a molecule of ADP. This is the power stroke that pulls the actin filament a distance of about 10 nm, and it comes to an end when another ATP molecule binds to the myosin head, inactivating the site. Thus each cycle requires expenditure of energy in the form of ATP (Figure 31-18).

Shortening will continue as long as nerve impulses arrive at the myoneural junction and free calcium remains available around the myofilaments. The attach-pull-release cycle can repeat again and again, 50 to 100 times per second, pulling thick and thin filaments past each other. While the distance each sarcomere can shorten is very small, this distance is multiplied by the thousands of sarcomeres lying end to end in a muscle fiber. Consequently, a strongly contracting muscle may shorten by as much as one-third its resting length.

When stimulation stops, calcium is quickly pumped back into the sarcoplasmic reticulum. Troponin resumes its original configuration; tropomyosin moves back into its blocking position on actin, and the muscle relaxes.

Energy for Contraction

Muscle contraction requires large amounts of energy. ATP is the immediate source of energy, but the amount present will sustain contraction for only a second or two. Muscle cells immediately call on the second level of energy reserve, **creatine phosphate.** Creatine phosphate is a high-energy phosphate compound that stores bond energy during periods of rest. As ADP is produced during contraction, creatine phosphate releases its stored bond energy to convert ADP to ATP. This reaction can be summarized as:

$$\text{Creatine phosphate} + \text{ADP} \rightarrow \text{ATP} + \text{Creatine}$$

Within a few seconds—perhaps as long as 30 seconds depending on the rapidity of muscle contraction—the reserves of creatine phosphate are depleted. The contracting muscle now must be fueled from its third and largest store of energy, **glycogen.** Glycogen is a polysaccharide chain of glucose molecules (p. 24) stored in both liver and muscle. Muscle has by far the larger store—some three-fourths of all the glycogen in the body is stored in muscle. As a supply of energy for contraction, glycogen has three important advantages: it is relatively abundant, it can be mobilized quickly, and it can provide energy under anoxic conditions. As soon as the muscle's store of creatine phosphate declines, enzymes break down glycogen, converting it into glucose-6-phosphate, the first stage of glycolysis that leads into mitochondrial respiration and the generation of ATP (p. 65).

If muscular contraction is not too vigorous or too prolonged, the glucose released from glycogen can be completely oxidized to carbon dioxide and water by **aerobic metabolism.** During prolonged or heavy exercise, however, blood flow to the muscles, although greatly increased above the resting level, cannot supply oxygen to the mitochondria rapidly enough to complete oxidation of glucose. The contractile machinery then receives its energy largely by **anaerobic glycolysis,** a process that does not require oxygen (p. 67). The ability to take advantage of this anaerobic pathway, although not nearly as efficient as the aerobic one, is of great importance; without it, all forms of heavy muscular exertion would be impossible.

During anaerobic glycolysis, glucose is degraded to lactic acid with release of energy. This is used to resynthesize creatine phosphate, which in turn passes the energy to ADP for the resynthesis of ATP. Lactic acid accumulates in the muscle and diffuses rapidly into the general circulation. If muscular exertion continues, the buildup of lactic acid causes enzyme inhibition and fatigue. Thus the anaerobic pathway is a self-limiting one, since continued heavy exertion leads to exhaustion. The muscles incur an **oxygen debt** because accumulated lactic acid must be oxidized by extra oxygen. After a period of exertion, oxygen consumption remains elevated until all of the lactic acid has

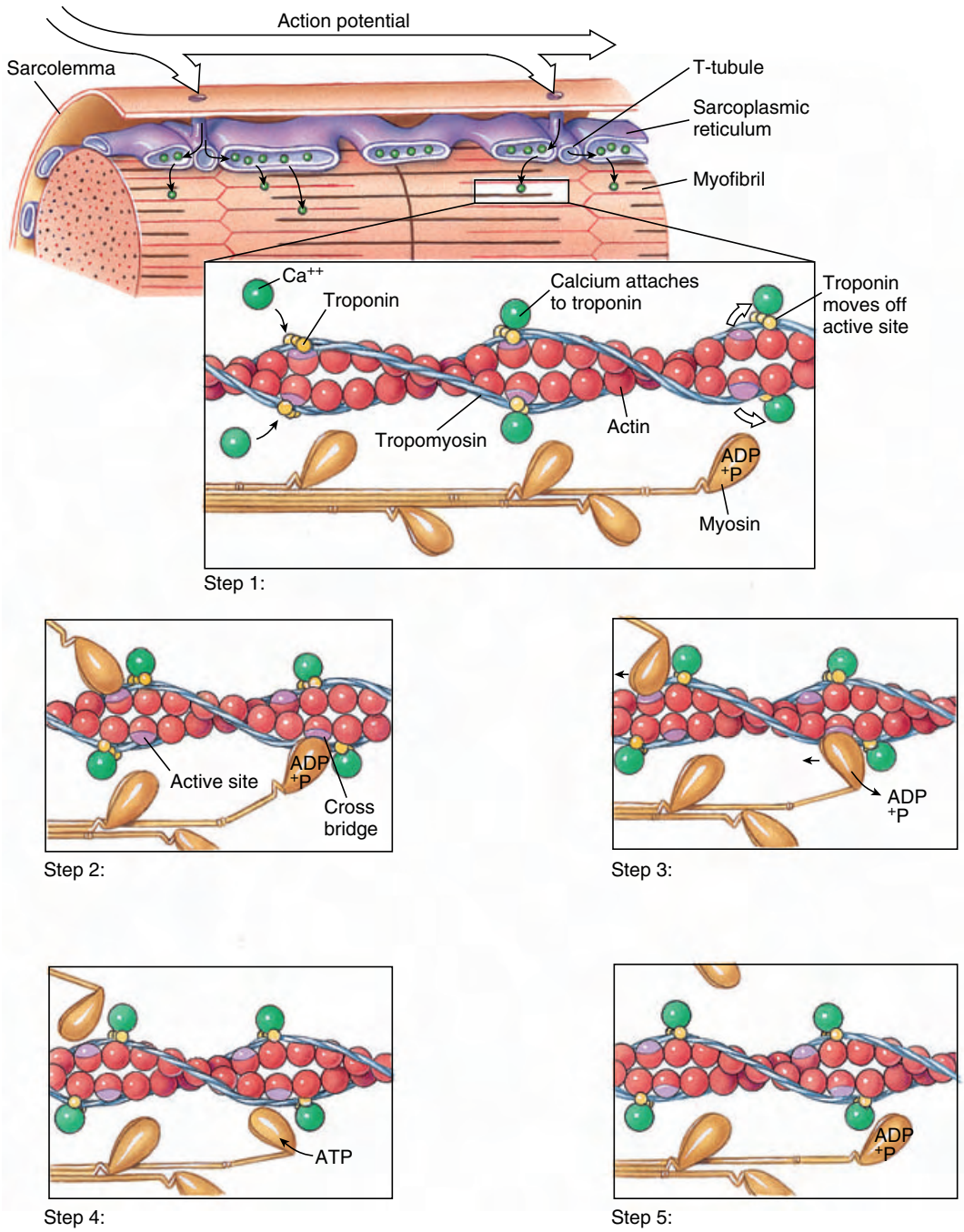

Figure 37-18

Excitation-contraction coupling in vertebrate skeletal muscle. **Step 1:** An action potential spreads along the sarcolemma and is conducted inward to the sarcoplasmic reticulum by way of T tubules (T-tubule system). Calcium ions released from the sarcoplasmic reticulum diffuse rapidly into the myofibrils and bind to troponin molecules on the actin molecule. Troponin molecules are moved away from the active sites. **Step 2:** Myosin cross bridges bind to the exposed active sites. **Step 3:** Using the energy stored in ATP, the myosin head swings toward the center of the sarcomere. ADP and a phosphate group are released. **Step 4:** The myosin head binds another ATP molecule; this frees the myosin head from the active site on actin. **Step 5:** The myosin head splits ATP, retaining the energy released as well as the ADP and the phosphate group. The cycle can now be repeated as long as calcium is present to open active sites on the actin molecules.

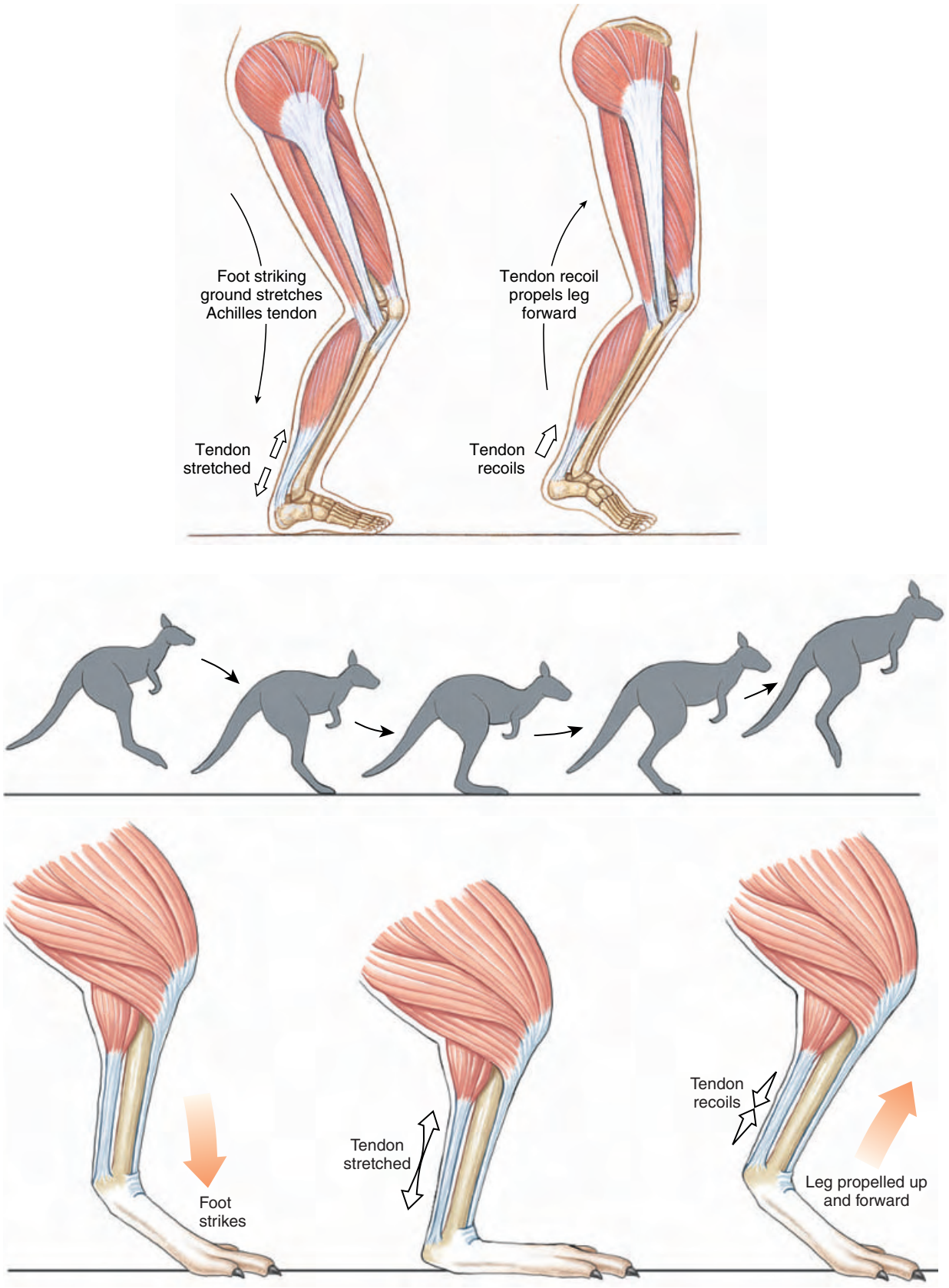

Figure 31-19
Energy storage in the Achilles tendon of human and kangaroo legs. During running, stretching of the Achilles tendon when the foot strikes the ground stores kinetic energy that is released to propel the leg forward.

been oxidized or resynthesized to glycogen.

Muscle Performance

Fast and Slow Fibers

Skeletal muscles of vertebrates consist of more than one type of fiber. **Slow fibers,** which are specialized for slow, sustained contractions without fatigue, are important in maintaining posture in terrestrial vertebrates. Such muscles are often called **red muscles** because they contain an extensive blood supply, a high density of mitochondria for supplying ATP, and abundant stored myoglobin which supplies oxygen reserves, all of which give the muscle a red color.

Two kinds of **fast fibers,** capable of fast, powerful contractions are known. One kind of fast fiber lacks an efficient blood supply and a high density of mitochondria and myoglobin. Muscles made up of these fibers (often referred to as white muscles) are usually pale in color, function anaerobically, and fatigue rapidly. The "white meat" of chicken is a familiar example. The other kind of fast fiber has an extensive blood supply and a high density of mitochondria and myoglobin, and functions largely aerobically. Animals use these for rapid, sustained activities. Most muscles possess a mixture of these different fiber types to provide for a range of activity. Geese, dogs, and ungulates (hoofed mammals), for example, have limb (or wing) muscles with a high percentage of fast aerobic fibers, and are capable of active locomotion for long periods of time. Members of the cat family, however, have running muscles made up almost entirely of fast fibers that operate anaerobically. During a chase, such muscles build up a substantial oxygen debt that is replenished after the chase. For example, a cheetah after a high-speed chase lasting less than a minute, will pant heavily for 30 to 40 minutes before its oxygen debt is paid off.

Importance of Tendons in Energy Storage

When mammals walk or run, much kinetic energy is stored from step to step as elastic strain energy in the tendons. For example, during running the Achilles tendon is stretched by a combination of downward force of the body on the foot and contraction of the calf muscles. The tendon then recoils, extending the foot while the muscle is still contracted, propelling the leg forward (Figure 31-19). An extreme example of this bouncing ball principle is the bounding of a kangaroo, which essentially bounces along on its tendons, utilizing the effect of gravity (Figure 31-19). This type of movement uses far less energy than would be required if every step relied solely on alternate muscle contraction and relaxation.

There are many examples of elastic storage in the animal kingdom. It is used in the ballistic jumps of grasshoppers and fleas, in the wing hinges of flying insects, in the hinge ligaments of bivalve molluscs, and in the highly elastic large dorsal ligament (ligamentum nuchae) that helps support the head of hoofed mammals.

Summary

An animal is wrapped in a protective covering, the integument, which may be as simple as the delicate plasma membrane of an ameba or as complex as the skin of a mammal. The arthropod exoskeleton is the most complex of invertebrate integuments, consisting of a two-layered cuticle secreted by a single-layered epidermis. It may be hardened by calcification or sclerotization and must be molted at intervals to permit body growth. Vertebrate integument consists of two layers: the epidermis, which gives rise to various derivatives such as hair, feathers, and claws; and the dermis, which supports and nourishes the epidermis. It also is the origin of bony derivatives such as fish scales and deer antlers.

Integument color is of two kinds: structural color, produced by refraction or scattering of light by particles in the integument, and pigmentary color, produced by pigments that are usually confined to special pigment cells (chromatophores).

Skeletons are supportive systems that may be hydrostatic or rigid. The hydrostatic skeletons of several soft-walled invertebrate groups depend on body-wall muscles that contract against a noncompressible internal fluid of constant volume. In a similar manner, muscular hydrostats, such as the tongue of mammals and reptiles, and the trunk of elephants, rely on muscle bundles arranged in complex patterns to produce movement without either skeletal support or a liquid-filled cavity. Rigid skeletons have evolved with attached muscles that act with the supportive skeleton to produce movement. Arthropods have an external skeleton, which must be shed periodically to make way for an enlarged replacement. The vertebrates developed an internal skeleton, a framework formed of cartilage or bone, that can grow with the animal, while, in the case of bone, additionally serving as a reservoir of calcium and phosphate.

Animal movement, whether in the form of cytoplasmic streaming, ameboid movement, or the contraction of an organized muscle mass, depends on specialized contractile proteins. The most important of these is the actomyosin system, which is usually organized into elongate thick and thin filaments that slide past one another during contraction. When a muscle is stimulated, an electrical depolarization is conducted into the muscle fibers through the sarcoplasmic reticulum, causing the release of calcium. Calcium binds to a protein troponin complex associated with the thin

actin filament. This causes tropomyosin to shift out of its blocking position and allows the myosin heads to cross-bridge with the actin filament. Powered by ATP, the myosin heads swivel back and forth to pull the thick and thin filaments past each other. Phosphate bond energy for contraction is supplied by carbohydrate fuels through a storage intermediate, creatine phosphate.

Vertebrate skeletal muscle consists of variable percentages of both slow fibers, used principally for sustained postural contractions, and fast fibers, used in locomotion. Tendons are important in locomotion because the kinetic energy stored in stretched tendons at one stage of a locomotory cycle is released at a subsequent stage.

Review Questions

1. The arthropod exoskeleton is the most complex of invertebrate integuments. Describe its structure, and explain the difference in the way cuticle is hardened in crustaceans and in insects.
2. Distinguish between epidermis and dermis in vertebrate integument, and describe the structural derivatives of these two layers.
3. What is the difference between structural colors and colors based on pigments? How do the chromatophores of vertebrates and cephalopod molluscs differ in structure and function?
4. As "naked apes" humans lack the protective investment of fur that shields other mammals from the damaging effects of sunlight. How does human skin respond to ultraviolet radiation in the short term and with continued exposure?
5. Hydrostatic skeletons have been defined as a mass of fluid enclosed within a muscular wall. How would you modify this definition to make it apply to a muscular hydrostat? Offer examples of both hydrostatic skeleton and muscular hydrostat.
6. One of the special qualities of vertebrate bone is that it is a living tissue that permits continuous remodeling. Explain how the structure of bone allows this remodeling to happen.
7. What is the difference between endochondral and membranous bone? Between spongy and compact bone?
8. Discuss the role of osteoclasts, osteoblasts, parathyroid hormone, and calcitonin in bone growth.
9. The laws of scaling tell us that doubling the length of an animal will increase its weight eightfold while the force its bones can bear increases only fourfold. What solutions to this problem have evolved that allow animals to become large, while maintaining bone stresses within margins of safety?
10. Name the major skeletal components included in the axial and in the appendicular skeleton.
11. An unexpected discovery from studies of ameboid movement is that the same proteins found in the contractile system of metazoan muscle—actin and myosin—are present in ameboid cells. Explain how these and other proteins are believed to interact during ameboid movement.
12. A "9 + 2" arrangement of microtubules is typical of both cilia and flagella. Explain how this system is thought to function to produce a bending motion. What is the difference between a cilium and a flagellum?
13. What functional features of molluscan smooth muscle and insect fibrillar muscle set them apart from any known vertebrate muscle?
14. The sliding filament model of skeletal muscle contraction assumes a sliding or slipping of interdigitating filaments of actin and myosin. Electron micrographs show that during contraction the thick and thin filaments remain of constant length while the distance between Z lines shortens. Explain how this happens in terms of the molecular structure of the muscle filaments. What is the role of regulatory proteins in contraction?
15. While the sarcoplasmic reticulum of muscle was first described by nineteenth-century microscopists, its true significance was not appreciated until its intricate structure was revealed much later by the electron microscope. What could you tell a nineteenth-century microscopist to enlighten him or her about the structure of the sarcoplasmic reticulum and its role in the coupling of excitation and contraction?
16. The filaments of skeletal muscle are moved by free energy derived from the hydrolysis of ATP. Yet the immediately available supply of ATP in muscle is exhausted within the first moments of muscle contraction. Explain where the energy for a sustained contraction originates. Under what circumstances is an oxygen debt incurred during muscle contraction?
17. During evolution, skeletal muscle became adapted to functional demands ranging from sudden, withdrawal movements of a startled worm, to the sustained contractions required to maintain mammalian posture, to supporting a long, fast chase across the African savanna. What are some of the fiber types in vertebrate muscle that evolved to support these kinds of activities?

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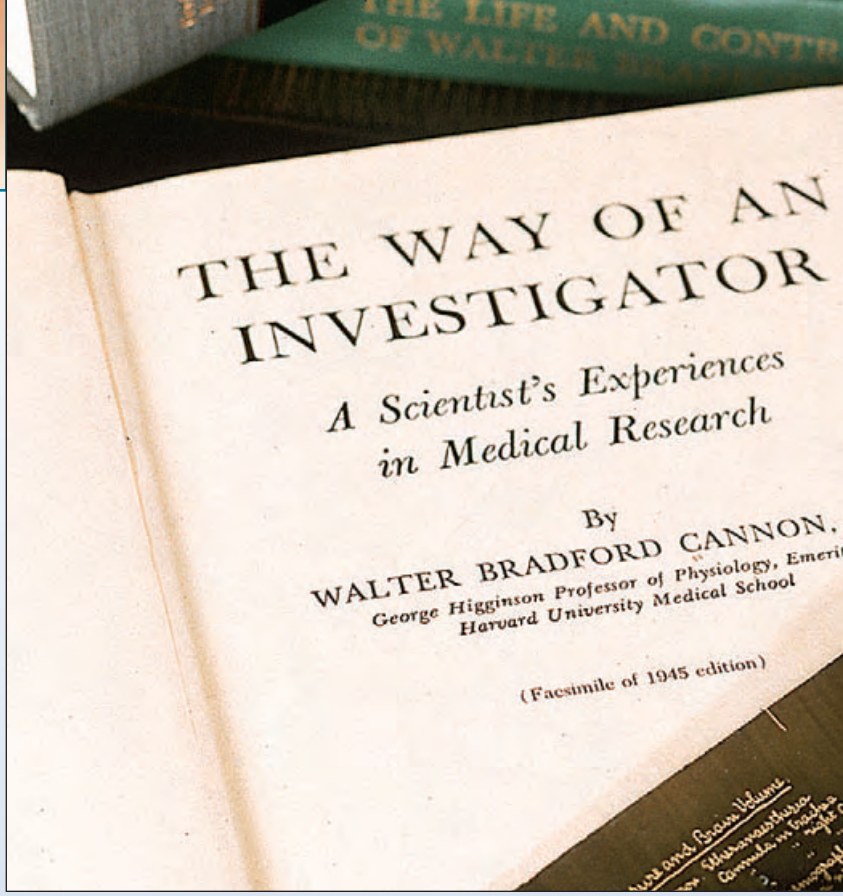
CHAPTER

32

Homeostasis

Osmotic Regulation, Excretion, and Temperature Regulation



Title page of Walter B. Cannon's autobiography.

Homeostasis: Birth of a Concept

The tendency toward internal stabilization of the animal body was first recognized by Claude Bernard, great French physiologist of the nineteenth century who, through his studies of blood glucose and liver glycogen, discovered the first internal secretions. Out of a lifetime of study and experimentation gradually grew the principle for which this retiring and lonely man is best remembered, that of constancy of the internal environment, a principle that in time would pervade physiology and medicine. Years later, at Harvard University, American physiologist Walter B. Cannon (Figure 32-1) reshaped and restated Bernard's idea. Developed out of his studies of the nervous system and reactions to stress, he described the ceaseless balancing and rebalancing of physiological processes that maintain stability and restore the normal state when it has been disturbed. He also gave it a name: homeostasis. The term soon flooded the medical literature of the 1930s. Physicians spoke of getting their patients back into homeostasis. Even politicians and sociologists saw what they considered deep nonphysiological implications. Cannon enjoyed this broadened application of the concept and later suggested that democracy was the form of government that took a homeostatic middle course. Despite the enduring importance of the homeostasis concept, Cannon never received the Nobel Prize—one of several acknowledged oversights of the Nobel Committee. Late in life, Cannon expressed his ideas about scientific research in his autobiography, *The Way of an Investigator*. This engaging book describes the resourceful career of a homespun man whose life embodied the traits that favor successful research. ■

Figure 32-1
Walter Bradford Cannon (1871 to 1945), Harvard professor of physiology who coined the term "homeostasis" and developed the concept originated by French physiologist Claude Bernard (Figure 33-2, p. 686).

The concept of homeostasis, described in the chapter opening essay, permeates all physiological thinking and is the theme of this and the following chapter. Although this concept was first developed from studies with mammals, it applies to single-celled organisms as well as to vertebrates. Potential changes in the internal environment arise from two sources. First, metabolic activities require a constant supply of materials, such as oxygen, nutrients, and salts, that cells withdraw from their surroundings and that must be replaced. Cellular activity also produces waste products that must be expelled. Second, the internal environment responds to changes in the organism's external environment. Changes from either source must be stabilized by the physiological mechanisms of homeostasis.

In more complex metazoans, homeostasis is maintained by the coordinated activities of the circulatory, nervous, and endocrine systems, and especially by organs that serve as sites of exchange with the external environment. These last include kidneys, lungs or gills, digestive tract, and integument. Through these organs oxygen, foodstuffs, minerals, and other constituents of body fluids enter, water is exchanged, heat is lost, and metabolic wastes are eliminated.

We look first at the problems of controlling the internal fluid environment of animals living in aquatic habitats. Next we briefly examine how these problems are solved by terrestrial animals and consider the function of the organs that regulate their internal state. Finally we look at strategies that have evolved for living in a world of changing temperatures.

Water and Osmotic Regulation

How Marine Invertebrates Meet Problems of Salt and Water Balance

Most marine invertebrates are in osmotic equilibrium with their seawater environment. They have body surfaces that are permeable to salts and water so that their body fluid concentration rises or falls in conformity with changes in concentrations of seawater. Because such animals are incapable of regulating osmotic pressure of their body fluid, they are called **osmotic conformers.** Invertebrates living in the open sea are seldom exposed to osmotic fluctuations because the ocean is a highly stable environment. Oceanic invertebrates have, in fact, very limited abilities to withstand osmotic change. If they should be exposed to dilute seawater, they die quickly because their body's cells cannot tolerate dilution and are helpless to prevent it. These animals are restricted to living in a narrow salinity range and are said to be **stenohaline** (Gr. *stenos*, narrow, + *hals*, salt). An example is the marine spider crab (Figure 32-2).

Conditions along coasts and in estuaries and river mouths are much less constant than those of the open ocean. Here animals must be able to withstand large and often abrupt changes in salinity as the tides ebb and flow and mix with fresh water draining from rivers. These animals are termed **euryhaline** (Gr. *eurys*, broad, + *hals*, salt), meaning that they can survive a wide range of salinity changes, mainly because they demonstrate varying powers of **osmotic regulation.** For example, the brackish-water shore crab can resist dilution of body fluids by dilute (brackish) seawater (Figure 32-2). Although the concentration of salts in the body fluids falls, it does so less rapidly than the fall in seawater concentration. This crab is a **hyperosmotic regulator,** meaning that it maintains its body fluids more concentrated (hence *hyper-*) than the surrounding water.

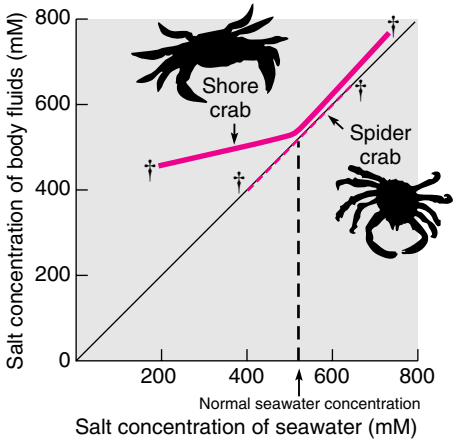


Figure 32-2
Salt concentration of body fluids of two crabs as affected by variations in seawater concentration. The 45-degree line represents equal concentration between body fluids and seawater. Since the spider crab cannot regulate the salt concentration of its fluids, it conforms to whatever changes happen in the seawater. The shore crab, however, can regulate osmotic concentration of its fluids to some degree in dilute seawater. For example, when seawater is 200 mM (millimolar), the shore crab's body fluid is approximately 430 mM. Crosses at ends of lines indicate limits of tolerance for each species.

By regulating against excessive dilution, thus protecting the cells from extreme changes, these crabs can live successfully in the physically unstable but biologically rich coastal environment. Nevertheless, with limited capacity for osmotic regulation, they will die if exposed to greatly diluted seawater. To understand how the brackish-water shore crab and other coastal invertebrates achieve hyperosmotic regulation, let us examine the

problems they face. First, because the crab's body fluids are osmotically more concentrated than the dilute seawater outside, water flows into its body, especially across the thin, permeable membranes of the gills. As with the membrane osmometer containing a salt solution (p. 48), water diffuses inward because it is more concentrated outside than inside. For the crab, were this inflow of water allowed to continue unchecked, its body fluids would soon become diluted and unbalanced. The problem is solved by the kidneys (antennal glands located in the crab's head), which can excrete the excess water as a dilute urine.

The second problem is salt loss. Again, because the animal is saltier than its environment, it cannot avoid loss of ions by outward diffusion across the gills. Salt is also lost in urine. This problem is solved by special salt-secreting cells in the gills that actively remove ions from dilute seawater and move them into the blood, thus maintaining the internal osmotic concentration. This is an **active transport** (p. 49) process that requires energy because ions must be transported against a concentration gradient from a lower salt concentration (in dilute seawater) to an already higher one (in blood).

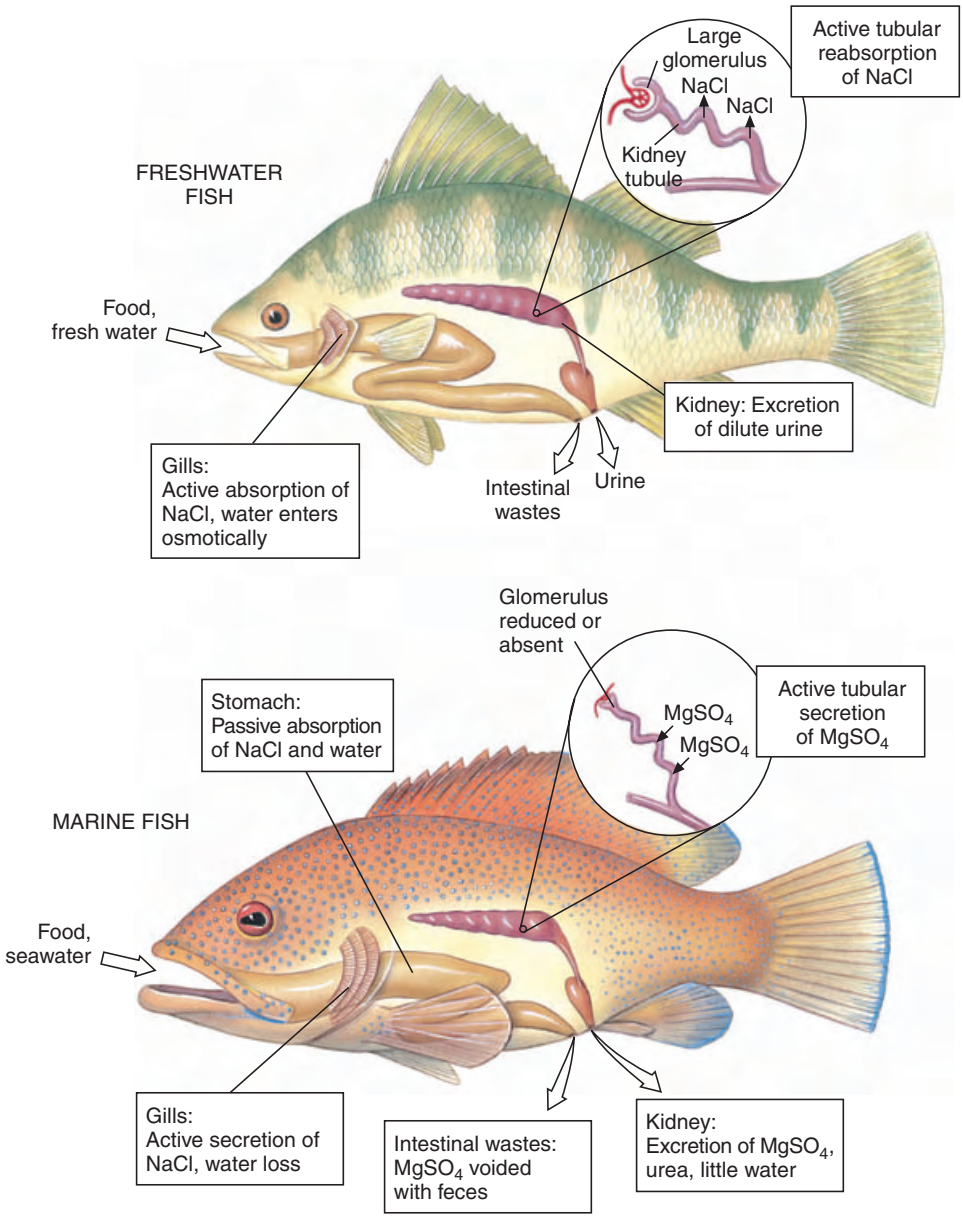


Figure 32-3
Osmotic regulation in freshwater and marine bony fishes. A freshwater fish maintains osmotic and ionic balance in its dilute environment by actively absorbing sodium chloride across the gills (some salt enters with food). To flush out excess water that constantly enters the body, the glomerular kidney produces a dilute urine by reabsorbing sodium chloride. A marine fish must drink seawater to replace water lost osmotically to its salty environment. Sodium chloride and water are absorbed from the stomach. Excess sodium chloride is secreted outward by the gills. Divalent sea salts, mostly magnesium sulfate, are eliminated with feces and secreted by the tubular kidney.

Invasion of Fresh Water

Some 400 million years ago, during the Silurian and Lower Devonian periods, the major groups of jawed fishes began to penetrate into brackish-water estuaries and then gradually into freshwater rivers. Before them lay a new, unexploited habitat already stocked with food in the form of insects and other invertebrates, which had preceded them into fresh water. However, the advantages of this new habitat were balanced by a tough physiological challenge: the necessity of developing effective osmotic regulation.

Freshwater animals must keep the salt concentration of their body fluids higher than that of the water in which they live. Water enters their bodies osmotically, and salt is lost by diffusion outward. Their problems are similar to those of the brackish-water crab, but more severe and unremitting. Fresh water is much more dilute than are coastal estuaries, and there is no retreat, no salty sanctuary into which a freshwater animal can retire for osmotic relief. It must and has become a permanent and highly efficient hyperosmotic regulator.

The scaled and mucus-covered body surface of a fish is about as waterproof as any flexible surface can be. In addition, freshwater fishes have several defenses against the problems of water gain and salt loss. First, water that inevitably enters by osmosis across the gills is pumped out by the kidney, which is capable of forming very dilute urine (Figure 32-3). Second, special

salt-absorbing cells located in the gills move salt ions, principally sodium and chloride (present in small quantities even in fresh water), from the water to the blood. This process, together with salt present in the fish's food, replaces diffusive salt loss. These mechanisms are so efficient that a freshwater fish devotes only a small part of its total energy expenditure to maintain osmotic balance.

Crayfishes, aquatic insect larvae, clams, and other freshwater animals are also hyperosmotic regulators and face the same hazards as freshwater fishes; they tend to gain too much water and lose too much salt. Like freshwater fishes, they solve these problems by excreting excess water as urine and replacing lost salt by some salt-transporting mechanism on the body surface.

Amphibians living in water also must compensate for salt loss by actively absorbing salt from the water (Figure 32-4). They use their skin for this purpose. Physiologists learned some years ago that pieces of frog skin continue to transport sodium and chloride actively for hours when removed and placed in a specially balanced salt solution. Fortunately for biologists, but unfortunately for frogs, these animals are so easily collected and maintained in the laboratory that frog skin became a favorite membrane system for studies of ion-transport phenomena.

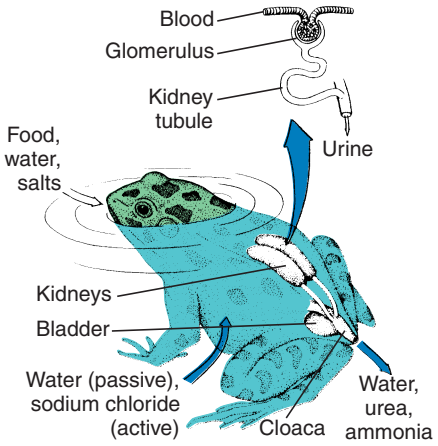


Figure 32-4
Exchange of water and solute in a frog. Water enters the highly permeable skin and is excreted by the kidney. The skin also actively transports ions (sodium chloride) from the environment. The kidney forms a dilute urine by reabsorbing sodium chloride. Urine flows into the urinary bladder, where, during temporary storage, most of the remaining sodium chloride is removed and returned to the blood.

Return of Fishes to the Sea

Marine bony fishes maintain the salt concentration of their body fluids at approximately one-third that of seawater (body fluids = 0.3 to 0.4 gram mole per liter [M]; seawater = 1 M). They are **hypoosmotic regulators** because they maintain their body fluids at a lower concentration (hence *hypo-*) than their seawater environment. Bony fishes living in the oceans today are descendants of earlier freshwater bony fishes that moved back into the sea during the Triassic period approximately 200 million years ago. During many millions of years that freshwater fishes were adapting themselves so well to their environment, they established an ionic concentration in the body fluid equivalent to approximately one-third that of seawater. The body fluid of terrestrial vertebrates is remarkably similar to that of dilute seawater too, a fact that is undoubtedly related to their ancient marine heritage.

By expressing concentration of salt in seawater or body fluids in molarity, we are saying that the osmotic strength is equivalent to the molar concentration of an ideal solute having the same osmotic strength. In fact, seawater and animal body fluids are not ideal solutions because they contain electrolytes that dissociate in solution. A 1 M solution of sodium chloride (which dissociates in solution) has a much greater osmotic strength than a 1 M solution of glucose, an ideal solute (nonelectrolyte) that does not dissociate in solution. Consequently, biologists usually express osmotic strength of a biological solution in osmolarity rather than molarity. A 1 osmolar solution exerts the same osmotic pressure as a 1 M solution of a nonelectrolyte.

When some freshwater bony fishes of the Triassic period ventured back to the sea, they encountered a new set of problems. Having a much lower internal osmotic concentration than the seawater around them, they lost water and gained salt. Indeed a marine bony fish literally risks drying out, much like a desert mammal deprived of water.

To compensate for water loss a marine fish drinks seawater (Figure 32-3). This seawater is absorbed from the intestine, and the major sea salt, sodium chloride, is carried by the blood to the gills, where specialized salt-secreting cells transport it back into the surrounding sea. Ions remaining in the intestinal residue, especially magnesium, sulfate, and calcium, are voided with the feces or excreted by the kidney. In this indirect way, marine fishes rid themselves of the excess sea salts they have drunk, and replace water lost by osmosis. Samuel Taylor Coleridge's ancient mariner, surrounded by "water, water, everywhere, nor any drop to drink" undoubtedly would have been tormented even more had he known of the marine fishes' ingenious solution for thirst. A marine fish regulates the amount of seawater it drinks, consuming only enough to replace water loss and no more.

The cartilaginous sharks and rays (elasmobranchs) achieve osmotic balance differently. This group is almost totally marine. The salt composition of shark's blood is similar to that of the bony fishes, but the blood also carries a large content of organic compounds, especially urea and trimethylamine oxide. Urea is a metabolic waste that most animals quickly excrete. The shark kidney, however, conserves urea, allowing it to accumulate in the blood and raising the blood osmolarity to equal or slightly exceed that of seawater. With osmotic difference between blood and seawater eliminated, water balance is not a problem for sharks and their kin; they are in osmotic equilibrium with their environment.

The high concentration of urea in the blood of sharks and rays—more than 100 times as high as in mammals—could not be tolerated by most other vertebrates. In the latter, such high concentrations of urea disrupt peptide bonds of proteins, altering protein configuration. Sharks have adapted

biochemically to the presence of urea that permeates all their body fluids, even penetrating freely into cells. So accommodated are elasmobranchs to urea that their tissues cannot function without it, and their heart will stop beating in its absence.

How Terrestrial Animals Maintain Salt and Water Balance

The problems of living in an aquatic environment seem small indeed compared with the problems of life on land. Since animal bodies are mostly water, all metabolic activities proceed in water, and life itself was conceived in water, it might seem that animals were meant to stay in water. Yet many animals, like the plants preceding them, moved onto land, carrying their watery composition with them. Once on land, terrestrial animals continued their adaptive radiation, solving the threat of desiccation, until they became abundant even in some of the most arid parts of the earth.

Terrestrial animals lose water by evaporation from respiratory and body surfaces, excretion in urine, and elimination in the feces. They replace such losses by water in the food, drinking water when available, and retaining **metabolic water** formed in cells by oxidation of foods, especially carbohydrates. Certain insects—for example, desert roaches, certain ticks and mites, and the mealworm—are able to absorb water vapor directly from atmospheric air. In some desert rodents, metabolic water gain may constitute most of the animals' water intake.

Particularly revealing is a comparison of water balance in human beings, nondesert mammals that drink water, with that of kangaroo rats, desert rodents that may drink no water at all (Table 32-1). Kangaroo rats acquire all their water from their food: 90% is metabolic water derived from oxidation of foods (see Figure 4-14, p. 68, and accompanying discussion of water yield during oxidative phosphorylation) and 10% as free moisture in food. Even though we eat foods with a much higher water content than the dry seeds that make up much of a kangaroo rat's diet, we still must drink half our total water requirement.

TABLE 32.1

Water Balance in a Human and a Kangaroo Rat, a Desert Rodent

	Human (%)	Kangaroo Rat (%)
Gains		
Drinking	48	0
Free water in food	40	10
Metabolic water	12	90
Losses		
Urine	60	25
Evaporation (lungs and skin)	34	70
Feces	6	5

Source: Some data from K. Schmidt-Nielsen, *How animals work*. Cambridge University Press, 1972.

Given ample water to drink, humans can tolerate extremely high temperatures while preventing a rise in body temperature. Our ability to keep cool by evaporation was impressively demonstrated more than 200 years ago by a British scientist who remained for 45 minutes in a room heated to 260° F (126° C). A steak he carried in with him was thoroughly cooked, but he remained uninjured and his body temperature did not rise. Sweating rates may exceed 3 liters of water per hour under such conditions and cannot be tolerated unless the lost water is replaced by drinking. Without water, a human continues to sweat unabatedly until the water deficit exceeds 10% of the body weight, when collapse occurs. With a water deficit of 12% a human is unable to swallow even if offered water, and death occurs when the water deficit reaches about 15% to 20%. Few people can survive more than a day or two in a desert without water. Thus people are not physiologically well adapted for desert climates but prosper there nonetheless by virtue of their technological culture.

The excretion of wastes presents a special problem in water conservation. The primary end product of protein breakdown is ammonia, a highly toxic material. Fishes easily excrete ammonia by diffusion across their gills, since there is an abundance of water to wash it away. Terrestrial insects, reptiles, and birds have no convenient way to rid themselves of toxic ammonia; instead, they convert it into uric acid, a nontoxic, almost insoluble compound. This conversion enables them to excrete a semisolid urine with little water loss. The use of uric acid has another important benefit. Reptiles and birds lay amniotic eggs enclosing their embryos (Figure 28-4, p. 564), together with their stores of food and water, and wastes that accumulate during development. By converting ammonia to uric acid, a developing embryo's waste can be precipitated into solid crystals, which are stored harmlessly within the egg until hatching.

Marine birds and turtles have evolved an effective solution for excreting large loads of salt eaten with their food. Located above each eye is a special **salt gland** capable of excreting a highly concentrated solution of sodium chloride—up to twice the concentration of seawater. In birds the salt solution runs out the nares (see p. 593 and Figure 29-13). Marine lizards and turtles, like *Alice in Wonderland's* Mock Turtle, shed their salt gland secretion as salty tears. Salt glands are important accessory organs of salt excretion in these animals because their kidneys cannot produce a concentrated urine, as can mammalian kidneys.

Invertebrate Excretory Structures

Many protozoa and some freshwater sponges have special excretory organelles called contractile vacuoles. More complex invertebrates have

excretory organs that are basically tubular structures forming urine by first producing an ultrafiltrate or fluid secretion of the blood. This fluid secretion enters the proximal end of the tubule and is modified continuously as it flows down the tubule. The final product is urine.

Contractile Vacuole

The tiny, spherical, intracellular vacuole of protozoa and freshwater sponges is not a true excretory organ, since ammonia and other nitrogenous wastes of metabolism readily enter the surrounding water by direct diffusion across the cell membrane. The contractile vacuole is an organ of water balance. It expels excess water that freshwater protozoa gain by osmosis. As water enters the protozoan, the vacuole grows and finally collapses, emptying its contents through a pore on the surface. The cycle is repeated rhythmically. Although the mechanism for filling the vacuole is not fully understood, recent research suggests that contractile vacuoles are surrounded by a network of membranous channels populated with numerous proton pumps (proton pumps were described in connection with the electron transport chain in Chapter 4, p. 66 and following). Proton pumps apparently create H^+ and HCO^- gradients that draw water into the vacuole, forming an isosmotic solution. These ions are excreted when the vacuole empties.

Contractile vacuoles are common in freshwater protozoa, sponges, and radiate animals (such as hydra), but rare or absent in marine forms of these groups, which are isosmotic with seawater and consequently neither lose nor gain too much water.

Nephridium

The most common type of invertebrate excretory organ is the nephridium, a tubular structure designed to maintain appropriate osmotic balance. One of the simplest arrangements is the flame cell system (or **protonephridium**) of acoelomates (flatworms) and some pseudocoelomates.

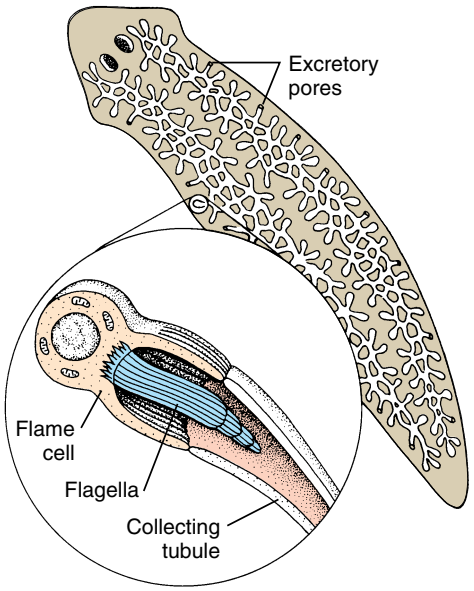


Figure 32-5
Flame cell system of a flatworm. Body fluids collected by flame cells (protonephridia) are passed down a system of ducts to excretory pores on the body surface.

In planaria and other flatworms the protonephridial system takes the form of two highly branched duct systems distributed throughout the body (Figure 32-5). Fluid enters the system through specialized "flame cells," moves slowly into and down the tubules, and is excreted through pores that open at intervals on the body surface. The rhythmical beat of the flagellar tuft, suggestive of a tiny flickering flame, creates a negative pressure that draws fluid into the tubular portion of the system. In the tubule, water and metabolites valuable to the body are recovered by reabsorption, leaving wastes behind to be expelled. Nitrogenous wastes (mainly ammonia) diffuse across the surface of the body.

The flame-cell system is extensively branched throughout a flatworm's body because these acoelomate animals have no circulatory system to deliver wastes to a centralized excretory system (such as the kidneys of vertebrates and many invertebrates).

The protonephridium just described is a **closed** system. The tubules are closed on the inner end and urine is formed from a fluid that must first enter the tubules by being transported across flame cells. A more advanced type of nephridium is the **open,** or "true," nephridium **(metanephridium)** that is found in several eucoelomate phyla such as annelids (Figure 32-6), molluscs, and several smaller phyla. A metanephridium is more advanced than a protonephridium in two important ways. First, the tubule is open at *both* ends, allowing fluid to be swept into the tubule through a ciliated funnel-like opening, the **nephrostome.** Second, a metanephridium is surrounded by a network of blood vessels that assists in the reclamation of water and valuable materials such as salts, sugars, and amino acids from the tubular fluid.

Despite these differences, the basic process of urine formation is the same in protonephridia and metanephridia: fluid enters and flows continuously through a tubule where the fluid is selectively modified by (1) withdrawing valuable solutes from it and returning these to the body (reabsorption) and (2) adding waste solutes to it (secretion). The sequence ensures removal of wastes from the body without loss of materials valuable to the body. We will see that kidneys of vertebrates operate in basically the same way.

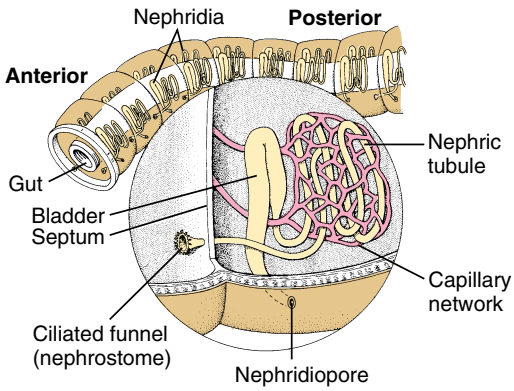


Figure 32-6
Excretory system of an earthworm. Each segment has a pair of large nephridia suspended in a fluid-filled coelom. Each nephridium occupies two segments because the ciliated funnel (nephrostome) drains the segment anterior to the segment containing the rest of the nephridium.

Arthropod Kidneys

The paired **antennal glands** of crustaceans, located in the ventral part of the head (Figure 32-7), are an advanced design of the basic nephridial organ. However, they lack open nephrostomes. Instead, hydrostatic pressure of the blood forms a protein-free filtrate of the blood (ultrafiltrate) in the end sac. In the tubular portion of the gland, selective reabsorption of certain salts and active secretion of others modifies the filtrate. Thus crustaceans have excretory organs that are basically vertebrate-like in the functional sequence of urine formation.

Insects and spiders have a unique excretory system consisting of **Malpighian tubules** that operate in conjunction with specialized glands in the wall of the rectum (Figure 32-8). These thin, elastic, blind Malpighian tubules are closed and lack an arterial supply. Urine formation is initiated by active secretion of salts, largely potassium, into the tubules from the hemolymph (blood). This primary secretion of ions creates an osmotic drag that pulls water, solutes, and nitrogenous wastes, especially uric acid, into the tubule. Uric acid enters the upper end of the tubule as soluble potassium urate, which precipitates as insoluble uric acid in the proximal end of the tubule. Once the formative urine drains into the rectum, most of the water and potassium are reabsorbed by specialized rectal glands, leaving behind uric acid and other wastes that are expelled in the feces. The Malpighian tubule excretory system is ideally suited for life in dry environments and has contributed to the adaptive radiation of insects on land.

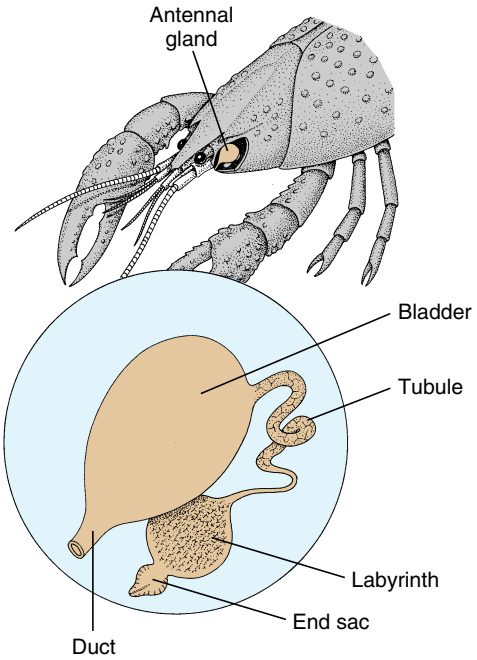


Figure 32-7
Antennal glands of a crayfish. These are filtration kidneys in which a filtrate of the blood is formed in the end sac. The filtrate is converted into urine as it passes down the tubule toward the bladder.

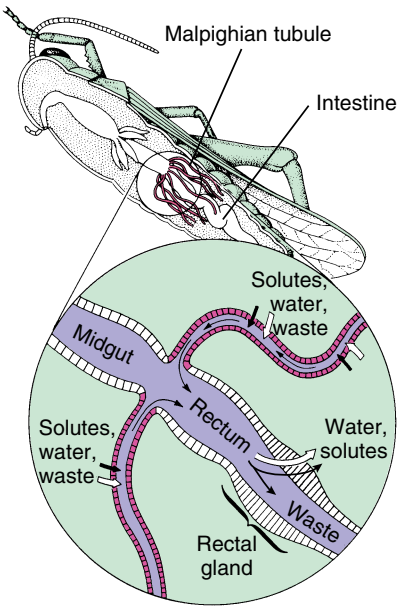


Figure 32-8
Malpighian tubules of insects. Malpighian tubules are located at the juncture of the midgut and hindgut (rectum). Solutes, especially potassium, are actively secreted into the tubules from the surrounding arthropod hemolymph. Water and wastes follow. This fluid drains into the rectum, where solutes and water are actively reabsorbed, leaving wastes to be excreted.

Vertebrate Kidney

Ancestry and Embryology

From comparative studies of development, biologists believe that the kidney of the earliest vertebrates extended the length of the coelomic cavity and was composed of segmentally arranged tubules, each resembling an invertebrate nephridium. Each tubule opened at one end into the coelom by a nephrostome and at the other end into a common **archinephric duct.** This ancestral kidney is called an **archinephros** ("ancient kidney"), and we find a segmented kidney very similar to an archinephros in embryos of hagfishes and caecilians (Figure 32-9). Almost from the beginning, the reproductive system, which develops beside the excretory system from the same segmental blocks of trunk mesoderm, used the nephric ducts as a convenient conducting system for reproductive products. Thus even though the two systems have nothing functionally in common, they are closely associated in their use of common ducts.

Kidneys of living vertebrates developed from this primitive plan. During embryonic development of amniote vertebrates, there is a succession of three developmental stages of kidneys: **pronephros, mesonephros,** and **metanephros** (Figure 32-9). Some, but not all, of these stages are observed in other vertebrate groups. In all vertebrate embryos, the pronephros is the first kidney to appear. It is located anteriorly in the body and becomes part of the persistent kidney only in adult hagfishes. In all other vertebrates the pronephros degenerates during development and is replaced by a more centrally located mesonephros. The mesonephros is the functional kidney of embryonic amniotes (reptiles, birds, and mammals), and contributes to the adult kidney (called an **opisthonephros**) of fishes and amphibians.

The metanephros, characteristic of adult amniotes, is distinguished in several ways from the pronephros and mesonephros. It is more caudally located and it is a much larger, more compact structure containing a very large number of nephric tubules. It is drained by a new duct, the **ureter,** which developed when the old archinephric duct was relinquished to the reproductive system of the male for sperm transport. Thus three successive kidney types—pronephros,

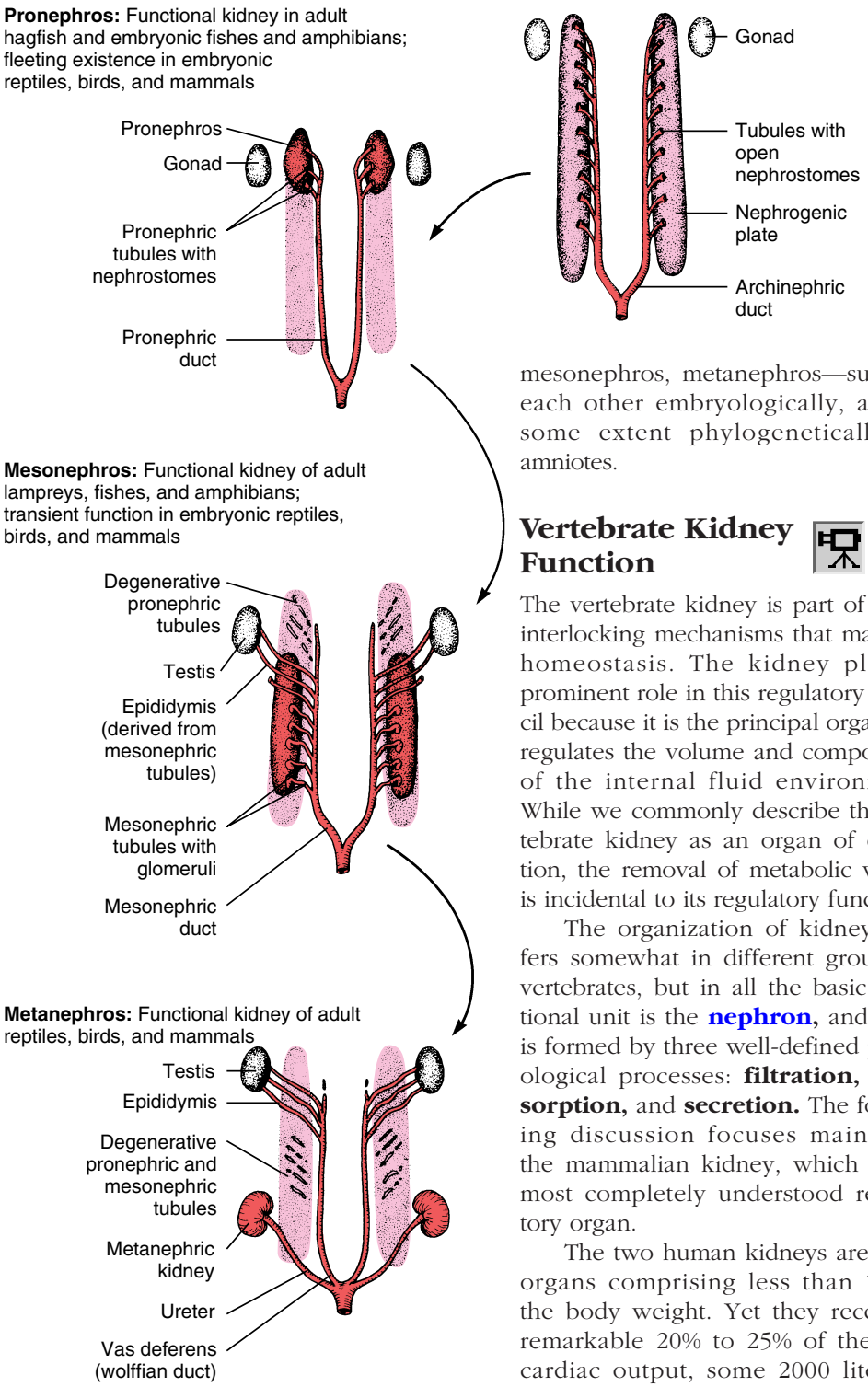


Figure 32-9
Comparative development of male vertebrate kidney. *Red*, functional structures. *Light red*, degenerative or undeveloped parts.

mesonephros, metanephros—succeed each other embryologically, and to some extent phylogenetically, in amniotes.

Vertebrate Kidney Function

The vertebrate kidney is part of many interlocking mechanisms that maintain homeostasis. The kidney plays a prominent role in this regulatory council because it is the principal organ that regulates the volume and composition of the internal fluid environment. While we commonly describe the vertebrate kidney as an organ of excretion, the removal of metabolic wastes is incidental to its regulatory function.

The organization of kidneys differs somewhat in different groups of vertebrates, but in all the basic functional unit is the **nephron,** and urine is formed by three well-defined physiological processes: **filtration, reabsorption,** and **secretion.** The following discussion focuses mainly on the mammalian kidney, which is the most completely understood regulatory organ.

The two human kidneys are small organs comprising less than 1% of the body weight. Yet they receive a remarkable 20% to 25% of the total cardiac output, some 2000 liters of blood each day. This vast blood flow is channeled to approximately 2 million nephrons, which make up the bulk of the two kidneys. Each nephron begins with an expanded chamber, the **renal corpuscle,** containing a tuft of capillaries called the **glomerulus** (glo-mer′yoo-lus). Blood pressure in the capillaries forces a protein-free **filtrate** into a **renal tubule,** consisting of several segments that perform different functions in the process of urine formation. The filtrate passes first into a **proximal convoluted tubule,** then into a long, thin-walled **loop of Henle,** which drops deep into the inner portion of the kidney (the **medulla**) before returning to the outer portion (the **cortex**) where it joins a **distal convoluted tubule.** From the distal tubule the fluid empties into a **collecting duct** which drains into the **renal pelvis.** Here the urine is collected before being carried by the **ureter** to the **urinary bladder.** These anatomical relationships are shown in Figure 32-10.

The urine that leaves the collecting duct is very different from the filtrate produced in the renal corpuscle. During its travels through the renal tubule and collecting duct, both the composition and concentration of the original filtrate change. Some solutes such as glucose and sodium have been reabsorbed while other materials, such as hydrogen ions and urea, have been concentrated in the urine.

The nephron, with its pressure filter and tubule, is intimately associated with blood circulation (Figure 32-11). Blood from the aorta enters each kidney through a large **renal artery,** which divides into a branching system of smaller arteries. The arterial blood reaches the renal corpuscle through an **afferent arteriole** and leaves by way of an **efferent arteriole.** From the efferent arteriole the blood travels to an extensive capillary network that surrounds and supplies the proximal and distal convoluted tubules and the loop of Henle (Figure 32-10). This

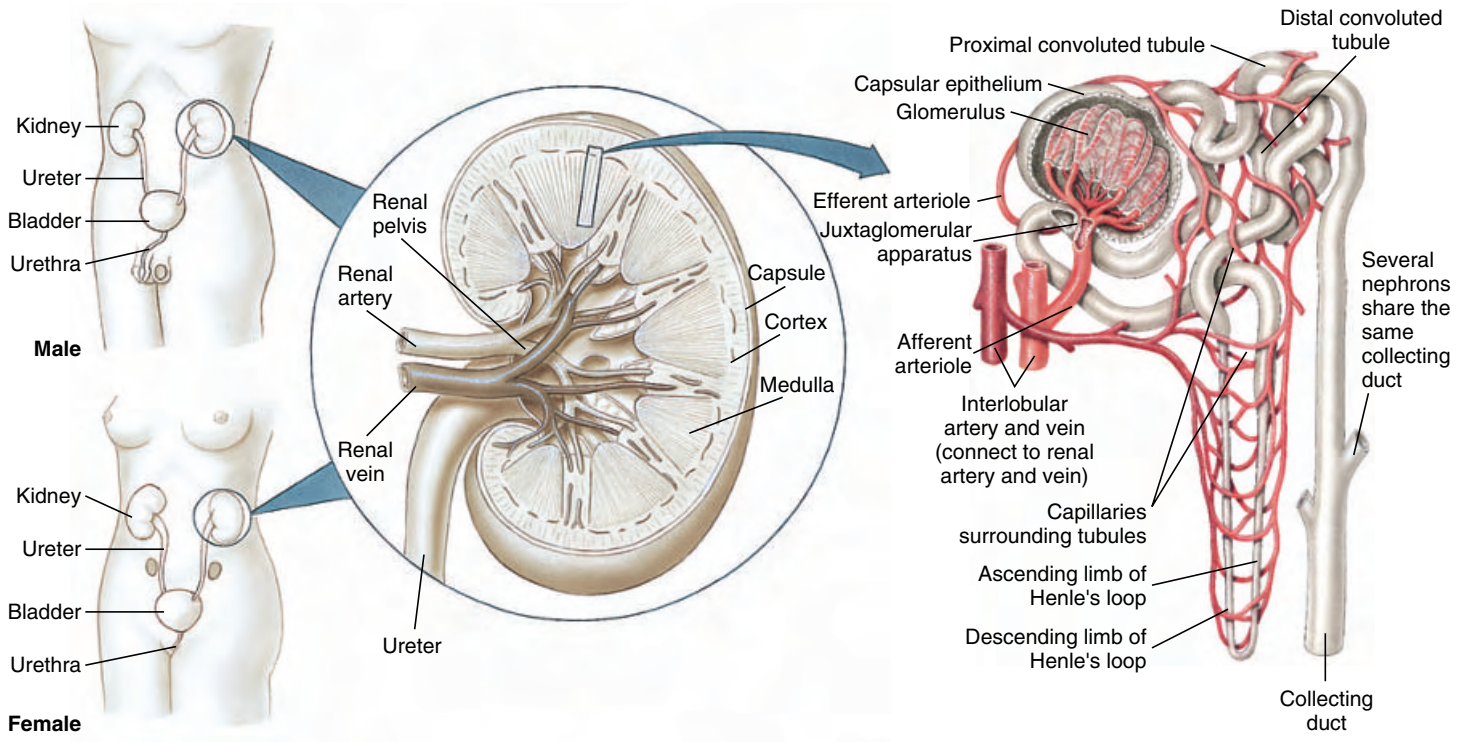


Figure 32-10
Urinary system of humans, with enlargements showing detail of the kidney and a single nephron.

capillary network provides a means for the pickup and delivery of materials that are reabsorbed or secreted by the kidney tubules. From these capillaries blood is collected by veins that unite to form the **renal vein.** This vein returns the blood to the vena cava.

Glomerular Filtration

Let us now return to the glomerulus, where the process of urine formation begins. The glomerulus acts as a specialized mechanical filter in which a protein-free filtrate of the plasma is driven by the blood pressure across the capillary walls and into the fluid-filled space of the renal corpuscle. Solute molecules small enough to pass through the slit pores of the capillary wall are carried through with the water in which they are dissolved. Red blood cells and plasma proteins, however, are withheld because they are too large to pass through these pores (Figure 32-12).

The filtrate continues through the renal tubular system where it will undergo extensive modification before becoming urine. Human kidneys form approximately 180 liters (nearly 50 gallons) of filtrate each day, a volume many times exceeding the total blood volume. If this volume of water and the valuable nutrients and salts it contains were lost, the body would soon be depleted of these compounds. Depletion does not happen because nearly all of the filtrate is reabsorbed. The final urine volume in humans averages 1.2 liters per day.

Conversion of filtrate into urine involves two processes: (1) modification of the composition of the filtrate through tubular reabsorption and secretion, and (2) changes in the total osmotic concentration of the urine through the regulation of water excretion.

Tubular Reabsorption

Approximately 60% of the filtrate volume and virtually all of the glucose, amino acids, vitamins and other valuable nutrients are reabsorbed in the proximal convoluted tubule. Much of this reabsorption is by **active transport,** in which cellular energy is used to transport materials from tubular fluid to the surrounding capillary network from which they will reenter the blood circulation. Electrolytes such as sodium, potassium, calcium, bicarbonate, and phosphate are reabsorbed by ion pumps, which are carrier proteins

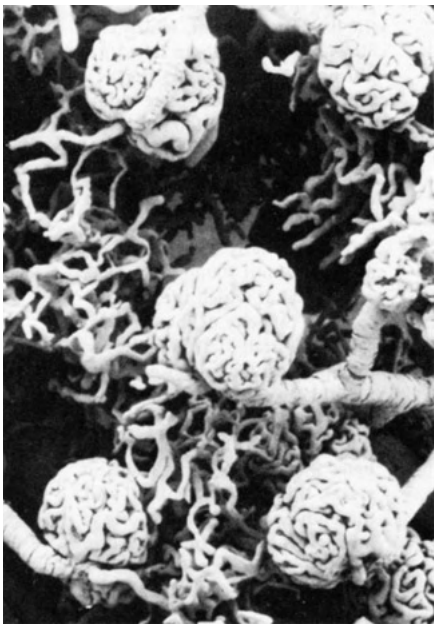


Figure 32-11
Scanning electron micrograph of a cast of the microcirculation of the mammalian kidney, showing several glomeruli and associated blood vessels. The capsular epithelium, which normally surrounds each glomerulus, has been digested away in preparing the cast.

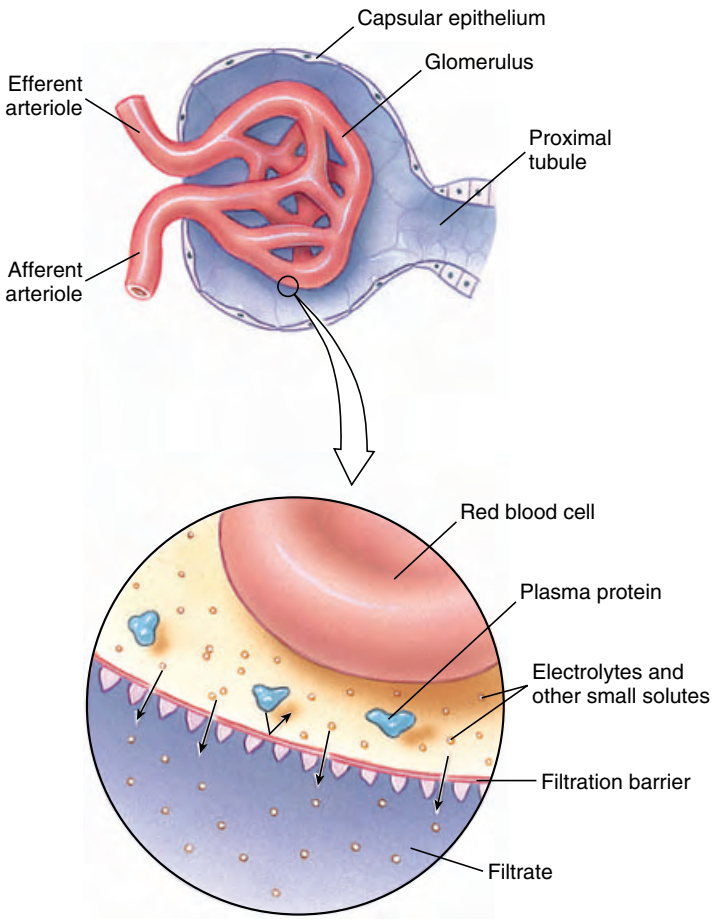


Figure 32-12

Renal corpuscle, showing (*enlargement*) the filtration of fluid through the glomerular capillary membrane. Water, electrolytes, and other small molecules pass the porous filtration barrier, but the plasma proteins are too large to pass the barrier. The filtrate is thus protein free.

driven by the hydrolysis of ATP (ion pumps are described on p. 49). Because an essential function of the kidney is to regulate the plasma concentrations of electrolytes, all are individually reabsorbed by ion pumps specific for each electrolyte. Some are strongly reabsorbed and others weakly reabsorbed, depending on the body's need to conserve each mineral. Some materials are passively reabsorbed. Negatively charged chloride ions, for example, passively accompany active reabsorption of positively charged sodium ions in the proximal convoluted tubule. Water, too, is withdrawn passively from the tubule, as it follows osmotically the active reabsorption of solutes.

In the disease diabetes mellitus ("sweet running through"), glucose rises to abnormally high concentrations in the blood plasma (hyperglycemia) because the hormone insulin, which enables body cells to take up glucose, is deficient. As blood glucose rises above a normal level of about 100 mg/100 ml of plasma, the concentration of glucose in the filtrate also rises, and more glucose must be reabsorbed by the proximal tubule. Eventually a point is reached (about 300 mg/100 ml of plasma) at which reabsorptive capacity of the tubular cells is saturated. This point is the transport maximum for glucose. Should plasma glucose continue to rise, glucose spills into the urine. In untreated diabetes mellitus the victim's urine tastes sweet, thirst is unrelenting, and the body wastes away despite a large food intake. In England the disease for centuries was appropriately called the "pissing evil."

For most substances there is an upper limit to the amount of substance that can be reabsorbed. This upper limit is termed the **transport maximum** (renal threshold) for that substance. For example, glucose normally is reabsorbed completely by the kidney because the transport maximum for glucose is poised well above the amount of glucose usually present in the plasma filtrate. Should the plasma glucose concentration exceed this threshold level, as in the disease diabetes mellitus, glucose appears in the urine (Figure 32-13).

Unlike glucose, most electrolytes are excreted in the urine in variable amounts. The reabsorption of sodium, the dominant cation in the plasma, illustrates the flexibility of the reabsorption process. The human kidney filters approximately 600 g of sodium every 24 hours. Nearly all of this sodium is reabsorbed, but the exact amount is matched precisely to sodium intake. With a normal sodium intake of 4 g per day, the kidney excretes 4 g and reabsorbs 596 g each day. A person on a low-salt diet of 0.3 g of sodium per day still maintains salt balance because only 0.3 g escapes reabsorption. But with a very high salt intake, much above 20 g per day, the kidney cannot excrete sodium as fast as it enters. The unexcreted sodium chloride holds additional water in the body fluids, and the person begins to gain weight. (The salt intake of the average North American is about 6 to 18 g per day, approximately 20 times more than the body needs, and three times more than is considered acceptable for those predisposed to high blood pressure.)

The human kidney can adapt to excrete large quantities of salt (sodium chloride) under conditions of high salt intake. In societies accustomed to widespread use of foods heavily salted for preservation (for example, salted pork and salt herring) daily intakes may approach or even exceed 100 g. Body weight remains normal under such conditions. However, the acute ingestion of 20 to 40 g/day by volunteers unadapted to such large intakes of salt caused swelling of tissues, increase in body weight, and some increase in blood pressure.

The distal convoluted tubule carries out the final adjustment of filtrate composition. Sodium reabsorbed by

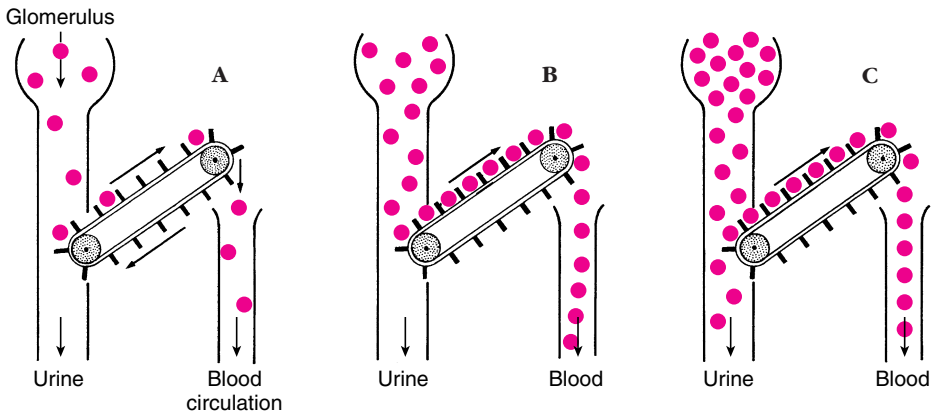


Figure 32-13

The mechanism for the tubular reabsorption of glucose can be likened to a conveyor belt running at constant speed. **A,** When the concentration of glucose in the filtrate is low, all is reabsorbed. **B,** When the glucose concentration in the filtrate has reached the transport maximum, all carrier sites for glucose are occupied. If the glucose rises further, **C,** as in the disease diabetes mellitus, some glucose escapes the carriers and appears in the urine.

the proximal convoluted tubule—some 85% of the total filtered—is obligatory reabsorption; this amount will be reabsorbed independent of sodium intake. In the distal convoluted tubule, however, sodium reabsorption is controlled by **aldosterone,** a steroid hormone from the adrenal gland (p. 764). Aldosterone increases active reabsorption of sodium by the distal tubules and thus decreases loss of sodium in the urine. The secretion of aldosterone is regulated mainly by the enzyme **renin,** produced by the **juxtaglomerular apparatus,** a complex of cells located in the afferent arteriole at its junction with the glomerulus (Figure 32-10). Renin is released in response to a low blood sodium level or to low blood pressure (which can occur if the blood volume drops too low). Renin then initiates a series of enzymatic events culminating in the production of **angiotensin,** a blood protein that has several related effects. First, it stimulates the release of aldosterone, which acts in turn to increase sodium reabsorption by the distal tubule. Second, it increases the secretion of **antidiuretic hormone** (vasopressin, discussed later in the chapter), which promotes water conservation by the kidney. Third, it increases blood pressure. Finally, it stimulates thirst. These actions of angiotensin tend to reverse the circumstances (low blood sodium and low blood pressure and/or blood volume) that triggered the secretion of renin. Sodium and water are conserved, and blood volume and blood pressure are restored to normal.

The flexibility of distal reabsorption of sodium varies considerably in different animals: it is restricted in humans but very broad in many rodents. These differences have appeared because selective pressures during evolution have resulted in rodents adapted for dry environments. They must conserve water and at the same time excrete considerable sodium. Humans, however, were not designed to accommodate the large salt appetites many have. Our closest relatives, the great apes, are vegetarians with an average salt intake of less than 0.5 g per day.

Tubular Secretion

In addition to reabsorbing materials from plasma filtrate, the nephron can secrete materials across the tubular epithelium and *into* the filtrate. In this process, the reverse of tubular reabsorption, carrier proteins in the tubular epithelial cells selectively transport substances from blood in capillaries outside the tubule to the filtrate inside the tubule. Tubular secretion enables the kidney to build up the urine concentrations of materials to be excreted, such as hydrogen and potassium ions, drugs, and various foreign organic materials. The distal convoluted tubule is the site of most tubular secretion.

In the kidneys of bony marine fishes, reptiles, and birds, tubular secretion is a much more highly developed process than it is in mammalian kidneys. Marine bony fishes actively secrete large amounts of magnesium and sulfate, seawater salts that are by-products of their mode of osmotic regulation. Reptiles and birds excrete uric acid instead of urea as their major nitrogenous waste. The material is actively secreted by the tubular epithelium. Since uric acid is nearly insoluble, it forms crystals in the urine and requires little water for excretion. Thus excretion of uric acid is an important adaptation for water conservation.

Water Excretion

The kidney closely regulates the osmotic pressure of the blood. When fluid intake is high, the kidney excretes a dilute urine, saving salts and excreting water. When fluid intake is low, the kidney conserves water by forming a concentrated urine. A dehydrated person can concentrate urine to approximately four times blood osmotic concentration. This important ability to concentrate urine enables us to excrete wastes with minimal loss of water.

The capacity of the kidney of mammals and some birds to produce a concentrated urine involves an interaction between the loop of Henle and the collecting ducts. This interplay results in the formation of an osmotic gradient in the kidney, as shown in Figure 32-14. In the cortex, the interstitial fluid is isosmotic with the blood, but deep in the medulla the osmotic concentration is 4 times greater than that of the blood (in rodents and desert mammals that can produce highly concentrated urine the osmotic gradient is much greater than in humans). The high osmotic concentrations in the medulla are produced by an exchange of ions in the loop of Henle by **countercurrent multiplication.** "Countercurrent" refers to the

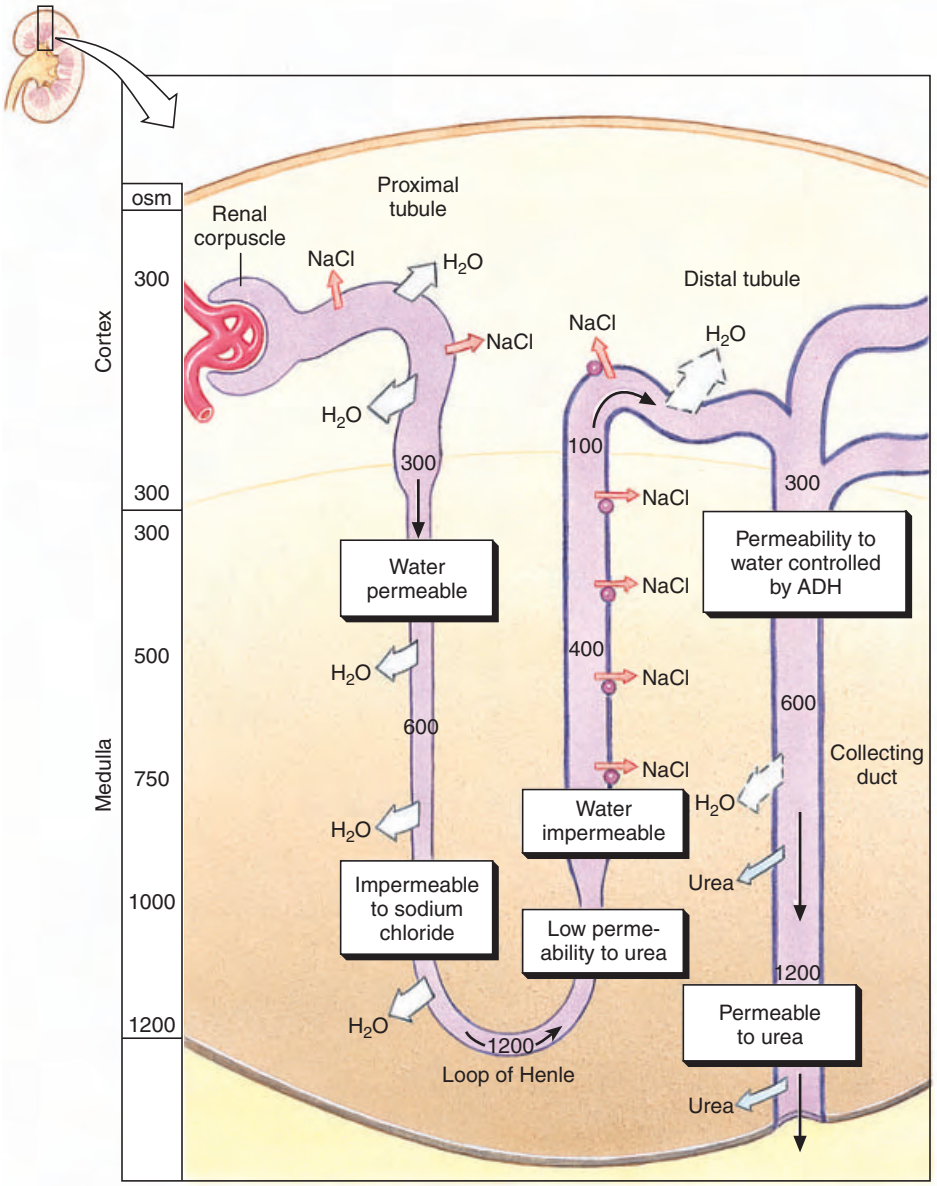


Figure 32-14

Mechanism of urine concentration in mammals. Sodium and chloride are pumped from the ascending limb of the loop of Henle, and water is withdrawn passively from the descending limb, which is impermeable to sodium chloride. Sodium chloride and urea reabsorbed from the collecting duct raise the osmotic concentration in the kidney medulla, creating an osmotic gradient for the controlled reabsorption of water from the collecting duct.

opposite directions of fluid movement in the two limbs of the loop of Henle: down in the descending limb and up the ascending limb. "Multiplication" describes the increasing osmotic concentration in the medulla resulting from ion exchange between the two limbs of the loop.

The functional characteristics of this system are as follows. The descending limb of the loop of Henle is permeable to water but impermeable to solutes. The ascending limb is relatively impermeable to both water and solutes. Sodium chloride is actively transported out of the thick portion of the ascending limb and into the surrounding tissue fluid (Figure 32-14). As the interstitium surrounding the loop becomes more concentrated with solute, water is withdrawn from the descending limb by osmosis. The tubular fluid in the base of the loop, now more concentrated, moves up the ascending limb, where still more sodium chloride is pumped out. In this way the effect of active ion transport in the ascending limb is multiplied as more water is withdrawn from the descending limb and more concentrated fluid is presented to the ascending limb ion pump (Figures 32-14 and 32-15).

Final adjustment of urine concentration occurs not in the loops of Henle but in the collecting ducts. Formative urine that enters the distal tubule from the loop of Henle is dilute (because of active salt withdrawal) and is diluted still more by active reabsorption of more sodium chloride in the distal tubule. The formative urine, low in solutes but carrying urea, now flows down into the collecting duct. Because of the high concentration of solutes surrounding the collecting duct, water is withdrawn from the urine. As the urine becomes more concentrated, urea also diffuses out and adds to the high osmotic pressure in the kidney medulla (Figure 32-15).

The amount of water reabsorbed and the final concentration of the urine depend on the permeability of the walls of the distal convoluted tubule and the collecting duct. This is controlled by the **antidiuretic hormone** (ADH, or vasopressin), which is released by the posterior pituitary gland (neurohypophysis). In turn, special receptors in the brain that constantly sense the osmotic pressure of the body fluids govern the release of this hormone. When the blood osmotic pressure increases, as during dehydration, the pituitary gland releases more ADH. ADH increases the permeability of the collecting duct, probably by expanding the size of pores in the walls of the duct. Then, as the fluid in the collecting duct passes through the hyperosmotic region of the kidney medulla, water diffuses through the pores into the surrounding interstitial fluid and is carried away by the blood circulation. The urine loses water and becomes more concentrated. Given this sequence of events for dehydration, it is not difficult to anticipate how the system responds to overhydration: the pituitary stops releasing ADH,

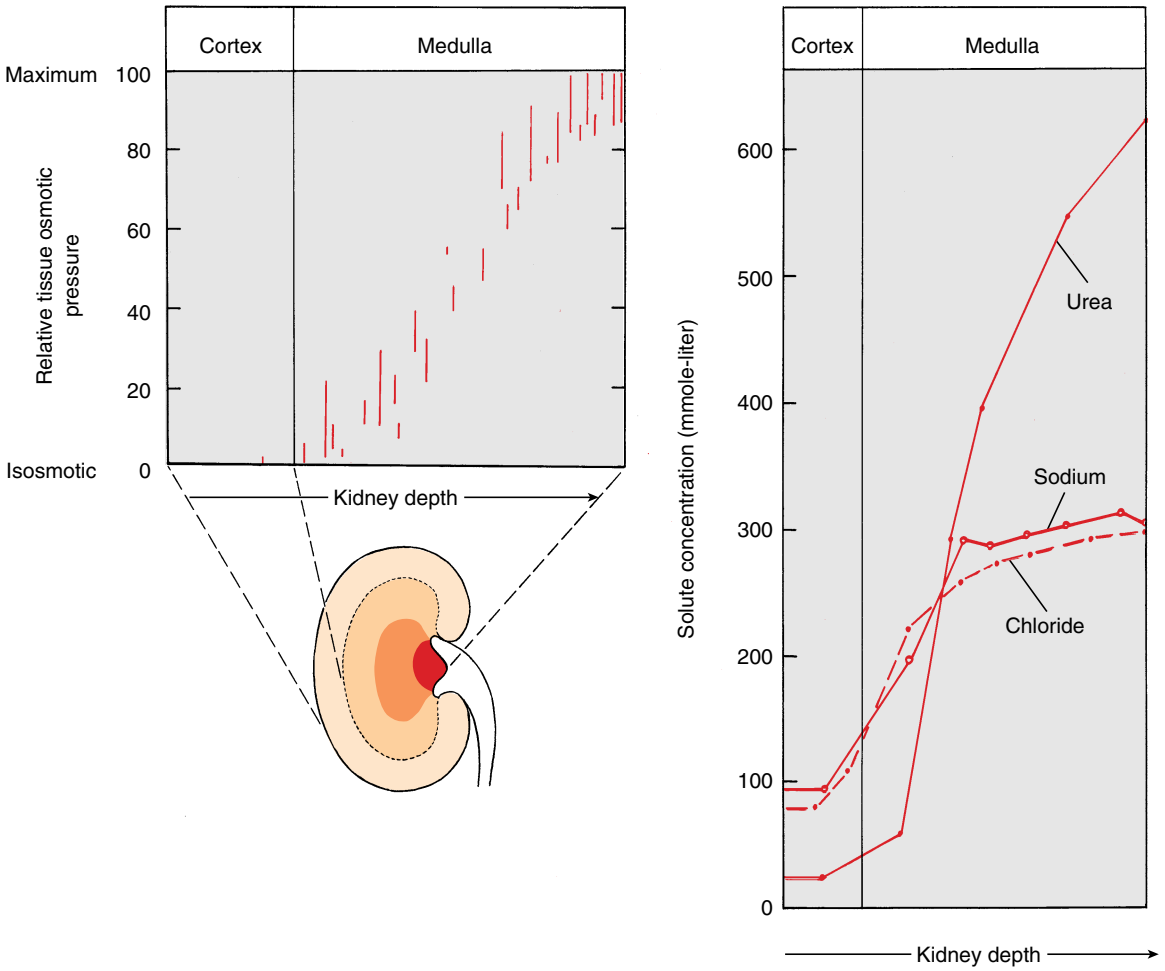


Figure 32-15

Osmotic concentration of tissue fluid in the mammalian kidney. Tissue fluid is isosmotic in the kidney cortex (*to left in diagram*) but osmotic concentration increases continuously through the medulla, reaching a maximum at the papilla where the urine drains into the ureter.

the pores in the collecting duct walls close, and a large volume of dilute urine is excreted.

The varying ability of different mammals to form a concentrated urine correlates closely with length of the loops of Henle. The beaver, which has no need to conserve water in its aquatic environment, has short loops and can concentrate its urine only to about twice the osmolarity of its blood plasma. Humans, with relatively longer loops, can concentrate urine 4.2 times that of the blood. As we would anticipate, desert mammals have much greater urine concentrating powers. A camel can produce a urine 8 times the plasma concentration, a gerbil 14 times, and an Australian hopping mouse 22 times. In this creature, the greatest urine concentrator of all, the loops of Henle extend to the tip of a long renal papilla that pushes out into the mouth of the ureter.

Temperature Regulation

We have seen that a fundamental problem facing an animal is keeping its internal environment in a state that permits normal cell function. Biochemical activities are sensitive to the chemical environment and our discussion thus far has examined how the chemical environment is stabilized. Biochemical reactions are also extremely sensitive to temperature. All enzymes have an optimum temperature; at temperatures above or below this optimum, enzyme function is impaired. Temperature therefore is a severe constraint for animals, all of which must maintain biochemical stability. When body temperature drops too low, metabolic processes slow, reducing the amount of energy the animal can muster for activity and reproduction. If body temperature rises too high, metabolic reactions become unbalanced and enzymatic activity is hampered or even destroyed. Thus animals can succeed only in a restricted range of temperature, usually between 0° to 40° C. Animals must either find a habitat where they do not have to contend with temperature extremes, or they must develop means of stabilizing their metabolism independent of temperature extremes.

A temperature difference of 10° C has become a standard used to measure the temperature sensitivity of a biological function. This value, called the Q_{10}, is

determined (for temperature intervals of exactly 10° C) simply by dividing the value of a rate function (such as metabolic rate or rate of an enzymatic reaction) at the higher temperature by the value of the rate function at the lower temperature. In general, metabolic reactions have Q_{10} values of about 2.0 to 3.0. Purely physical processes, such as diffusion, have much lower Q_{10} values, usually close to 1.0.

Ectothermy and Endothermy

The terms "cold-blooded" and "warm-blooded" have long been used to divide animals into two groups: invertebrates and vertebrates that feel cold to the touch, and those, such as humans, other mammals, and birds, that do not. It is true that body temperature of mammals and birds is usually (though not always) warmer than the air temperature, but a "cold-blooded" animal is not necessarily cold. Tropical fishes, and insects and reptiles basking in the sun, may have body temperatures equaling or surpassing those of mammals. Conversely, many "warm-blooded" mammals hibernate, allowing their body temperature to approach the freezing point of water. Thus the terms "warm-blooded" and "cold-blooded" are hopelessly subjective and nonspecific but are so firmly entrenched in our vocabulary that most biologists find it easier to accept the usage than to try to change people.

The term **poikilothermic** (variable body temperature) and **homeothermic** (constant body temperature) are frequently used by zoologists as alternatives to "cold-blooded" and "warm-blooded," respectively. These terms, which refer to variability of body temperature, are more precise and more informative, but still offer difficulties. For example, deep-sea fishes live in an environment having no perceptible temperature change. Even though their body temperature is absolutely stable, day in and day out, to call such fishes homeotherms would distort the intended application of the term. Furthermore, among the homeothermic birds and mammals there are many that allow their body temperature to change between day and night, or, as with hibernators, between seasons.

Physiologists prefer yet another way to describe body temperatures, one that reflects the fact that an animal's body temperature is a balance between heat gain and heat loss. All animals produce heat from cellular metabolism, but in most the heat is conducted away as fast as it is produced. In these animals, the **ectotherms**—and the overwhelming majority of animals belong to this group—body temperature is determined solely by the environment. Many ectotherms exploit their environment behaviorally to select areas of more favorable temperature (such as basking in the sun) but the source of energy used to increase body temperature comes from the environment, not from within the body. Alternatively some animals are able to generate and retain enough heat to elevate their own body temperature to a high but stable level. Because the source of their body heat is internal, they are called **endotherms.** These favored few in the animal kingdom are the birds and mammals, as well as a few reptiles and fast-swimming fishes, and certain insects that are at least partially endothermic. Endothermy allows birds and mammals to stabilize their internal temperature so that biochemical processes and nervous system functions can proceed at steady high levels of activity. Endotherms can thus remain active in winter and exploit habitats denied to ectotherms.

How Ectotherms Achieve Temperature Independence

Behavioral Adjustments

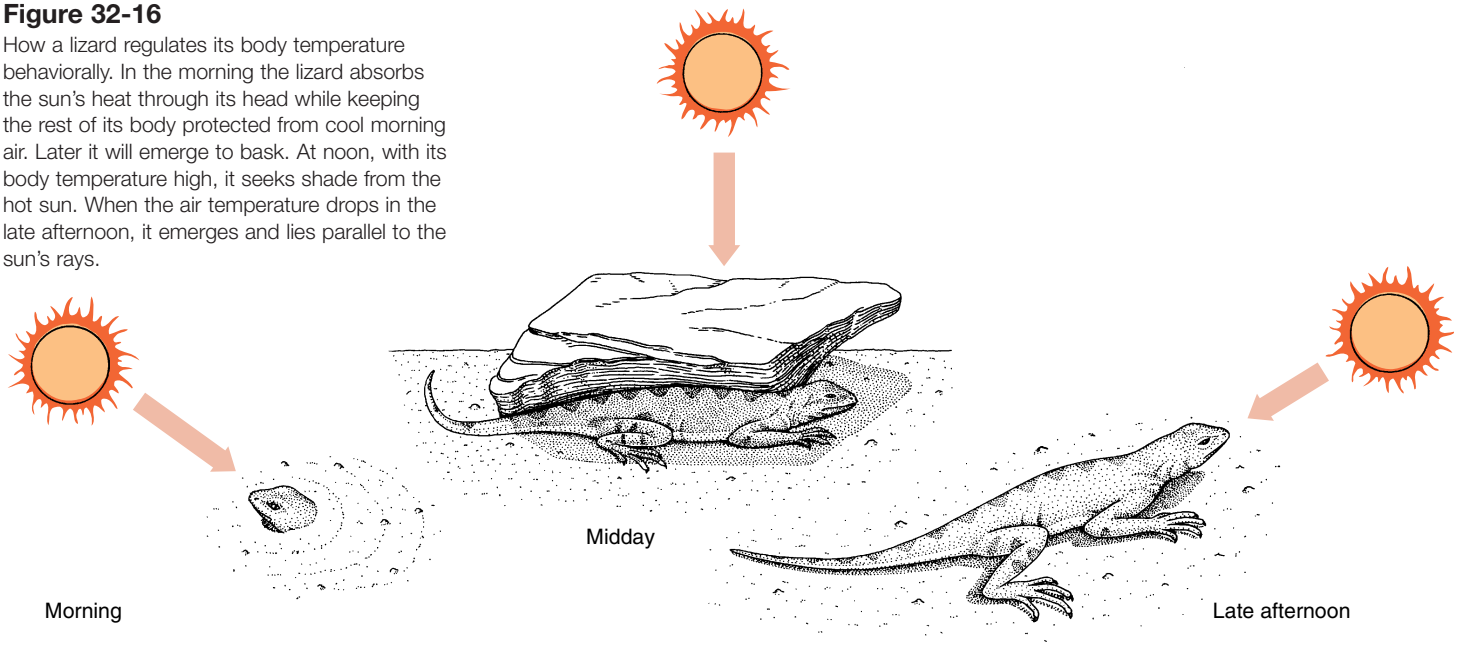
Although ectotherms cannot control their body temperature physiologically, many are able to regulate their body temperature behaviorally with considerable precision. Ectotherms often have the option of seeking areas in their environment where the temperature is favorable to their activities. Some ectotherms, such as desert lizards, exploit hour-to-hour changes in solar radiation to keep their body temperatures relatively constant (Figure 32-16). In the early morning they emerge from their burrows and bask in the sun with their bodies flattened to absorb heat. As the day warms, they turn to face the sun to reduce exposure, and raise their bodies from the hot substrate. In the hottest part of the day they may retreat to their burrows. Later they emerge to bask as the sun sinks lower and the air temperature drops.

These behavioral patterns help to maintain a relatively steady body temperature of 36° to 39° C while the air temperature varies between 29° and 44° C. Some lizards can tolerate intense midday heat without shelter. The desert iguana of the southwestern United States prefers a body temperature of 42° C when active and can tolerate a rise to 47° C, a temperature that is lethal to all birds and mammals and most other lizards. The term "cold-blooded" clearly does not apply to these animals!

Metabolic Adjustments

Even without the help of the behavioral adjustments just described, most ectotherms can adjust their metabolic rates to the prevailing temperature such that the intensity of metabolism remains mostly unchanged. This is called **temperature compensation** and involves complex biochemical and cellular adjustments. These adjustments enable a fish or a salamander, for example, to benefit from almost the same level of activity in both warm and cold environments. Thus, whereas endotherms achieve metabolic homeostasis by maintaining their body temperature independent of environmental temperature, ectotherms accomplish much the same by directly maintaining their metabolism independent of body temperature. This metabolic regulation also is a form of homeostasis.

Figure 32-16
How a lizard regulates its body temperature behaviorally. In the morning the lizard absorbs the sun's heat through its head while keeping the rest of its body protected from cool morning air. Later it will emerge to bask. At noon, with its body temperature high, it seeks shade from the hot sun. When the air temperature drops in the late afternoon, it emerges and lies parallel to the sun's rays.



Temperature Regulation in Endotherms

Most mammals have body temperatures between 36° and 38° C, somewhat lower than those of birds, which range between 40° and 42° C. Constant temperature is maintained by a delicate balance between heat production and heat loss—not a simple matter when these animals are alternating between periods of rest and bursts of activity.

Heat is produced by the animal's metabolism. This includes oxidation of foods, basal cellular metabolism, and muscular contraction. Because much of an endotherm's daily caloric intake is required to generate heat, especially in cold weather, the endotherm must eat more food than an ectotherm of the same size. Heat is lost by radiation, conduction, and convection (air movement) to a cooler environment and by evaporation of water (Figure 32-17). A bird or mammal can control both processes of heat production and heat loss within rather wide limits. If the animal becomes too cool, it can generate heat by increasing muscular activity (exercise or shivering) and by decreasing heat loss by increasing its insulation. If it becomes too warm, it decreases heat production and increases heat loss. We will examine these processes in the following examples.

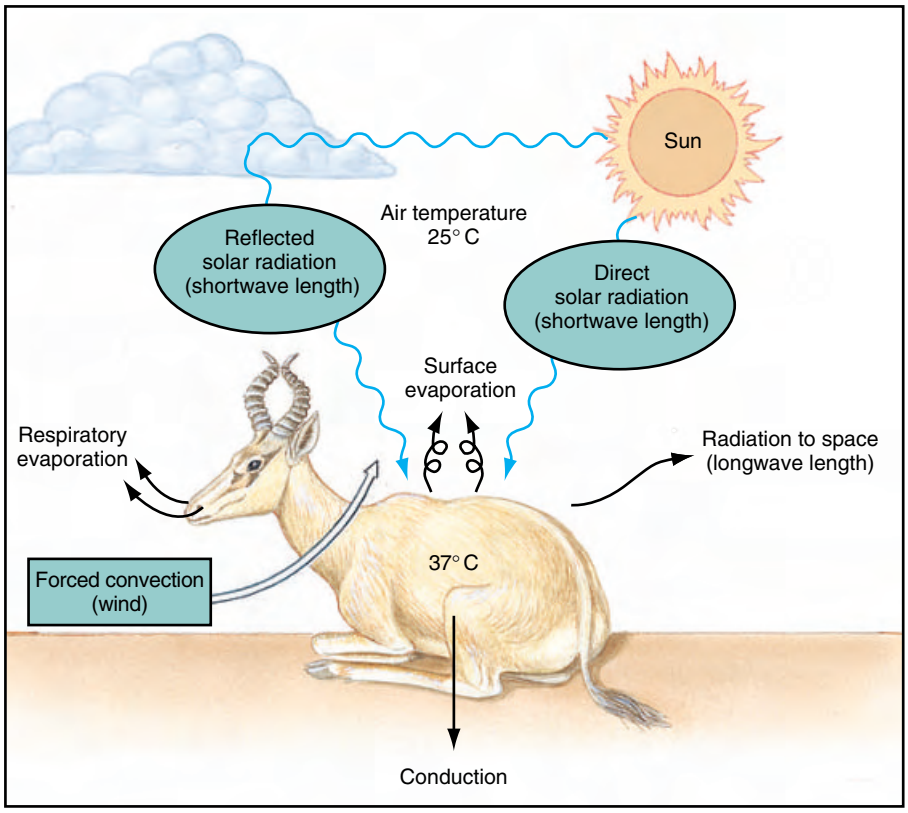


Figure 32-17
Exchange of heat between the animal and its environment on a warm day. Blue arrows indicate sources of net heat gain by the animal (all radiation); black arrows are avenues of net heat loss (evaporative cooling, conduction to the ground, longwave radiation into space, and forced convection by the wind). If air and ground temperatures were warmer than the animal, the arrows for forced convection, conduction, and radiation would be reversed. Then the animal could lose heat only by evaporative cooling.

Adaptations for Hot Environments

Despite the harsh conditions of deserts—intense heat during the day, cold at night, and scarcity of water, vegetation, and cover—many kinds of animals live there successfully. The smaller desert mammals are mostly **fossorial** (living mainly in the ground) or **nocturnal** (active at night). The lower temperature and higher humidity of burrows help to reduce water loss by evaporation. As explained earlier in this chapter (p. 668), desert animals such as the kangaroo rat and the American desert ground squirrels can, if necessary, derive the water they need from their dry food, drinking no water at all. Such animals produce a highly concentrated urine and form almost completely dry feces.

Large desert ungulates (hooved mammals that chew their cud) obviously cannot escape desert heat by living in burrows. Animals such as camels and desert antelopes (gazelle, oryx, and eland) possess a number of adaptations for coping with heat and dehydration. Figure 32-18 shows those of the eland. Mechanisms for controlling water loss and preventing overheating are closely linked. The glossy, pallid color of fur reflects direct sunlight, and fur itself is an excellent insulation that resists heat. Heat is lost by convection and conduction from the underside of elands where the fur is very thin. Fat tissue, an essential food reserve, is concentrated in a single hump on the back, instead of being uniformly distributed under the skin where it would impair loss of heat by radiation. Elands avoid evaporative water loss—the only means an animal has for cooling itself when the environmental temperature is higher than that of the body—by permitting their body temperature to drop during the cool night and then to rise slowly during the day as the body stores heat. Only when the body temperature reaches 41° C must elands prevent further rise through **evaporative cooling** by sweating and panting. They conserve water by producing a concentrated urine and dry feces.

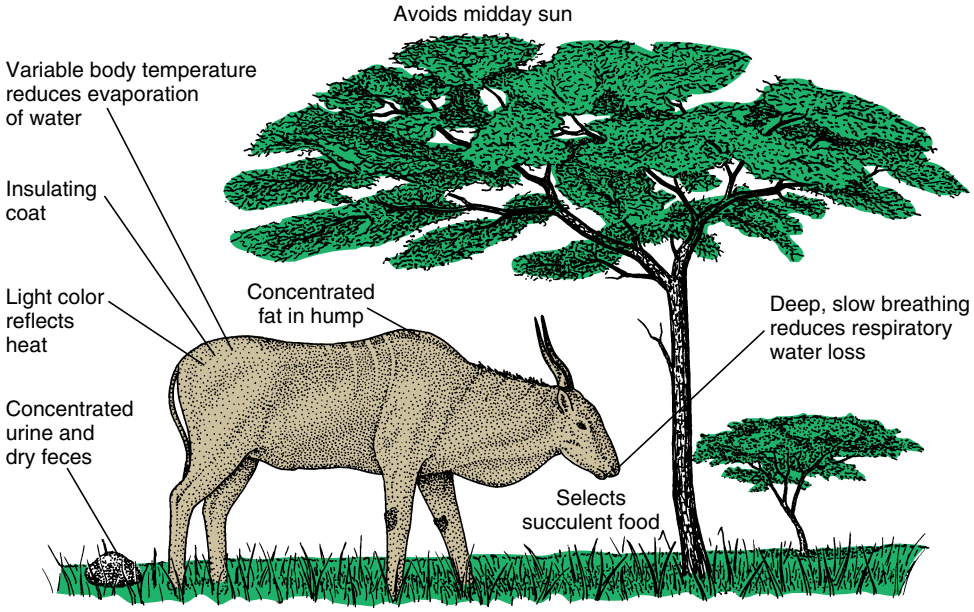


Figure 32-18
Physiological and behavioral adaptations of the common eland for regulating temperature in the hot, arid savanna of central Africa.

Camels have all of these adaptations developed to a similar or even greater degree; they are perhaps the most perfectly adapted of all large desert mammals.

Adaptations for Cold Environments

In cold environments mammals and birds use two major mechanisms to maintain homeothermy: (1) **decreased conductance,** reduction of heat loss by increasing the effectiveness of the insulation, and (2) **increased heat production.**

In all mammals living in the cold regions of the earth, fur thickness increases in winter, sometimes by as much as 50%. Thick underhair is the principal insulating layer, whereas the longer and more visible guard hair serves as protection against wear and for protective coloration. However, unlike the well-insulated trunk of the body, the body extremities (legs, tail, ears, nose) of arctic mammals are thinly insulated and exposed to rapid cooling. To prevent these parts from becoming major avenues of heat loss, they are allowed to cool to low temperatures, often approaching the freezing point. The heat in the warm arterial blood is not lost from the body, however. Instead, a **countercurrent heat exchange** between the outgoing warm blood and the returning cold blood prevents heat loss. Arterial blood in the leg of an arctic mammal or bird passes in close contact with a network of small veins. Because arterial blood flow is opposite to that of returning venous blood, heat is exchanged very efficiently from artery to veins. By the time the arterial blood reaches the foot it has transferred nearly all of its heat to the veins returning blood to the body core (Figure 32-19). Thus little heat is lost from poorly insulated distal regions of the leg to the surrounding cold air. Countercurrent heat exchangers in appendages also are common in aquatic mammals such as seals and whales, which have thinly insulated flippers and flukes that would be avenues of excessive heat loss in the absence of this heat-salvaging arrangement.

A consequence of peripheral heat exchange is that legs and feet of mammals and birds living in cold environments must function at low temperatures. Temperatures of the feet of arctic foxes and barren-ground caribou are just above the freezing point; in fact, the temperature may be below 0° C in

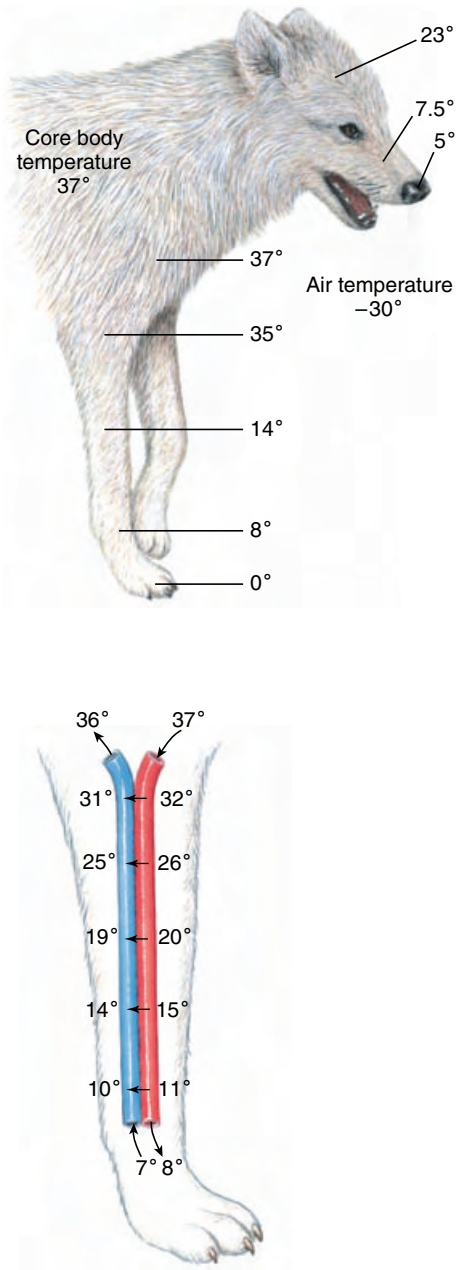


Figure 32-19
Countercurrent heat exchange in the leg of an arctic wolf. The upper diagram shows how the extremities cool when the animal is exposed to low air temperatures. The lower diagram depicts a portion of the front leg artery and vein, showing how heat is exchanged between arterial and venous blood. Heat is shunted back into the body and conserved.

footpads and hooves. To keep feet supple and flexible at such low temperatures, fats in the extremities have very low melting points, perhaps 30° C lower than ordinary body fats.

In severely cold conditions all mammals can produce more heat by **augmented muscular activity** through exercise or shivering. We are all familiar with the effectiveness of both activities. A person can increase heat production as much as 18-fold by violent shivering when maximally stressed by cold. Another source of heat is increased oxidation of foods, especially from stores of brown fat (brown fat is described on p. 718). This mechanism is called **nonshivering thermogenesis.**

Small mammals the size of lemmings, voles, and mice meet the challenge of cold environments in a different way. Small mammals are not as well insulated as large mammals because thickness of fur is limited by the need to maintain mobility. Consequently these forms exploit the excellent insulating qualities of snow by living under it in runways on the forest floor, where incidentally, their food also is located. In this **subnivean environment** the temperature seldom drops below −5° C even though the air temperature above may fall to −50° C. Snow insulation decreases thermal conductance from small mammals just as thick pelage does for large mammals. Living beneath the snow is really a type of avoidance response to cold.

Adaptive Hypothermia in Birds and Mammals

Endothermy is energetically expensive. Whereas an ectotherm can survive for weeks in a cold environment without eating, an endotherm must always have energy resources to supply its high metabolic rate. The problem is especially acute for small birds and mammals which, because of their intense metabolism, may require a daily intake of food each day approaching their own body weight to maintain homeothermy (food consumption by birds is related on p. 591, and by mammals on p. 621). It is not surprising then that a few small birds and mammals have evolved ways to abandon homeothermy for periods ranging from a few hours to several months, allowing their body temperature to fall until it approaches or equals the temperature of surrounding air.

Some very small mammals, such as bats, maintain high body temperatures when active but allow their body temperature to drop profoundly when inactive and asleep. This is called **daily torpor,** an adaptive hypothermia that provides enormous saving of energy to small endotherms that are never more than a few hours away from starvation at normal body temperatures. Hummingbirds also may drop their body temperature at night when food supplies are low (Figure 32-20).

Many small and medium-sized mammals in northern temperate regions solve the problem of winter scarcity of food and low temperature by entering a prolonged and controlled state of dormancy: **hibernation.** True hibernators, such as ground squirrels, jumping mice, marmots, and woodchucks (Figure 32-21), prepare for hibernation by storing body fat. Entry into hibernation is gradual. After a series of "test drops" during which body temperature decreases a few degrees and then returns to normal, the animal cools to within a degree or less of the ambient temperature. Metabolism decreases to a fraction of normal. In ground squirrels, for example, the respiratory rate decreases from a normal rate of 200 per minute to 4 or 5 per minute, and the heart rate from 150 to 5 beats per minute. During arousal a hibernator both shivers violently and employs nonshivering thermogenesis to produce heat.

Some mammals, such as bears, badgers, raccoons, and opossums, enter a state of prolonged sleep in winter with little or no decrease in body temperature. Prolonged sleep is not true hibernation. Bears of the northern forest sleep for several months. A bear's heart rate may decrease from 40 to 10 beats per minute, but body temperature remains normal and the bear is awakened if sufficiently disturbed. One intrepid but reckless biologist narrowly escaped injury when he crawled into a den and attempted to measure the bear's rectal temperature with a thermometer!

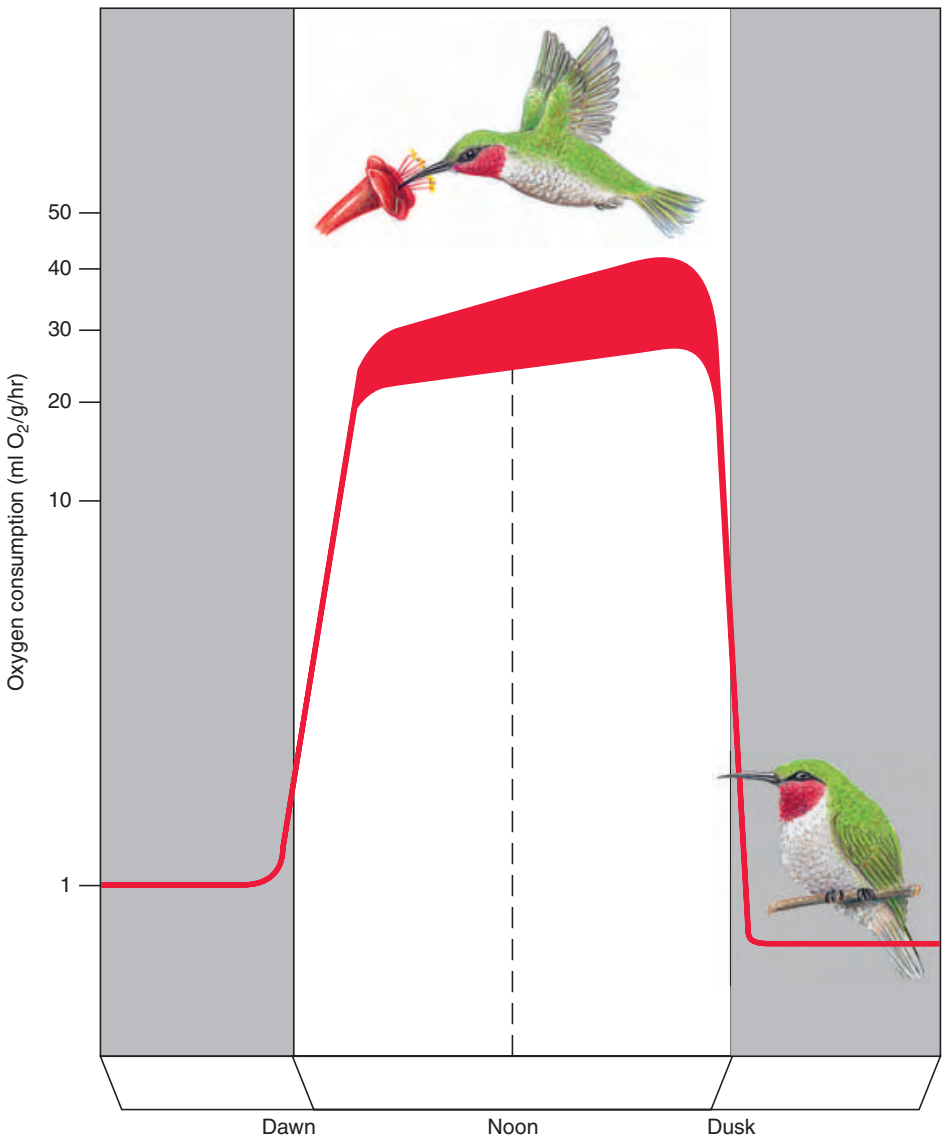


Figure 32-20
Torpor in hummingbirds. Body temperature and oxygen consumption (red line) are high when hummingbirds are active during the day but may drop to one-twentieth these levels during periods of food shortage. Torpor vastly lowers demands on the bird's limited energy reserves.

Figure 32-21
Hibernating woodchuck *Marmota monax* (order Rodentia) in den exposed by road-building work sleeps on, unaware of the intrusion. Woodchucks begin hibernating in late September while the weather is still warm and may sleep six months. The animal is rigid and decidedly cold to the touch. Breathing is imperceptible, as slow as one breath every five minutes. Although it appears to be dead, it will awaken if the den temperature drops dangerously low.

Summary

Throughout life, matter and energy pass through the body, potentially disturbing the internal physiological state. Homeostasis, the ability of an organism to maintain internal stability despite such challenges, is a characteristic of all living systems. Homeostasis involves the coordinated activity of several physiological and biochemical mechanisms, and it is possible to relate some major events in animal evolution to increasing internal independence from the consequences of environmental change. In this chapter we have examined two aspects of homeostasis: (1) the varying ability of animals to stabilize the osmotic and chemical composition of the blood, and (2) the capacity of animals to regulate their temperatures in thermally challenging environments.

Most marine invertebrates must either depend on the osmotic stability of the ocean to which they conform, or be able to tolerate wide fluctuations in environmental salinity. Some of the latter show limited powers of osmotic regulation, the capacity to resist internal osmotic change through the evolution of specialized regulatory organs. All animals living in fresh water are hyperosmotic to their environment and have developed mechanisms for recovering salt from the environment and eliminating excess water that enters the body osmotically.

All vertebrate animals, except hagfishes, show excellent osmotic homeostasis. Marine bony fishes maintain their body fluids distinctly hypoosmotic to their environment by drinking seawater and physiologically distilling it. Elasmobranchs (sharks

and rays) have adopted a strategy of near-osmotic conformity by retaining urea in the blood.

The kidney is the most important organ for regulating the chemical and osmotic composition of the blood. In all metazoa kidneys are some variation on a basic theme: a tubular structure that forms urine by introducing a fluid secretion or filtrate of the blood or interstitial fluid into a tubule in which it is selectively modified to form urine. Terrestrial vertebrates have especially sophisticated kidneys, since they must be able to regulate closely the water content of the blood by balancing gains and expenditures. The basic excretory unit is the nephron, composed of a glomerulus in which an ultrafiltrate of the blood is formed, and a long nephric tubule in which the formative urine is selectively modified by the tubular epithelium. Water, salts, and other valuable materials pass by reabsorption to the peritubular circulation, and certain wastes pass by secretion from the circulation to the tubular urine. All mammals and some birds can produce urine more concentrated than blood by means of a countercurrent multiplier system localized in the loops of Henle, a specialization not found in other vertebrates.

Temperature has a profound effect on the rate of biochemical reactions and, consequently, on the metabolism and activity of all animals. Animals may be classified according to whether body temperature is variable (poikilothermic) or stable (homeothermic), or by the source of body heat, whether external (ectothermic) or internal (endothermic).

Ectotherms partially free themselves from thermal constraints by seeking out habitats with favorable temperatures, by behavioral thermoregulation, or by adjusting their metabolism to the prevailing temperature through biochemical alterations.

Endothermic birds and mammals differ from ectotherms in having a much higher production of metabolic heat and a much lower conductance of heat from the body. They maintain constant body temperature by balancing heat production with loss.

Small mammals in hot environments for the most part escape intense heat and reduce evaporative water loss by burrowing. Large mammals employ several strategies for dealing with direct exposure to heat, including reflective insulation, heat storage by the body, and evaporative cooling.

Endotherms in cold environments maintain body temperature by decreasing heat loss with thickened pelage or plumage, by peripheral cooling, and by increasing heat production through shivering or nonshivering thermogenesis. Small endotherms may avoid exposure to low temperatures by living under the snow.

Adaptive hypothermia is a strategy used by small mammals and birds to blunt energy demands during periods of inactivity (daily torpor) or periods of prolonged cold and minimal food availability (hibernation).

Review Questions

1. Define homeostasis. What evolutionary advantages for a species might result from the successful maintenance of internal homeostasis?
2. The problems of water balance may have arisen when the early metazoan animals began invading estuaries and rivers. Describe the physiological challenges confronting marine invertebrates entering fresh water and, using crustaceans as an example, suggest solutions to these challenges.
3. Distinguish between the following pairs of terms: osmotic conformity and osmotic regulation; stenohaline and euryhaline; hyperosmotic and hypoosmotic.
4. Young downstream salmon migrants moving from their freshwater natal streams into the sea leave an environment nearly free of salt to enter one containing three times as much salt as their body fluids. Describe the osmotic challenges of each environment and the physiological adjustments salmon must make in moving from fresh water to the sea.
5. Most marine invertebrates are osmotic conformers. How does their body fluid differ from that of the cartilaginous sharks and rays, which are also in near osmotic equilibrium with their environment?
6. What strategy does a kangaroo rat use that allows it to exist in the desert without drinking any water?
7. In what animals would you expect to find a salt gland? What is its function?
8. Relate the function of contractile vacuoles to the following experimental observations: to expel an amount of fluid equal in volume to the volume of the animal required 4 to 53 minutes for some freshwater protozoa, and between 2 and 5 hours for some marine species.
9. How does a protonephridium differ structurally and functionally from a true nephridium (metanephridium)? In what ways are they similar?
10. Describe the developmental stages of kidneys in amniotes. How does the developmental sequence for amniotes differ from that of amphibians and fishes?
11. In what ways does the nephridium of an earthworm parallel the human nephron in structure and function?
12. Describe what happens during the following stages in urine formation in the mammalian nephron: filtration, tubular reabsorption, tubular secretion.
13. Explain how the cycling of sodium chloride between the descending and ascending limbs of the loop of Henle in the mammalian kidney, and the special permeability of these tubules, produces high osmotic concentrations in interstitial fluids in the kidney medulla.
14. Explain how the antidiuretic hormone (vasopressin) controls the excretion of water in mammalian kidneys.
15. Define the following terms and comment on the limitations (if any) of each in describing the thermal relationships of animals to their environments: poikilothermy, homeothermy, ectothermy, endothermy.
16. Defend the statement: "Both ectotherms and endotherms achieve metabolic homeostasis in unstable thermal environments, but they do so by employing different physiological strategies."
17. Large mammals live successfully in deserts and in the arctic. Describe the different adaptations mammals use to maintain homeothermy in each environment.
18. Explain why it is advantageous for certain small birds and mammals to abandon homeothermy during brief or extended periods of their lives.

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Animal Survival. Information on animals (amphibians, reptiles, birds, and mammals) adapted to desert environments. Links to relevant organizations.

Normal Anatomy and Physiology. Learn more about the normal human male and female urinary tracts and normal bladder anatomy and physiology.

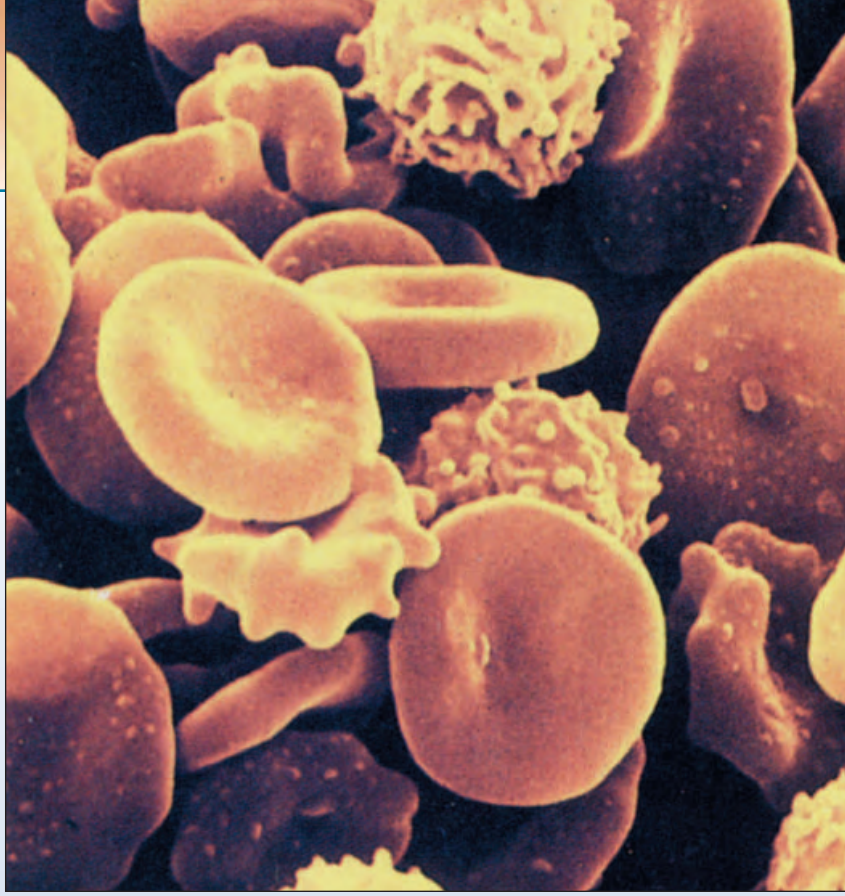
The Basics of the Kidney. A good introduction to the basic function of the kidney.

OLC Student Center Website

CHAPTER

33

Internal Fluids and Respiration



Scanning electron micrograph of blood cells.

William Harvey's Discovery

Ceaselessly, during a human life, the heart pumps blood through arteries, capillaries, and veins: about 5 liters per minute, until by the end of a normal life the heart has contracted some 2.5 billion times and pumped 300,000 tons of blood. When the heart stops its contractions, life also ends.

The crucial importance of the heart and its contractions for human life has been known since antiquity, probably almost as long as humans have existed. However, the circuit flow of blood, the notion that the heart pumps blood into arteries through the circulation and receives it back in veins became known only a few hundred years ago. The first correct description of blood flow by the English physician William Harvey initially received vigorous opposition when published in 1628. Centuries earlier, the Greek anatomist Galen had taught that air enters the heart from the windpipe and that blood was able to pass from one ventricle to the other through "pores" in the interventricular septum. He also believed that blood first flowed out of the heart into all vessels, then returned—a kind of ebb and flow of blood. Even though there was almost nothing correct about this concept, it was still doggedly trusted at the time of Harvey's publication. Harvey's conclusions were based on sound experimental evidence. He used a variety of animals for his experiments and chided human anatomists, saying that if only they had acquainted themselves with anatomy of lower vertebrates, they would have understood the blood's circuit. By tying ligatures on arteries, he noticed that the region between the heart and ligature swelled up. When veins were tied off, the swelling occurred beyond the ligature. When blood vessels were cut, blood flowed in arteries from the cut end nearest the heart; the reverse happened in veins. By means of such experiments, Harvey discovered the correct scheme of blood circulation, even though he could not see the capillaries that connected the arterial and venous flows. ■

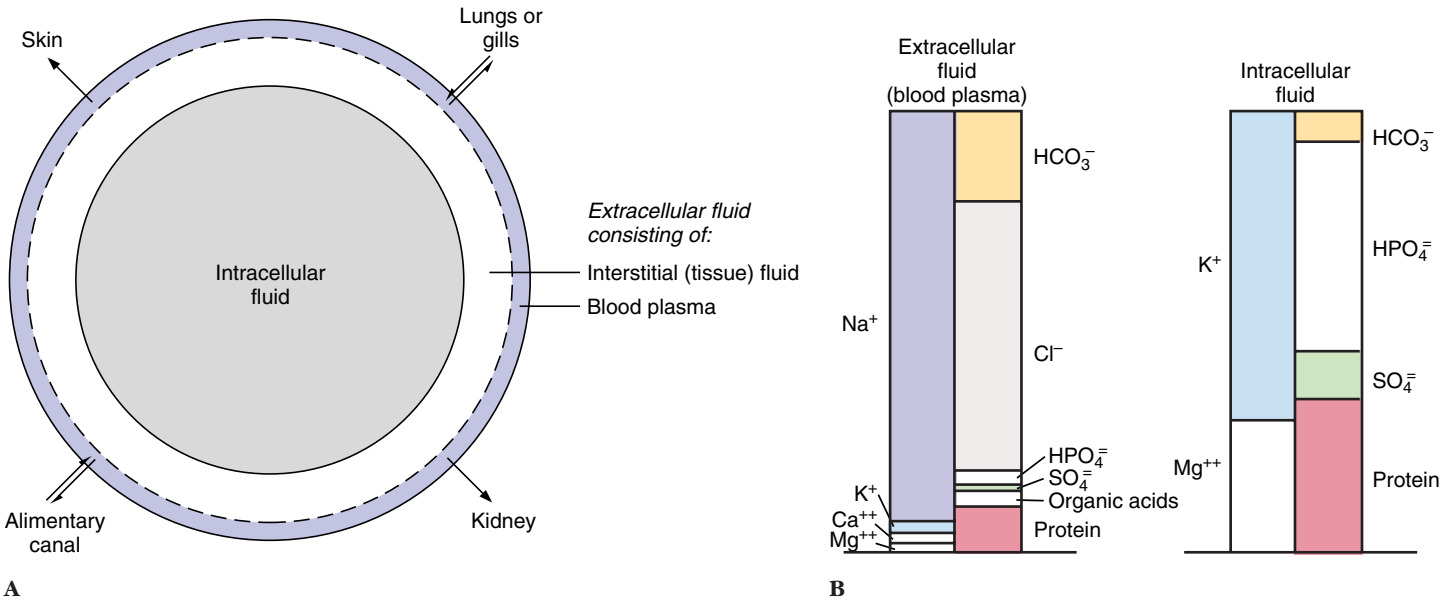


Figure 33-1

Fluid compartments of the body. **A,** All body cells can be represented as belonging to a single large fluid compartment that is completely surrounded and protected by extracellular fluid (*milieu intérieur*). This fluid is further subdivided into plasma and interstitial fluid. All exchanges with the environment occur across the plasma compartment. **B,** Electrolyte composition of extracellular and intracellular fluids. Total equivalent concentration of each major constituent is shown. Equal amounts of anions (negatively charged ions) and cations (positively charged ions) are in each fluid compartment. Note that sodium and chloride, major plasma electrolytes, are virtually absent from intracellular fluid (actually they are present in low concentration). Note the much higher concentration of protein inside cells.

Single-celled organisms live in direct contact with their environment. They obtain nutrients and oxygen and release wastes directly across the cell surface. These organisms as so small that no special internal system of transport, beyond normal streaming movements of cytoplasm, is required. Even some simple multicellular forms, such as sponges, cnidarians, and flatworms, lack the internal complexity and metabolic demands that would require a circulatory system. Most other multicellular organisms, because of their size, activity, and complexity, need a specialized circulatory system to transport nutrients and respiratory gases to and from all tissues of the body. In addition to serving these primary transport needs, circulatory systems have acquired additional functions; hormones are moved from the glands that produce them, to target organs where they assist the nervous system to integrate organismal function. Water, electrolytes, and the many other constituents of body fluids are distributed and exchanged between different organs and tissues. An effective response to disease and injury is vastly accelerated by an efficient circulatory system. Homeothermic birds and mammals depend heavily on blood circulation to conserve or dissipate heat as required for maintenance of constant body temperature.

Internal Fluid Environment

The body fluid of a single-celled organism is cellular cytoplasm, a liquid-gel substance in which the various membrane systems and organelles are suspended. In multicellular animals body fluids are divided into two main phases, **intracellular** and **extracellular.** The intracellular phase (also called intracellular fluid) is the collective fluid inside all the body's cells. The extracellular phase (or fluid) is the fluid outside and surrounding the cells (Figure 33-1A). Thus the cells, sites of the body's crucial metabolic activities, are bathed by their own aqueous environment, the extracellular fluid that buffers them from the often harsh physical and chemical changes occurring outside the body. The importance of extracellular fluid was first emphasized by the great French physiologist Claude Bernard (Figure 33-2). In animals having closed circulatory systems (vertebrates, annelids, and a few other invertebrate groups; see p. 346) extracellular fluid is further subdivided into **blood plasma** and **interstitial (intercellular) fluid** (Figure 33-1A). Blood vessels contain plasma, whereas interstitial fluid, or tissue fluid as it is sometimes called, occupies spaces surrounding the cells in the body. Nutrients and gases passing between vascular plasma and cells must traverse this narrow fluid separation. Interstitial fluid is constantly formed from plasma by filtration through capillary walls.

Composition of the Body Fluids

All these fluid spaces—plasma, interstitial, and intracellular—differ from each other in solute composition, but all have one feature in common: they are mostly water. Despite their firm appearance, animals are 70% to 90% water. Humans, for example, are approximately 70% water by weight.

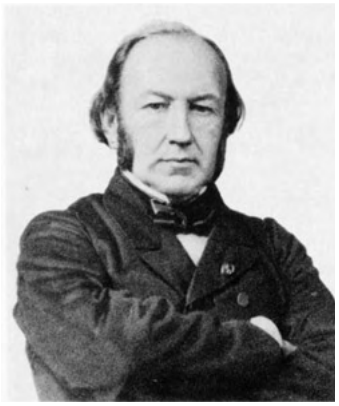


Figure 33-2
French physiologist Claude Bernard (1813 to 1878), one of the most influential of nineteenth-century physiologists. Bernard believed in the constancy of the *milieu intérieur* ("internal environment"), which is the extracellular fluid bathing the cells. He pointed out that it is through the *milieu intérieur* that foods and wastes and gases are exchanged and through which chemical messengers are distributed. He wrote, "The living organism does not really exist in the external environment (the outside air or water) but in the liquid *milieu intérieur* . . . that bathes the tissue elements."

Of this, 50% is cell water, 15% is interstitial fluid water, and the remaining 5% is in blood plasma. Plasma spaces serve as the pathway of exchange between the cells of the body and the outside world. This exchange of respiratory gases, nutrients, and wastes is accomplished by specialized organs (kidney, lung, gill, alimentary canal), as well as by the skin (Figure 33-1A).

Body fluids contain many inorganic and organic substances in solution. Principal among these are inorganic electrolytes and proteins. **Sodium, chloride,** and **bicarbonate ions** are the chief extracellular electrolytes, whereas **potassium, magnesium,** and **phosphate ions** and **proteins** are the major intracellular electrolytes (Figure 33-1B). These differences are dramatic; they are always maintained despite continuous flow of materials into and out of cells of the body. The two subdivisions of extracellular fluid—plasma and interstitial fluid—have similar compositions except that plasma has more proteins, which are mostly too large to filter through capillary walls into interstitial fluid.

Composition of Blood

Among invertebrates that lack a circulatory system (such as flatworms and cnidarians) it is not possible to distinguish a true "blood." These forms possess a clear, watery tissue fluid containing some phagocytic cells, a little protein, and a mixture of salts similar to seawater. The "blood" of invertebrates with open circulatory systems is more complex and is often called hemolymph (Gr. *haimo,* blood, + L. *lympha,* water). Invertebrates with closed circulatory systems, on the other hand, maintain a clear separation between blood contained within blood vessels and tissue (interstitial) fluid surrounding blood vessels.

In vertebrates, blood is a complex liquid tissue composed of plasma and formed elements, mostly red cells (also called corpuscles), suspended in plasma. If we separate red blood corpuscles and other formed elements from the fluid components by centrifugation, we find that blood is approximately 55% plasma and 45% formed elements.

The composition of mammalian blood is as follows:

Plasma

1. Water 90%
2. Dissolved solids, consisting of plasma proteins (albumin, globulins, fibrinogen), glucose, amino acids, electrolytes, various enzymes, antibodies, hormones, metabolic wastes, and traces of many other organic and inorganic materials
3. Dissolved gases, especially oxygen, carbon dioxide, and nitrogen

Formed elements (Figure 33-3)

1. Red blood cells (erythrocytes), containing hemoglobin for transport of oxygen and carbon dioxide
2. White blood cells (leukocytes), serving as scavengers and as defensive cells
3. Cell fragments (platelets in mammals) or cells (thrombocytes in other vertebrates) that function in blood coagulation

Plasma proteins are a diverse group of large and small proteins that perform numerous functions. The major protein groups are (1) **albumins,** the most abundant group, constituting 60% of the total, which help to keep plasma in osmotic equilibrium with the cells of the body; (2) **globulins,** a diverse group of high-molecular weight proteins (35% of total) that includes immunoglobulins and various metal-binding proteins; and (3) **fibrinogen,** a very large protein that functions in blood coagulation. Blood **serum** is plasma minus the proteins involved in clot formation (see the following).

Red blood cells, or **erythrocytes,** are present in enormous numbers in blood, approximately 5.4 billion per milliliter of blood in adult men and 4.8 billion in adult women. In mammals and birds, red cells form continuously from large nucleated **erythroblasts** in red bone marrow (in other vertebrates kidneys and spleen are the principal sites of red blood cell production). During erythrocyte formation hemoglobin is synthesized and the precursor cells divide several times. In mammals the nucleus shrinks during development to a small remnant and eventually disappears altogether. Many other characteristics of a typical cell also are lost: ribosomes, mitochondria, and most enzyme systems. What is left is a biconcave disc consisting of a baglike membrane packed with about 280 million molecules of the blood-transporting pigment hemoglobin. Approximately 33% of an erythrocyte by weight is hemoglobin. The biconcave shape (Figure 33-3) is a mammalian innovation that provides a larger surface for gas diffusion than would a flat or spherical shape. All other vertebrates have nucleated erythrocytes that are usually ellipsoidal in shape (Figure 33-4).

An erythrocyte enters the circulation for an average life span of approximately 4 months. During this time it may journey 11,000 km, squeezing

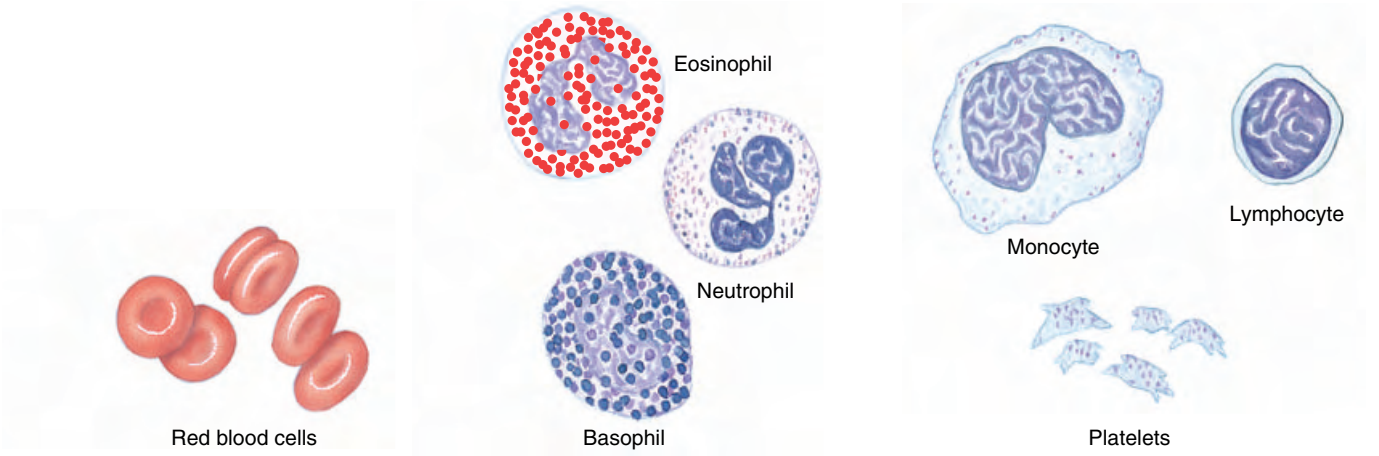


Figure 33-3

Formed elements of human blood. Hemoglobin-containing red blood cells of humans and other mammals lack nuclei, but those of all other vertebrates have nuclei. Various leukocytes provide a wandering system of protection for the body. Platelets participate in the blood's clotting mechanism.

repeatedly through capillaries, which are sometimes so narrow that the erythrocyte must bend to pass through. At last it fragments and is quickly engulfed by large scavenger cells called **macrophages** located in the liver, bone marrow, and spleen. Iron from hemoglobin is salvaged to be used again; the rest of the heme is converted to **bilirubin,** a bile pigment. It is estimated that a human body produces 10 million erythrocytes and destroys another 10 million every second.

White blood cells, or **leukocytes,** form a wandering system of protection for the body. In adults they number only approximately 7.5 million per milliliter of blood, a ratio of 1 white cell to 700 red cells. There are several kinds of white blood cells: **granulocytes** (subdivided into **neutrophils, basophils,** and **eosinophils**), and **agranulocytes,** the lymphocytes and monocytes (Figure 33-3). We discuss the role of leukocytes in the body's defense mechanisms in Chapter 37.

Hemostasis: Prevention of Blood Loss

It is essential that animals have ways of preventing rapid loss of body fluids after an injury. Since blood is flowing and is under considerable hydrostatic pressure, it is especially vulnerable to hemorrhagic loss.

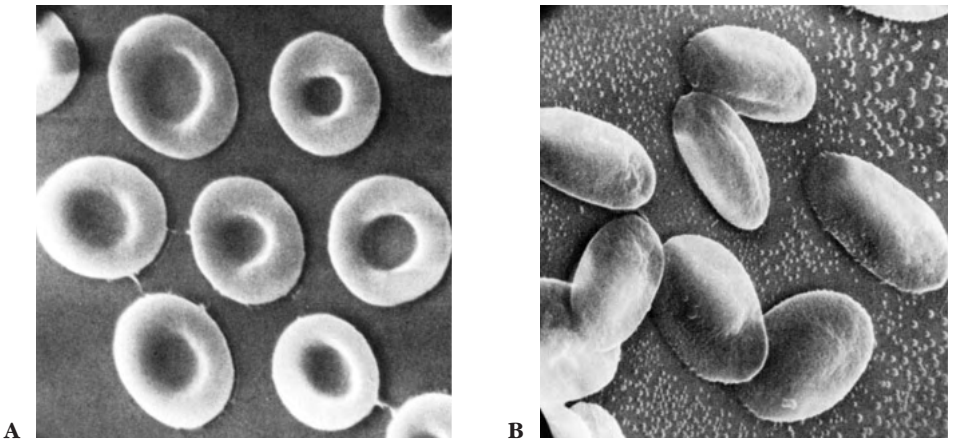


Figure 33-4

Mammalian and amphibian red blood cells. **A,** Erythrocytes of a gerbil are biconcave discs containing hemoglobin and surrounded by a tough stroma. **B,** Frog erythrocytes are convex discs, each containing a nucleus, which is plainly visible in the scanning electron micrograph as a bulge in the center of each cell. (Magnifications: mammalian erythrocytes, ×6300; frog erythrocytes, ×2400.)

When a vessel is damaged, smooth muscle in the wall of the vessel contracts, which causes the vessel lumen to narrow, sometimes so strongly that blood flow is completely stopped. This simple but highly effective means of preventing hemorrhage is used by invertebrates and vertebrates alike. Beyond this first defense against blood loss, all vertebrates, as well as some larger, active invertebrates with high blood pressures, have in the blood special cellular elements and proteins that are capable of forming plugs, or clots, at the injury site.

In vertebrates **blood coagulation** is the dominant hemostatic defense. Blood clots form as a tangled network of fibers from one of the plasma proteins, **fibrinogen.** The transformation of fibrinogen into a **fibrin** meshwork (Figure 33-5) that entangles blood cells to form a gel-like clot is catalyzed by the enzyme thrombin. Thrombin is normally present in blood in an inactive form called **prothrombin,** which must be activated for coagulation to occur.

In this process, blood platelets (Figure 33-3) play a vital role. Platelets form in red bone marrow from certain large cells that regularly pinch off bits of their cytoplasm; thus they are fragments of cells. There are 150,000 to

Figure 33-5
Human red blood cells trapped in fibrin clot. Clotting is initiated after tissue damage by disintegration of platelets in blood, resulting in a complex series of intravascular reactions that end with conversion of a plasma protein, fibrinogen, into long, tough, insoluble polymers of fibrin. Fibrin and entangled erythrocytes form the blood clot, which arrests bleeding.

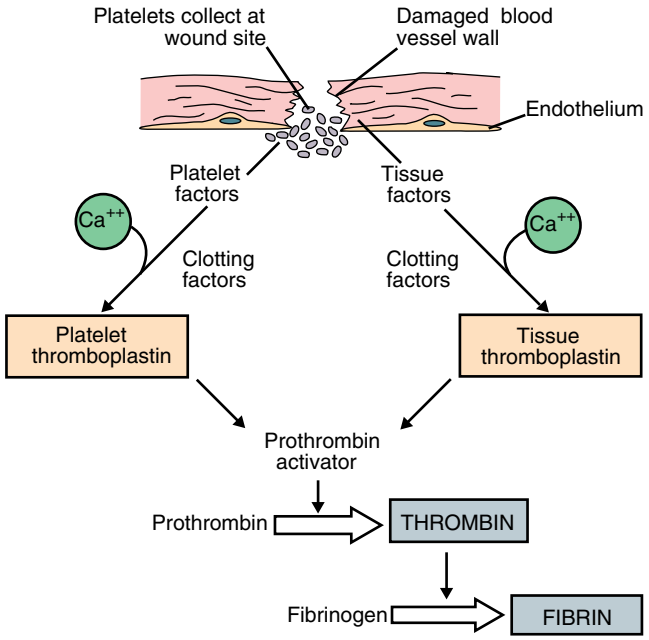


Figure 33-6
Stages in formation of fibrin.

300,000 platelets per cubic millimeter of blood. When the normally smooth inner surface of a blood vessel is disrupted, either by a break or by deposits of a cholesterol-lipid material, platelets rapidly adhere to the surface and release **thromboplastin** and other clotting factors. These factors, along with factors released from damaged tissue and with calcium ions, initiate conversion of prothrombin to active thrombin (Figure 33-6).

The catalytic sequence in this scheme is unexpectedly complex, involving a series of plasma protein factors, each normally inactive until activated by a previous factor in the sequence. The sequence behaves like a "cascade" with each reactant in the sequence leading to a large increase in the amount of the next reactant. At least 13 different plasma coagulation factors have been identified. A deficiency of only a single factor can delay or prevent the clotting process. Why has such a complex clotting mechanism evolved? Probably it is necessary to provide a fail-safe system capable of responding to any kind of internal or external hemorrhage that might occur and yet a system that cannot be activated into forming dangerous intravascular clots in the absence of injury.

Several kinds of clotting abnormalities in humans are known. One of these, hemophilia is a condition characterized by failure of blood to clot, so that even insignificant wounds can cause continuous severe bleeding. It is caused by a rare mutation (the condition occurs in about 1 in 10,000 males) on the X sex chromosome, resulting in an inherited lack of one of the platelet factors in males and in homozygous females. Called the "disease of kings," it once ran through several interrelated royal families of Europe, apparently having originated from a mutation in one of Queen Victoria's parents.

Hemophilia is one of the best known cases of sex-linked inheritance in humans (p. 86). Actually two different loci on the X chromosome are involved. Classic hemophilia (hemophilia A) accounts for about 80% of persons with the condition, and the remainder are caused by Christmas disease (hemophilia B). The allele at each locus results in a deficiency of a different platelet factor.

Circulation

We pointed out in the opening to this chapter that most animals have evolved mechanisms, in addition to simple diffusion, for transporting materials among various regions of the body. For sponges and radiates the water in which they live provides the medium for transport. Water, propelled by ciliary, flagellar, or body movements, passes through channels or compartments to facilitate the movement of food, respiratory gases, and wastes. True circulatory systems—containing vessels through which blood moves—are essential to animals so large or so active that diffusional processes alone cannot supply their oxygen needs. An animal's shape obviously is important. The flattened and leaflike acoelomate flatworms, even though many are relatively large animals, have no need for a circulatory system because the distance of any body part from the surface is short; respiratory gases and metabolic wastes transfer by simple diffusion.

A circulatory system having a full complement of components—

propulsive organ, arterial distribution system, capillaries, and venous reservoir and return system—is fully recognizable in annelid worms. In earthworms (Figure 33-7) there are two main vessels, a dorsal vessel carrying blood toward the head, and a ventral vessel that flows posteriorly, delivering blood throughout the body by way of segmental vessels and a dense capillary network. The dorsal vessel drives the blood forward by peristalsis (see p. 712) and thus serves as a heart. Five aortic arches that on each side connect the dorsal and ventral vessels are also contractile and serve as accessory hearts to maintain a steady flow of blood into the ventral vessel. Many smaller segmental vessels that deliver blood to tissue capillaries are actively contractile as well. We see then that there is no localized pump pushing the blood through a system of passive tubes; instead the power of contraction is widely distributed throughout the vascular system.

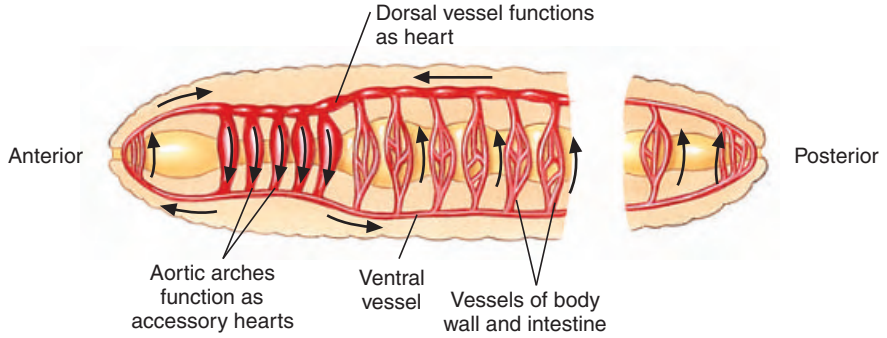


Figure 33-7
Blood flow through the closed vascular system of an earthworm.

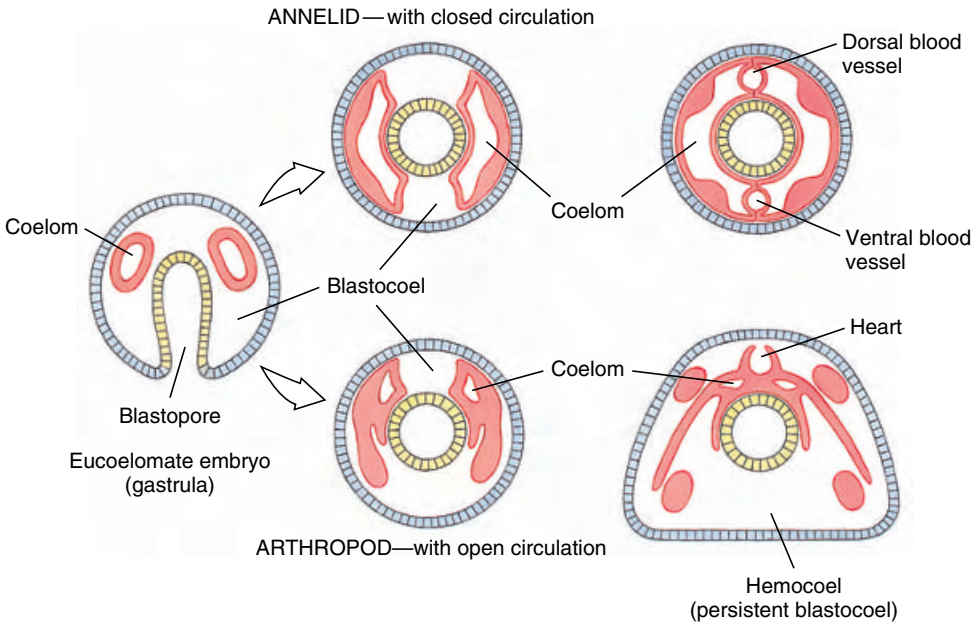


Figure 33-8
Diagrams showing how open and closed circulatory systems develop. The principal body cavity of arthropods is the persistent blastocoel which becomes a hemocoel; the true coelom remains mostly undeveloped.

Open and Closed Circulations

The system just described is a **closed circulation** because the circulating medium, **blood,** is confined to vessels throughout its journey through the vascular system. Many invertebrates have an **open circulation** in which there are no small blood vessels or capillaries connecting arteries with veins. In insects and other arthropods, in most molluscs, and in many smaller invertebrate groups blood sinuses, collectively called a **hemocoel,** replace capillary beds found in animals with closed systems. During development of the body cavity in these groups, the blastocoel is not completely obliterated by the expanding mesoderm. This space be-comes the hemocoel, which is nothing more than the primary body cavity (persistent blastocoel) through which blood (also called **hemolymph**) freely circulates (bottom diagrams in Figure 33-8). Since there is no separation of the extracellular fluid into blood plasma and lymph (as there is in a closed circulation, p. 694) the blood volume is large and may constitute 20% to 40% of body volume. By contrast, blood volume in animals with closed circulations (vertebrates, for example) is only about 5% to 10% of body volume.

In arthropods, the heart and all viscera lie in the hemocoel, bathed by blood (Figure 33-8). Blood enters the heart through valved openings, the ostia, and the heart's contractions, which resemble a forward-moving peristaltic wave, propel blood into a limited arterial system. Blood is distributed to the head and other organs, then escapes into the hemocoel. It is routed through the body and appendages by a system of baffles and longitudinal membranes (septa) before returning to the heart. Because the blood pressure is very low in open systems, seldom exceeding 4 to 10 mm Hg, many arthropods have auxiliary hearts or contractile vessels to boost blood flow (Figure 33-9).

During embryonic development of animals with closed circulatory systems (most annelids, cephalopod molluscs, and all vertebrates) the coelom increases in size to obliterate the blastocoel and forms a secondary body cavity (top diagrams in Figure 33-8). A system of continuously connected blood vessels develops within the mesoderm. All closed systems have

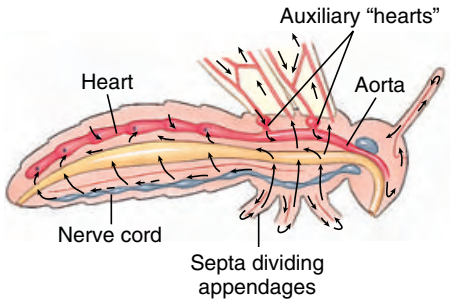


Figure 33-9
Circulatory system of an insect. Although the circulatory system is open, blood is directed through the appendages in channels formed by longitudinal septa. Arrows indicate the course of circulation.

certain features in common. A **heart** pumps blood into **arteries** that branch and narrow into **arterioles** and then into a vast system of **capillaries.** Blood leaving capillaries enters **venules** and then **veins** that return the blood to the heart. Capillary walls are thin, permitting rapid rates of transfer of materials between blood and tissues. Closed systems are more suitable for large and active animals because blood can be moved rapidly to tissues needing it. In addition, flow to various organs can be readjusted to meet changing needs by varying the diameters of blood vessels.

Because blood pressures are much higher in closed than in open systems, fluid is constantly filtered across capillary walls into the surrounding tissue spaces. Most of this fluid is drawn back into capillaries by osmosis (see p. 694). The remainder is recovered by the **lymphatic system** which has evolved in parallel with the high-pressure system of vertebrates.

Plan of Vertebrate Circulatory Systems

In vertebrates the principal differences in the blood vascular system involve the gradual separation of the heart into two separate pumps as vertebrates evolved from aquatic life with gill breathing to fully terrestrial life with lung breathing. These changes are shown in Figure 33-10 which compares the circulation of fish, amphibians, and mammals.

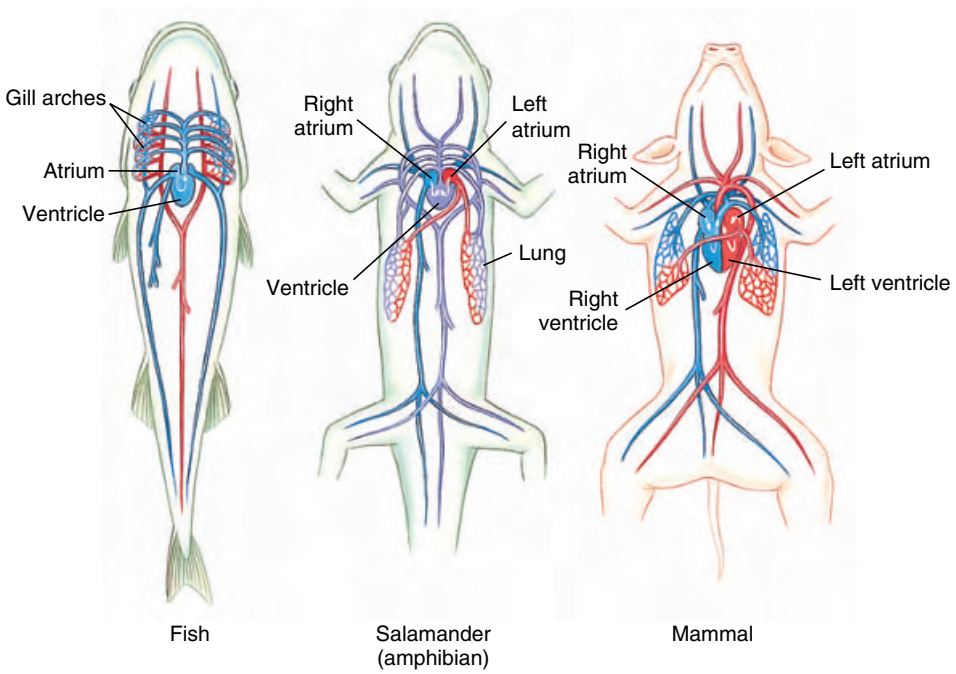


Figure 33-10
Circulatory systems of fish, amphibian, and mammal, showing evolution of separate systemic and pulmonary circuits in lung-breathing vertebrates.

A fish heart contains two main chambers in series, an **atrium** and a **ventricle.** The atrium is preceded by an enlarged chamber, the **sinus venosus,** which collects blood from the venous system to assure a smooth delivery of blood to the heart. Blood makes a single circuit through a fish's vascular system; it is pumped from the heart to the gills, where it is oxygenated, then flows into the dorsal aorta to be distributed to body organs, and finally returns by veins to the heart. In this circuit the heart must provide sufficient pressure to push the blood through two sequential capillary systems, first that of the gills, and then that of the remainder of the body. The principal disadvantage of the single-circuit system is that the gill capillaries offer so much resistance to blood flow that blood pressures to the body tissues are greatly reduced.

With evolution of lung breathing and elimination of gills between the heart and aorta, vertebrates developed a high-pressure **double circulation:** a **systemic circuit** that provides oxygenated blood to the capillary beds of the body organs; and a **pulmonary circuit** that serves the lungs. The beginning of this major evolutionary change probably resembled the condition seen in lungfishes and amphibians. In modern amphibians (frogs, toads, salamanders) the atrium is completely separated by a partition into two atria (Figure 33-11). The right atrium receives venous blood from the body while the left atrium receives oxygenated blood from the lungs. The ventricle is undivided, but venous and arterial blood remain mostly separate by the arrangement of vessels leaving the heart. Separation of the ventricles is nearly complete in some reptiles (crocodilians) and is completely separate in birds and mammals (Figure 33-12). Systemic and pulmonary circuits are now separate circulations, each served by one half of a dual heart (Figure 33-12).

Mammalian Heart

The four-chambered mammalian heart (Figure 33-12) is a muscular organ located in the thorax and covered by a tough, fibrous sac, the **pericardium.** Blood returning from the lungs collects in the **left atrium,** passes into the **left ventricle,** and is pumped into the

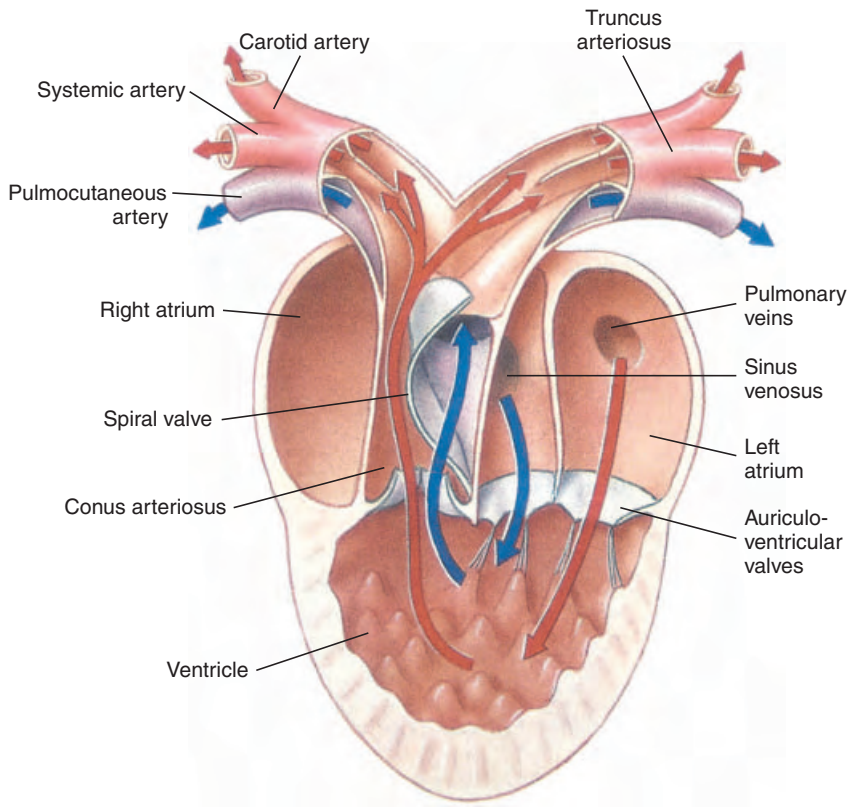


Figure 33-11
Route of blood through a frog heart. Atria are completely separated, and the spiral valve helps to route blood to lungs and systemic circulation.

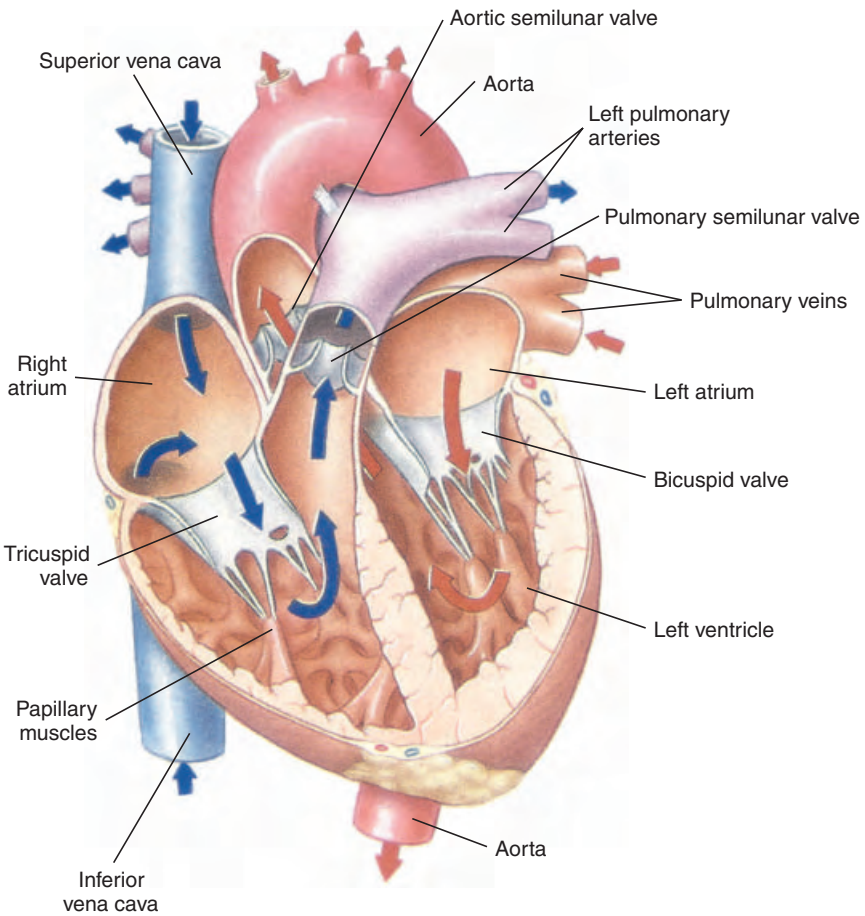


Figure 33-12
Human heart. Deoxygenated blood enters right side of heart and is pumped to the lungs. Oxygenated blood returning from the lungs enters left side of the heart and is pumped to the body. The left ventricular wall is thicker than that of the right ventricle, which needs less muscular force to pump blood into the nearby lungs.

body (systemic) circulation. Blood returning from the body flows into the **right atrium,** and passes into the **right ventricle,** which pumps it into the lungs. Backflow of blood is prevented by two sets of valves that open and close passively in response to pressure differences between the heart chambers. The **bicuspid** (between left atrium and ventricle) and **tricuspid** (between right atrium and ventricle) valves separate the cavities of the atrium and ventricle in each half of the heart. Where the great arteries, the **pulmonary** from the right ventricle and the **aorta** from the left ventricle, leave the heart, **semilunar valves** prevent backflow into the ventricles.

Contraction is called **systole** (sis′to-lee), and relaxation, **diastole** (dy-as′to-lee) (Figure 33-13). When the atria contract (atrial systole), the ventricles relax (ventricular diastole), and ventricular systole is accompanied by atrial diastole. Rate of the heartbeat depends on age, sex, and especially exercise. Exercise may increase **cardiac output** (volume of blood forced from either ventricle each minute) more than fivefold. Both heart **rate** and **stroke volume** increase. Heart rates among vertebrates vary with general level of metabolism and body size. Ectothermic codfish have a heart rate of approximately 30 beats per minute; endothermic rabbits of about the same weight have a rate of 200 beats per minute. Small animals have higher heart rates than do large animals. The heart rate in an elephant is 25 beats per minute, in a human 70 per minute, in a cat 125 per minute, in a mouse 400 per minute, and in the tiny 4 g shrew, the smallest mammal, the heart rate approaches a prodigious 800 beats per minute. We must marvel that the shrew's heart can sustain such a frantic pace throughout this animal's life, brief as it is.

Excitation and Control of the Heart

The vertebrate heart is a muscular pump composed of **cardiac muscle.** Cardiac muscle resembles skeletal muscle—both are types of striated muscle—but the cells are branched and joined end-to-end by junctional complexes to form a complex branching network (see Figure 9-7, p. 188). Unlike skeletal muscle, vertebrate cardiac muscle does not depend on nerve activity to initiate a contraction. Instead, regular contractions are established by specialized cardiac muscle cells, called **pacemaker cells.** In a tetrapod heart the pacemaker is in the **sinus node,** a remnant of the sinus venosus in the fishlike ancestor. Electrical activity initiated in the pacemaker spreads over the muscle of the two atria and then, after a slight delay, to the muscle of the ventricles. At this point electrical activity is conducted rapidly through the **atrioventricular bundle** to the apex of the ventricle and then continues through specialized fibers **(Purkinje fibers)** up the walls of the ventricles (Figure 33-14). This arrangement allows the contraction to begin at the apex or "tip" of the ventricles and spread upward to squeeze out the blood in the most efficient way; it also ensures that both ventricles contract simultaneously. Structural specializations in Purkinje fibers, such as well-developed intercalated discs (see Figure 9-7, p. 188) and numerous gap junctions, facilitate rapid conduction through these fibers.

The **control (cardiac) center** in the brain is located in the medulla and connects to two sets of nerves. Impulses sent along one set, the **vagus** nerves, apply a braking action to the heart rate, and impulses sent along the other set, the **accelerator** nerves, speed it up. Both sets of nerves terminate in the sinus node, thus guiding the activity of the pacemaker.

The cardiac center in turn receives sensory information about a variety of stimuli. Pressure receptors (sensitive to blood pressure) and chemical receptors (sensitive to carbon dioxide and pH) are located at strategic points in the vascular system. The cardiac center uses this information to increase or reduce heart rate and cardiac output in response to activity or changes in body position. Feedback mechanisms thus control the heart and keep its activity constantly attuned to needs of the body.

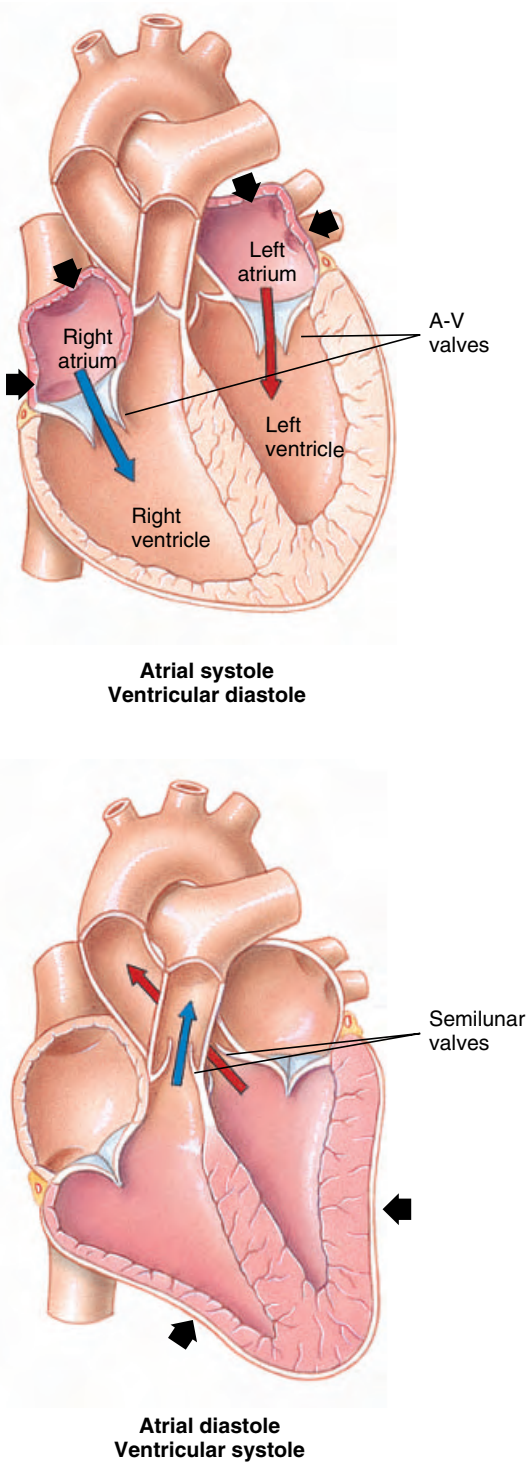


Figure 33-13
Human heart in systole and diastole.

Because the heartbeat is initiated in specialized muscle cells, vertebrate hearts, together with the hearts of molluscs and several other invertebrates,

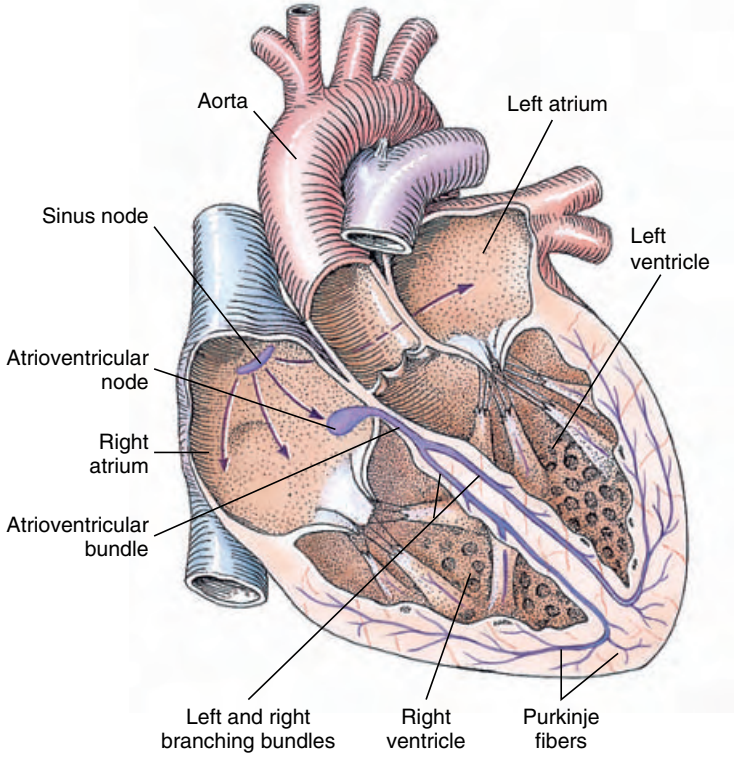


Figure 33-14

Neuromuscular mechanisms controlling heartbeat. Arrows indicate spread of excitation from the sinus node, across the atria, to the atrioventricular node. Wave of excitation is then conducted very rapidly to ventricular muscle over the specialized conducting bundles and Purkinje fiber system.

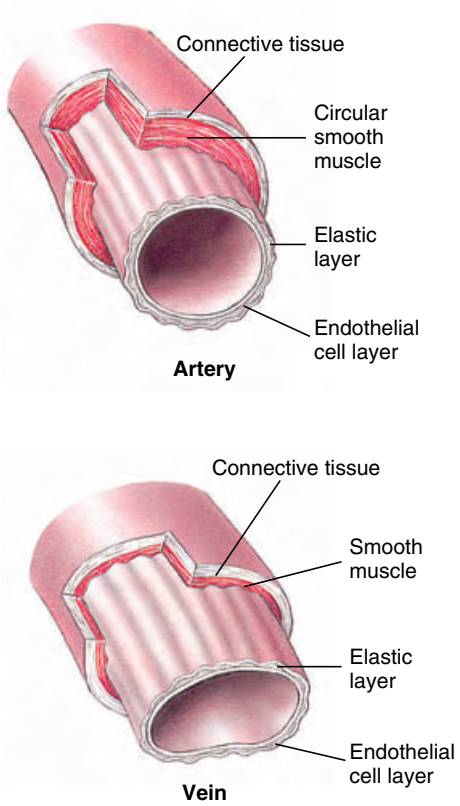


Figure 33-15

Artery and vein, showing layers. Note greater thickness of the muscularis layer (tunica media) in the artery.

are called **myogenic** ("muscle origin") hearts. Although the nervous system does alter pacemaker activity to slow down or speed up heart rate, a myogenic heart will beat spontaneously and involuntarily even if completely removed from the body. An isolated turtle or frog heart beats for hours if placed in a balanced salt solution. Some invertebrates, for example decapod crustaceans, have **neurogenic** ("nerve origin") hearts. In these hearts a cardiac ganglion located on the heart serves as pacemaker. If this ganglion is separated from the heart, the heart stops beating, even though the ganglion itself remains rhythmically active.

Coronary Circulation

It is no surprise that an organ as active as the heart needs a generous blood supply of its own. The heart muscle of frogs and other amphibians is so thoroughly channeled with spaces between muscle fibers that the heart's own pumping action squeezes through sufficient oxygenated blood. In birds and mammals, however, the thickness of the heart muscle and its high rate of metabolism require that the heart have its own vascular supply, the **coronary circulation.** Coronary arteries divide to form an extensive capillary network surrounding the muscle fibers and provide them with oxygen and nutrients. Heart muscle has an extremely high oxygen demand. Even at rest the heart removes 70% of oxygen from the blood, in contrast to most other body tissues, which remove only about 25%. Therefore, an increase in the work of the heart must be met by a massive increase in coronary blood flow—up to nine times the resting level during strenuous exercise. Any reduction in coronary circulation due to partial or complete blockage (coronary artery disease) may lead to a heart attack (myocardial infarction) in which heart cells die from lack of oxygen.

Thickening and loss of elasticity in arteries is known as *arteriosclerosis.* When arteriosclerosis is caused by fatty deposits of cholesterol in artery walls, the condition is *atherosclerosis.* Such irregularities in the walls of blood vessels often cause blood to clot around them, forming a *thrombus.* When a bit of the thrombus breaks off and is carried by the blood to lodge elsewhere, it is an *embolus.* If the embolus blocks one of the coronary arteries, the person has a heart attack (a "coronary"). The portion of the heart muscle served by the branch of the coronary artery that is blocked is starved for oxygen. It may be replaced by scar tissue if the person survives.

Arteries

All vessels leaving the heart are called arteries whether they carry oxygenated blood (aorta) or deoxygenated blood (pulmonary artery). To withstand high, pounding pressures, arteries are invested with layers of both elastic and tough inelastic connective fibers (Figure 33-15). The elasticity of arteries allows them to yield to the surge of

blood leaving the heart during ventricular systole and then to compress the fluid column during ventricular diastole. This elasticity prevents large changes in blood pressure. Thus the normal arterial pressure in humans varies only between 120 mm Hg (systole) and 80 mm Hg (diastole) (usually expressed as 120/80 or 120 over 80), rather than dropping to zero during diastole as we might expect in a fluid system with an intermittent pump.

As arteries branch and narrow into **arterioles,** the walls become mostly smooth muscle. Contraction of this muscle narrows the arterioles and reduces the flow of blood. Arterioles thus control blood flow to body organs, diverting it to where it is most needed. Blood must be pumped with a hydrostatic pressure sufficient to overcome resistance of the narrow passages through which it must flow. Consequently, large animals tend to have higher blood pressure than do small animals.

Blood pressure was first measured in 1733 by Stephan Hales, an English clergyman with unusual inventiveness and curiosity. He tied his mare, which was "to have been killed as unfit for service," on her back and exposed the femoral artery. This he cannulated with a brass tube, connecting it to a tall glass tube with the windpipe of a goose. The use of the windpipe was both imaginative and practical; it gave the apparatus flexibility "to avoid inconveniences that might arise if the mare struggled." The blood rose 8 feet in the glass tube and bobbed up and down with systolic and diastolic beats of the heart. The weight of the 8-foot column of blood was equal to the blood pressure. We now express blood pressure as the height of a column of mercury (Hg), which is 13.6 times heavier than water. Hales' figures, expressed in millimeters of mercury, indicate that he measured a blood pressure of 180 to 200 mm Hg, about normal for a horse.

Today, we measure blood pressure in humans most commonly and easily with an instrument called a **sphygmomanometer.** We inflate a cuff on the upper arm with air to a pressure sufficient to close the arteries in the arm. Holding a stethoscope over the brachial artery (in the crook of the elbow) and slowly releasing air from the cuff, we can hear the first spurts of blood through the artery as it opens slightly. This is equivalent to systolic pressure. As pressure in the cuff decreases, the sound finally disappears as blood runs smoothly through the artery. The pressure at which the sound disappears is diastolic pressure.

Capillaries

The Italian Marcello Malpighi was the first to describe capillaries in 1661, thus confirming the existence of the minute links between the arterial and venous systems that Harvey knew must exist but could not see. Malpighi studied capillaries of a living frog's lung, which is still one of the simplest and most vivid preparations for demonstrating capillary blood flow.

Capillaries are present in enormous numbers, forming extensive networks in nearly all tissues (Figure 33-16). In muscle there are more than 2000 per square millimeter (1,250,000 per square inch), but not all are open at the same time. Indeed, perhaps less than 1% are open in resting skeletal muscle. But when muscle is active, all capillaries may open to bring oxygen and nutrients to the working muscle fibers and to carry away metabolic wastes.

Capillaries are extremely narrow, averaging in mammals about 8 μm in diameter, which is only slightly wider than the red blood cells that must pass through them. Their walls are formed by a single layer of thin **endothelial** cells, held together by a delicate basement membrane and connective tissue fibers.

Capillary Exchange

Capillaries are quite permeable to small ions, nutrients, and water Blood pressure within a capillary tends to force fluids out through the capillary walls and into the surrounding interstitial space (p. 685). Because larger molecules such as plasma proteins cannot pass through the capillary wall, an almost protein-free filtrate is forced out. This fluid movement is important in irrigating the interstitial space, in providing tissue cells with oxygen, glucose, amino acids, and other nutrients, and in carrying away metabolic wastes. For capillary exchange to be effective, fluids that leave the capillaries must at some point reenter the circulation. If they did not, fluid would quickly accumulate in tissue spaces, causing edema. The delicate balance of fluid exchange across the capillary wall can be accounted for by the two opposing forces of hydrostatic (blood) pressure and osmotic pressure (Figure 33-17).

In a capillary, the blood pressure that pushes water molecules and solutes across the capillary wall is greatest at the arteriolar end of the capillary and declines along its length as blood pressure falls (Figure 33-17). Opposing the blood hydrostatic pressure is an osmotic pressure created by the proteins that cannot pass across the capillary wall. This **colloid osmotic pressure,** which is about 25 mm Hg in mammalian plasma, tends to draw

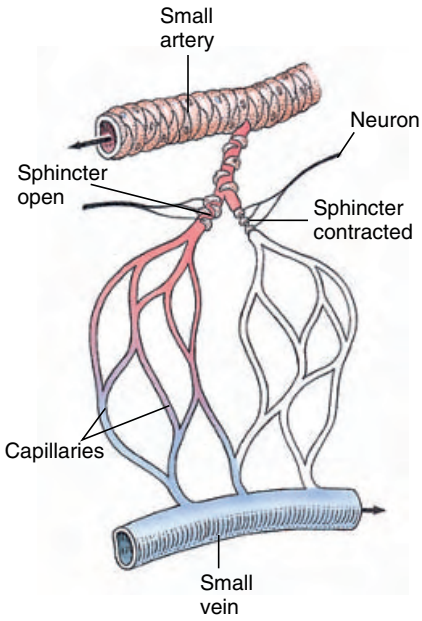


Figure 33-16
Capillary bed. Precapillary sphincters (muscles encircling an opening) control blood flow through capillaries.

water back into the capillary from the tissue fluid. The result of these two opposing forces is that water and solutes tend to be filtered out of the arteriolar end of the capillary where hydrostatic pressure exceeds osmotic pressure, and to be drawn in again at the venous end where osmotic pressure exceeds hydrostatic pressure.

The actual situation is a bit more complicated because there is a small hydrostatic pressure in the interstitial fluid, and a small amount of protein does leak through the capillary wall. The protein tends to accumulate at the venule end of the capillary, building up a small osmotic pressure there. Although actual calculation of the pressure differences must take into account interstitial fluid hydrostatic and osmotic pressures, the principle of capillary fluid shift is as we have presented it.

The amount of fluid filtered across the capillary wall fluctuates greatly among different capillaries. Usually outflow exceeds inflow, and the excess fluid, called **lymph,** remains in the interstitial spaces between tissue cells. This excess is picked up and removed by **lymph capillaries** of the lymphatic system and eventually returned to the circulatory system via larger lymph vessels (see the following text).

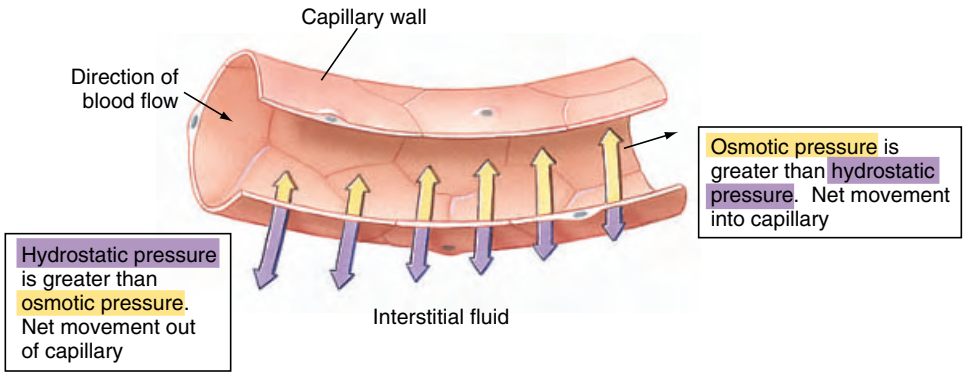


Figure 33-17

Fluid movement across the wall of a capillary. At the arterial end of the capillary, hydrostatic (blood) pressure exceeds colloid osmotic pressure contributed by plasma proteins, and a plasma filtrate is forced outside the capillary. At the venous end, colloid osmotic pressure exceeds the hydrostatic pressure, and fluid is drawn inside the capillary. In this way plasma nutrients are carried into the interstitial space where they can enter cells, and metabolic end products from the cells are drawn into the plasma and carried away.

Veins

Venules and veins into which the capillary blood drains for its return journey to the heart are thinner walled, less elastic, and of considerably larger diameter than their corresponding arteries and arterioles (Figure 33-15). Blood pressure in the venous system is low, from approximately 10 mm Hg, where capillaries drain into venules, to approximately zero in the right atrium. Because pressure is so low, venous return gets assistance from valves in the veins, body muscles surrounding the veins, and the rhythmical action of the lungs. Without these mechanisms, blood can pool in the lower extremities of a standing animal—a very real problem for people who must stand for long periods. Veins that lift blood from the extremities to the heart contain valves that divide the long column of blood into segments. When skeletal muscles contract, as in even slight activity, the veins are squeezed, and blood within them moves toward the heart because the valves within the veins keep blood from slipping back. The well-known risk of fainting while standing at stiff attention in hot weather usually can be prevented by deliberately pumping leg muscles. Negative pressure in the thorax created by inspiratory movements of the lungs also speeds venous return by sucking blood up the large vena cava into the heart.

Lymphatic System

The lymphatic system of vertebrates is an extensive network of thin-walled vessels that arise as blind-ended lymph capillaries in most tissues of the body. These unite to form a treelike structure of increasingly larger lymph vessels, which finally drain into veins in the lower neck (Figure 33-18). A principal function of the lymphatic system is to return to the blood the excess fluid (lymph) filtered across capillary walls into interstitial spaces. Lymph is similar to plasma but has a much lower concentration of protein. Large molecules, especially fats absorbed from the gut, also reach the circulatory system by way of the lymphatic system. The rate of lymph flow is very low, a minute fraction of blood flow.

The lymphatic system also plays a central role in the body's defenses. Located at intervals along the lymph vessels are **lymph nodes** (Figure 33-18) that have several defense-related functions (Chapter 37). Cells in the lymph glands such as macrophages remove foreign particles, especially bacteria, which might otherwise enter the general circulation. They are also centers (together with bone marrow and thymus gland) for production, maintenance, and distribution of lymphocytes that produce antibodies—essential components of the body's defense mechanisms

Respiration

Energy bound up in food is released by oxidative processes, usually with molecular oxygen as the terminal electron acceptor. Oxygen for this purpose is taken into the body across some respiratory surface. Physiologists find it is convenient to distinguish two separate but interrelated respiratory processes: **cellular respiration,** the oxidative processes that occur within cells (p. 63), and **external respiration,** the exchange of oxygen and carbon dioxide between the organism and its environment. In this section we

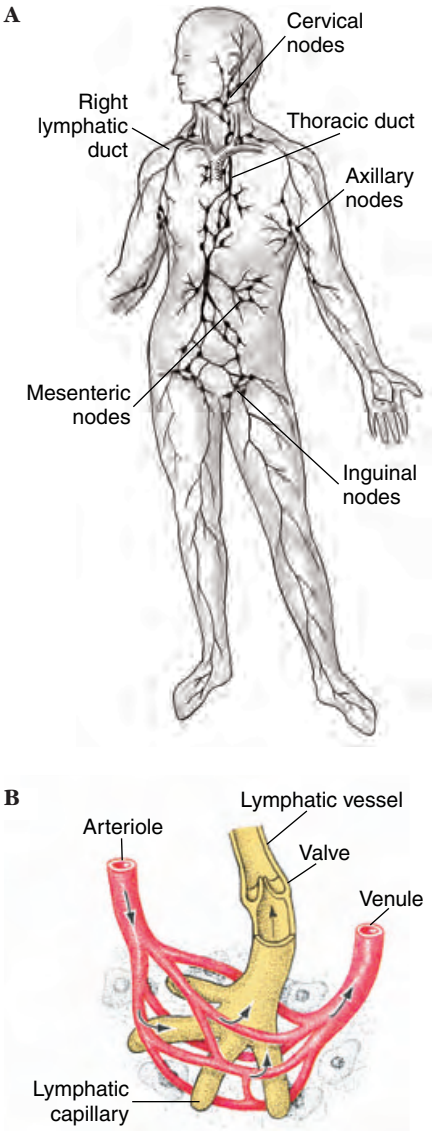


Figure 33-18
Human lymphatic system, showing major vessels, **A,** and a detail of the blood and lymphatic capillaries, **B.**

describe external respiration and transport of gases from respiratory surfaces to body tissues.

In single-celled organisms, oxygen is acquired and carbon dioxide liberated by direct diffusion across surface membranes. Gas exchange by diffusion alone is possible only for very small organisms less than 1 mm in diameter, where diffusion paths are short and the surface area of the organism is large relative to volume. As animals became larger and evolved a waterproof covering, specialized devices such as lungs and gills evolved to increase the effective surface for gas exchange. But, because gases diffuse so slowly through living tissue, a circulatory system was necessary to distribute gases to and from the deep tissues of the body. Even these adaptations were inadequate for complex animals with high rates of cellular respiration. The solubility of oxygen in the blood plasma is so low that plasma alone cannot carry enough oxygen to support metabolic demands. With evolution of special oxygen-transporting blood proteins such as hemoglobin, the oxygen-carrying capacity of blood increased greatly. Thus what began as a simple and easily satisfied requirement resulted in evolution of several complex and essential respiratory and circulatory adaptations.

Problems of Aquatic and Aerial Breathing

How an animal respires is determined largely by the nature of its environment. The two great arenas of animal evolution—water and land—are vastly different in their physical characteristics. The most obvious difference is that air contains far more oxygen—at least 20 times more—than does water. For example, water at 5° C (41° F) fully saturated with air contains approximately 9 ml of oxygen per liter (0.9%); by comparison air contains 209 ml of oxygen per 1000 ml (21%). The density and viscosity of water are approximately 800 and 50 times greater, respectively, than that of air. Furthermore, gas molecules diffuse 10,000 times more rapidly in air than in water. These differences mean that aquatic animals must have evolved very efficient ways of removing oxygen from water. Yet even the most advanced fishes with highly efficient gills and pumping mechanisms may use as much as 20% of their energy just extracting oxygen from water. By comparison, the cost for mammals to breathe is only 1% to 2% of their resting metabolism.

Respiratory surfaces must be thin and always kept wet with a fine film of fluid to allow diffusion of gases across an aqueous phase between the environment and the underlying circulation. This is hardly a problem for aquatic animals, immersed as they are in water, but it is a challenge for air breathers. To keep respiratory membranes moist and protected from injury, air breathers have in general developed invaginations of the body surface and then added pumping mechanisms to move air in and out of the body. The lung is the best example of a successful solution to breathing on land. In general **evaginations** of the body surface, such as gills, are most suitable for aquatic respiration; **invaginations,** such as lungs and tracheae, are best for air breathing. We now consider the specific kinds of respiratory organs employed by animals.

Respiratory Organs

Gas Exchange by Direct Diffusion

Protozoa, sponges, cnidarians, and many worms respire by direct diffusion of gases between organism and environment. We have noted that this kind of **cutaneous respiration** is not adequate when the cellular mass exceeds approximately 1 mm in diameter. However, by greatly increasing the surface of the body relative to its mass, many multicellular animals can supply part or all of their oxygen requirements by direct diffusion. Flatworms are an example of this strategy. Cutaneous respiration frequently supplements gill or lung breathing in larger animals such as amphibians and fishes. For example, an eel can exchange 60% of its oxygen and carbon dioxide through its highly vascular skin. During their winter hibernation, frogs and even turtles exchange all their respiratory gases through the skin while submerged in ponds or springs. Lungless salamanders comprise the largest family of salamanders. Some lungless salamanders have larvae with gills, and gills persist in the adults of some, but adults of most species have neither lungs nor gills.

Gas Exchange Through Tubes: Tracheal Systems

Insects and certain other terrestrial arthropods (centipedes, millipedes, and some spiders) have a highly specialized type of respiratory system, in many respects the simplest, most direct, and most efficient respiratory system found in active animals. It consists of a branching system of tubes **(tracheae)** that extends to all parts of the body (Figure 33-19). The smallest end channels are fluid-filled **tracheoles,** less than 1 μm in diameter, that sink into the plasma membranes of body cells. Air enters the tracheal system through valvelike openings **(spiracles).** Carbon dioxide diffuses out through spiracles. Some insects can ventilate the tracheal system with body movements; the familiar telescoping movement of the bee abdomen is an example. Because the cells have a direct pipeline to the outside, bringing oxygen in and carrying carbon dioxide out, an insect's respiration is independent of its circulatory system. Consequently, insect blood plays no direct role in oxygen transport.

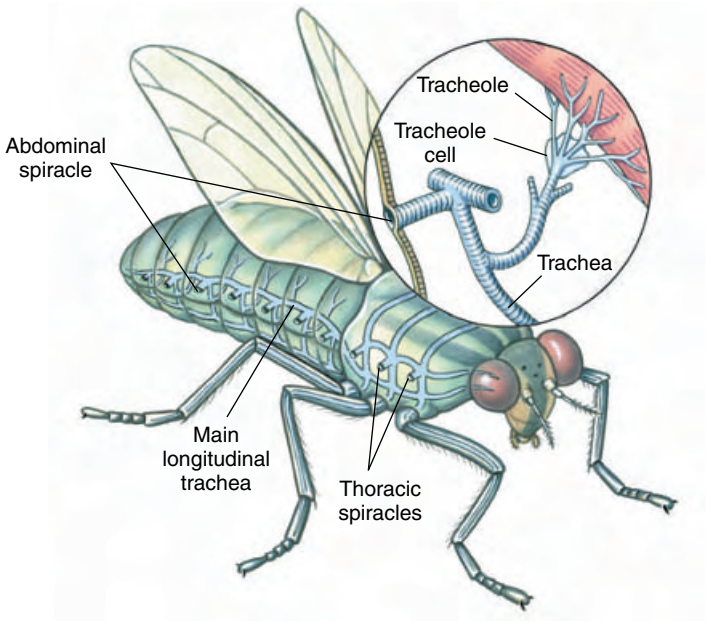


Figure 33-19

Tracheal system of insects. Air enters through spiracles, then travels through tracheae to reach tissues at tracheoles.

Efficient Exchange in Water: Gills

Gills of various types are effective respiratory devices for life in water. Gills may be simple **external** extensions of the body surface, such as **dermal papulae** of sea stars (p. 463) or **branchial tufts** of marine worms (p. 360) and aquatic amphibians (p. 545). Most efficient are **internal gills** of fishes (p. 527) and arthropods. Fish gills are thin filamentous structures, richly supplied with blood vessels arranged so that blood flow is opposite to the flow of water across the gills. This arrangement, called **countercurrent flow** (p. 674), provides the greatest possible extraction of oxygen from water. Water flows over the gills in a steady stream, pulled and pushed by an efficient, two-valved, branchial pump (Figure 33-20). Gill ventilation is often assisted by the fish's forward movement through the water.

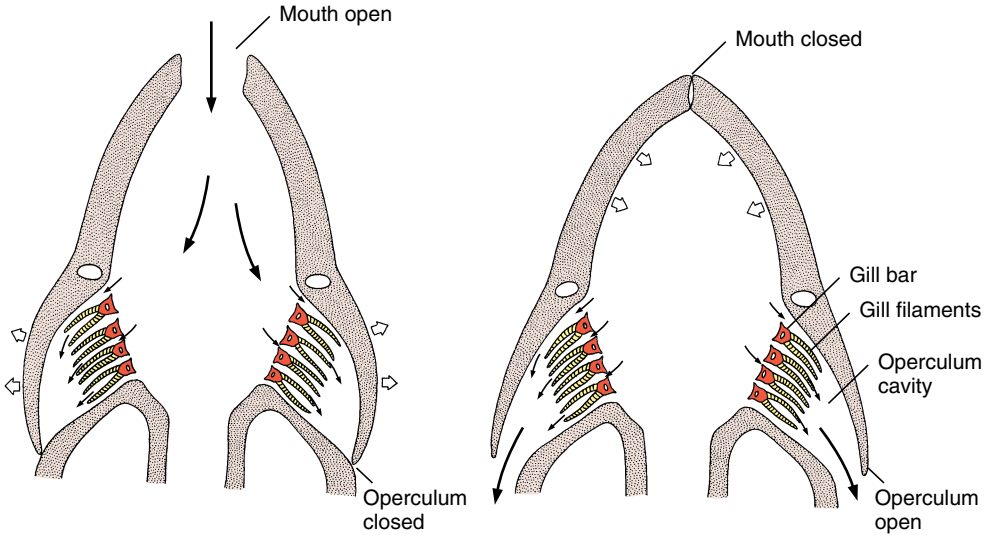


Figure 33-20

How a fish ventilates its gills. Through the action of two skeletal muscle pumps, one in the mouth cavity, the other in the opercular cavity, water is drawn into the mouth, passes over the gills, and exits through the gill covers (opercular clefts).

Lungs

Gills are unsuitable for life in air because, when removed from the buoying water medium, gill filaments collapse, dry, and stick together; a fish out of water rapidly asphyxiates despite the abundance of oxygen around it. Consequently most air-breathing vertebrates possess lungs, highly vascularized internal cavities. Lungs of a sort are found in certain invertebrates (pulmonate snails, scorpions, some spiders, some small crustaceans), but these structures cannot be very efficiently ventilated.

Lungs that can be ventilated by muscle movements to produce a rhythmic exchange of air are characteristic

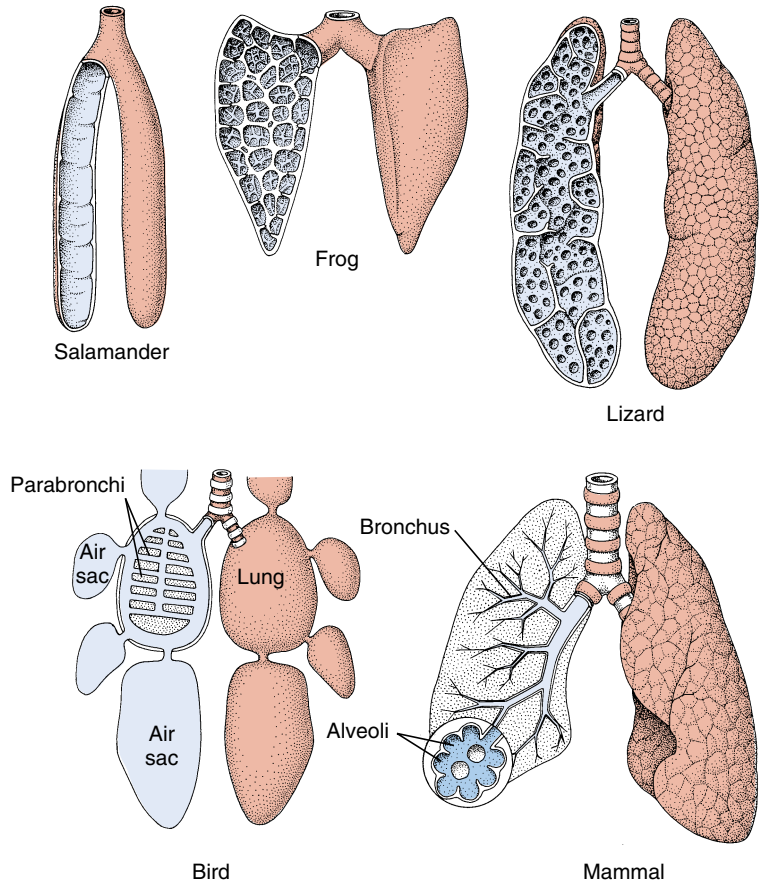


Figure 33-21

Internal structures of lungs among vertebrate groups. Generally, the evolutionary trend has been from simple sacs with little exchange surface between blood and air spaces to complex, lobulated structures, each with complex divisions and extensive exchange surfaces.

of terrestrial vertebrates. Most rudimentary of vertebrate lungs are those of lungfishes (Dipneusti), which use them to supplement, or even replace, gill respiration during periods of drought. Although of simple construction, a lungfish lung is supplied with a capillary network in its largely unfurrowed walls, a tubelike connection to the pharynx, and a primitive ventilating system for moving air in and out of the lung.

Amphibian lungs vary from simple, smooth-walled, baglike lungs of some salamanders to the subdivided lungs of frogs and toads (Figure 33-21). The total surface available for gas exchange is much increased in lungs of reptiles which are subdivided into numerous interconnecting air sacs. Most elaborate of all are mammalian lungs complexes of millions of small sacs, called **alveoli** (Figure 33-22), each veiled by a rich vascular network. Human lungs have a total surface area of from 50 to 90 m^2—50 times the area of the skin surface—and contain 1000 km of capillaries. A large surface area is essential for the high oxygen uptake required to support the elevated metabolic rate of endothermic mammals.

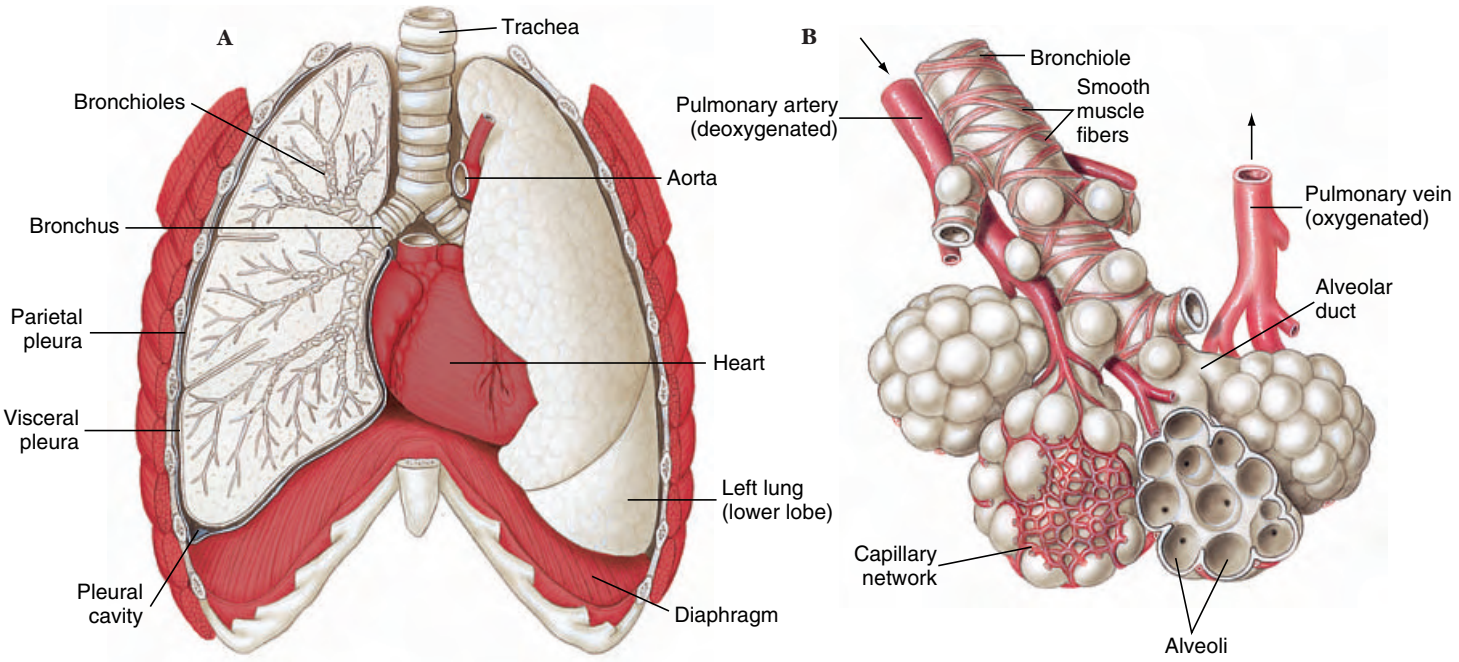


Figure 33-22

A, Lungs of human with right lung shown in section. **B,** Terminal portion of bronchiole showing air sacs with their blood supply. Arrows show direction of blood flow.

A disadvantage of lungs is that gas is exchanged between blood and air only in the alveoli, located at the ends of a branching tree of air tubes (trachea, bronchi, and bronchioles [Figure 33-22]). Unlike the efficient one-way flow of water across fish gills, air must enter and exit a lung through the same channel. After exhalation, the air tubes are filled with "used" air from the alveoli which, during the following inhalation, is pulled back into the lungs. The volume of air in a lung's passageways is called "dead space." This air shuttles back and forth with each breath, adding to the difficulty of properly ventilating lungs. In fact, lung ventilation in humans is so inefficient that in normal breathing only approximately one-sixth of the air in the lungs is replenished with each inspiration. Even after forced expiration, 20% to 35% of the air remains in the lungs.

In birds, lung efficiency is improved vastly by adding an extensive system of air sacs (Figure 33-21 and p. 593) that serve as air reservoirs during ventilation. On inspiration, some 75% of incoming air bypasses the lungs to enter the air sacs (gas exchange does not occur here). At expiration some of this fresh air passes directly through the lung passages and eventually into one-cell thick **air capillaries** where gas exchange occurs. Thus air capillaries receive nearly fresh air during both inspiration and expiration. The beautifully designed bird lung is a result of selective pressures during evolution of flight with its high metabolic demands.

Amphibians employ a **positive pressure** action to force air into their lungs, unlike most reptiles, birds, and mammals, which ventilate their lungs by **negative pressure,** in which air is pulled into the lungs by expansion of the thoracic cavity. Frogs ventilate the lungs by first drawing air into the mouth through the **external nares** (nostrils). Then, closing the nares and raising the floor of the mouth, they drive air into the lungs (Figure 33-23). Much of the time, however, frogs rhythmically ventilate only the mouth cavity, a well-vascularized respiratory surface that supplements pulmonary respiration.

Structure and Function of the Mammalian Respiratory System

Air enters a mammalian respiratory system through nostrils (external nares), passes through a **nasal chamber,** lined with mucus-secreting epithelium, and then through **internal nares,** nasal openings connected to the **pharynx.** Here, where pathways of digestion and respiration cross, inhaled air leaves the pharynx by passing into a narrow opening, the **glottis;** food enters the esophagus to pass to the stomach (see Figure 34-10, p. 714). The glottis opens into the **larynx,** or voice box, and then into the **trachea,** or windpipe. The trachea branches into two **bronchi,** one to each lung (Figure 33-22). Within the lungs each bronchus divides and subdivides into small tubes **(bronchioles)** that lead via **alveolar ducts** to the air sacs **(alveoli)** (Figure 33-22). The single-layered endothelial walls of the alveoli are thin and moist to facilitate exchange of gases between air sacs and adjacent blood capillaries. Air passageways are lined with both mucus-secreting and ciliated epithelial cells, which play an important role in conditioning the air before it reaches the alveoli. Partial cartilage rings in the walls of the tracheae, bronchi, and even some of the bronchioles prevent those structures from collapsing.

In its passage to the air sacs, air undergoes three important changes: (1) it is filtered free from most dust and other foreign substances, (2) it is warmed to body temperature, and (3) it is saturated with moisture.

The lungs consist of a great deal of elastic connective tissue and some muscle. They are covered by a thin layer of tough epithelium known as the **visceral pleura.** A similar layer, the **parietal pleura,** lines the inner surface of the walls of the chest (Figure 33-22). The two layers of the pleura are in contact and slide over one another as the lungs expand and contract. The "space" between the pleura, called the **pleural cavity,** maintains a partial vacuum, which helps keep the lungs expanded to fill the pleural cavity. Therefore no real pleural space exists; the two pleura rub together, lubricated by tissue fluid (lymph). The chest cavity is bounded by the spine, ribs, and breastbone, and floored by the **diaphragm,** a dome-shaped, muscular partition between the chest cavity and abdomen. A muscular diaphragm is found only in mammals.

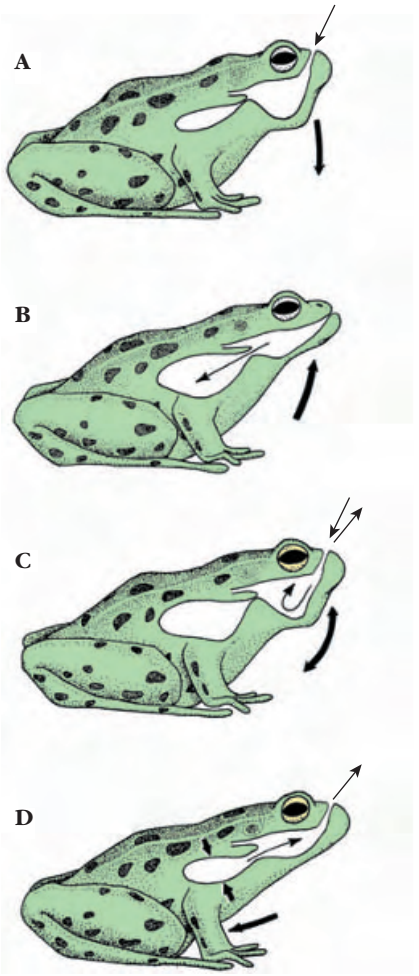


Figure 33-23
Breathing in frogs. Frogs, positive-pressure breathers, fill their lungs by forcing air into them. **A,** Floor of mouth is lowered, drawing air in through the nostrils. **B,** With nostrils closed and glottis open, frogs force air into lungs by elevating the floor of mouth. **C,** Mouth cavity is ventilated rhythmically for a period. **D,** Lungs are emptied by contraction of body-wall musculature and by elastic recoil of lungs.

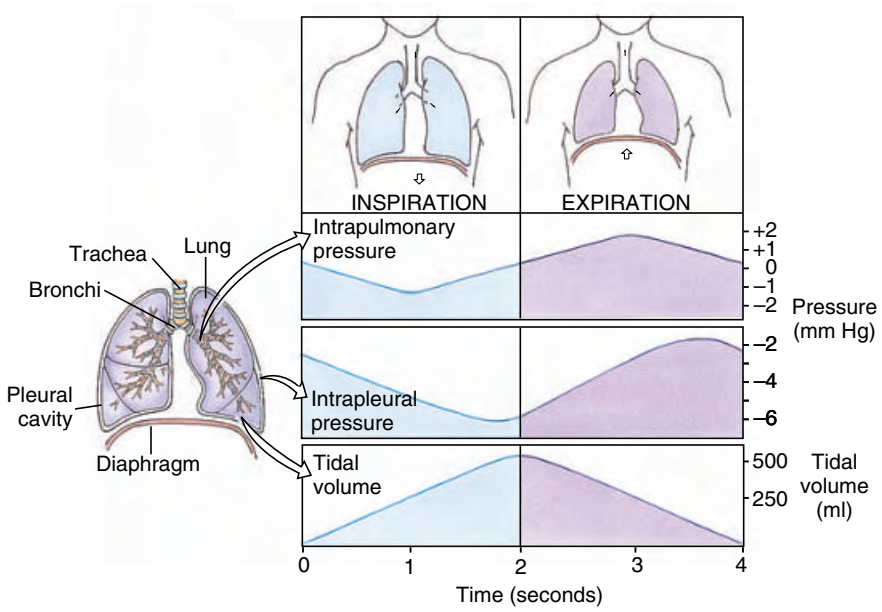


Figure 33-24
Mechanism of breathing in humans.

Ventilating the lungs

The chest cavity is an air-tight chamber. Inspiration pulls the ribs upward, flattens the diaphragm, and enlarges the chest cavity (Figure 33-24). The resultant increase in volume of the chest cavity causes air pressure in the lungs to fall below atmospheric pressure: air rushes in through passageways to equalize the pressure. Normal **expiration** is a less active process than inspiration. When the muscles relax, the ribs and diaphragm return to their original position, and the chest cavity decreases in size, the elastic lungs deflate, and air exits (Figure 33-24).

How Breathing Is Coordinated

Breathing is normally involuntary and automatic but can come under voluntary control. Neurons in the medulla of the brain regulate normal, quiet breathing. They spontaneously produce rhythmical bursts that stimulate contraction of the diaphragm and external intercostal muscles. However, respiration must adjust itself to changing requirements of the body for oxygen. Oddly, carbon dioxide rather than oxygen has the greatest effect on respiratory rate because under normal conditions arterial oxygen does not decline enough to stimulate oxygen receptors. Even a small rise in carbon dioxide level in the blood, however, has a powerful effect on respiratory activity. Actually, the stimulatory effects of carbon dioxide are due in part to an increase in hydrogen ion concentration in cerebrospinal fluid.

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow H^+ + HCO_3^-$$

This reaction shows that carbon dioxide combines with water to form carbonic acid. Carbonic acid then dissociates to release hydrogen ions, making the cerebrospinal fluid more acidic, and stimulating respiratory receptors in the medulla of the brain. Both rate and depth of respiration increase.

It is well known that swimmers can remain submerged much longer if they vigorously hyperventilate first to blow off carbon dioxide from the lungs, thereby delaying the overpowering urge to surface and breathe. The practice is dangerous because blood oxygen is depleted just as rapidly as without prior hyperventilation, and the swimmer may lose consciousness when the oxygen supply to the brain drops below a critical point. Several documented drownings among swimmers attempting long underwater swimming records have been caused by this practice.

Gaseous Exchange in Lungs and Body Tissues: Diffusion and Partial Pressure

Air (the atmosphere) is a mixture of gases: about 71% nitrogen, 20.9% oxygen, in addition to fractional percentages of other gases, such as carbon dioxide (0.03%). Gravity attracts the mass of the atmosphere to the earth. At sea level the atmosphere exerts a hydrostatic pressure due to gravity equal to the weight of a column of mercury (Hg) 760 mm high. Thus we can speak of atmospheric pressure (1 atm) as being equal to 760 mm Hg. But because air is not a single gas but a mixture, *part* of the 760 mm Hg pressure **(partial pressure)** is due to each component gas. For example, the partial pressure of oxygen is 0.209 × 760 = 159 mm, and that for carbon dioxide is 0.0003 × 760 = 0.23 mm in dry air. (In fact, atmospheric air is never completely dry, and the varying amount of water vapor present exerts a pressure in proportion to its concentration, like other gases.)

As soon as air enters the respiratory tract, its composition changes (Table 33-1, Figure 33-25). Inspired air becomes saturated with water vapor as it travels through the air-filled passageways toward the alveoli. When inspired air reaches the alveoli, it mixes with residual air remaining from the previous respiratory cycle. Partial pressure of oxygen drops and that of carbon dioxide rises. Upon expiration, air from the alveoli mixes with air in the dead space to produce still a different mixture (Table 33-1). Although no significant gas exchange takes place in the dead space, the air it contains is the first air to leave the body when expiration begins.

Because the partial pressure of oxygen in lung alveoli is greater (100 mm Hg) than it is in venous blood of lung capillaries (40 mm Hg), oxygen diffuses into the lung capillaries. In a similar manner carbon dioxide in blood of the lung capillaries has a higher concentration (46 mm Hg) than has this same gas in lung alveoli (40 mm Hg), so carbon dioxide diffuses from the blood into the alveoli.

TABLE 33.1

Partial Pressures and Gas Concentrations in Air and Body Fluids

	Nitrogen (N_2)	Oxygen (O_2)	Carbon Dioxide (CO_2)	Water Vapor (H_2O)
Inspired air (dry)	600 (79%)	159 (20.9%)	0.2 (0.03%)	—
Alveolar air (saturated)	573 (75.4%)	100 (13.2%)	40 (5.2%)	47 (6.2%)
Expired air (saturated)	569 (74.8%)	116 (15.3%)	28 (3.7%)	47 (6.2%)
Arterial blood	573	100	40	
Peripheral tissues	573	30	50	
Venous blood	573	40	46	

Note: Values expressed in millimeters of mercury (mm Hg). Percentages indicate proportion of total atmospheric pressure at sea level (760 mm Hg). Inspired air is shown as dry, although atmospheric air always contains variable amounts of water. If, for example, atmospheric air at 20° C were half saturated (relative humidity 50%), the partial pressures and percentages would be N_2 593.5 (78.1%); O_2 157 (20.6%); CO_2 0.2 (0.03%); and H_2O 8.75 (1.1%).

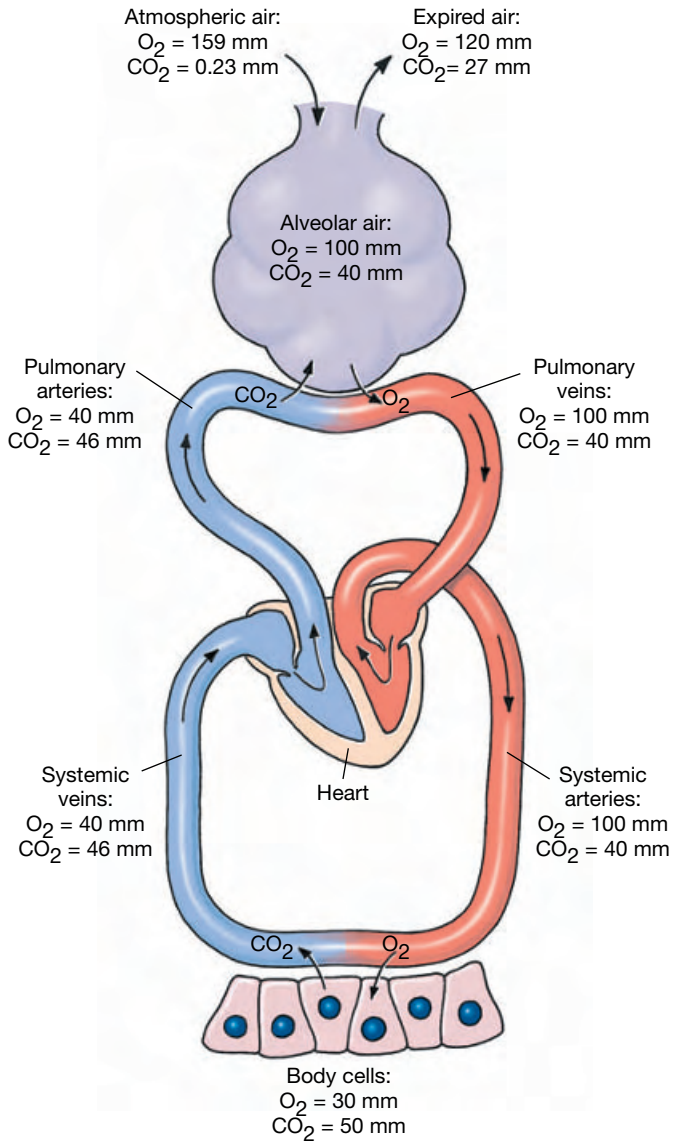


Figure 33-25

Exchange of respiratory gases in lungs and tissue cells. Numbers present partial pressures in millimeters of mercury (mm Hg).

In tissues respiratory gases also move along their concentration gradients (Figure 33-25). Partial pressure of oxygen in the blood (100 mm Hg) is greater than in the tissues (0 to 30 mm Hg), and partial pressure of carbon dioxide in tissues (45 to 68 mm Hg) is greater than that in blood (40 mm Hg). In each case gases diffuse from a location of higher concentration to one of lower concentration.

How Respiratory Gases Are Transported

In some invertebrates respiratory gases are simply carried, dissolved in body fluids. However, solubility of oxygen is so low in water that it is adequate only for animals with low rates of metabolism. For example, only approximately 1% of a human's oxygen requirement can be transported in this way. Consequently in many invertebrates and in virtually all vertebrates, nearly all oxygen and a significant amount of carbon dioxide are transported by special colored proteins, or **respiratory pigments,** in the blood. In most animals (all vertebrates) these respiratory pigments are packaged into blood cells.

Because of the weight of water, hydrostatic pressure increases the equivalent of 1 atmosphere for every 10 m of depth in seawater, and the pressure of the air supplied to a diver must be increased correspondingly so that it can be drawn into the lungs. Under the increased pressure, additional air dissolves

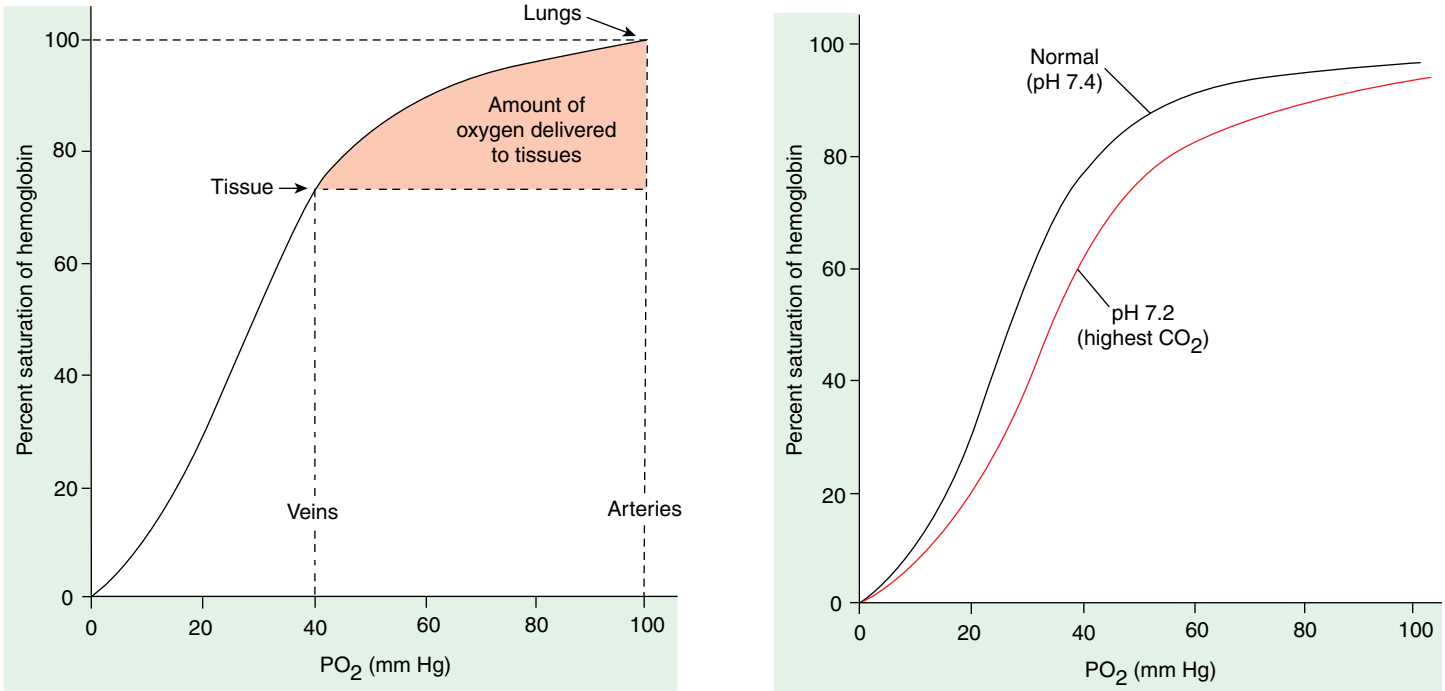


Figure 33-26

Hemoglobin saturation curves. Curves show how the amount of oxygen that can bind to hemoglobin is related to oxygen partial pressure. **A,** At the higher partial pressure in the lungs, hemoglobin can load with more oxygen. In the tissues the oxygen concentration is less, so hemoglobin can carry less; that is, it unloads more. **B,** Hemoglobin is also sensitive to carbon dioxide partial pressure (Bohr effect). As carbon dioxide enters blood from the tissues, it shifts the curve to the right, decreasing affinity of hemoglobin for oxygen. Thus the hemoglobin unloads more oxygen in the tissues where carbon dioxide concentration is higher.

in the blood, the amount depending on depth and time at depth of a dive. If a diver ascends slowly, the gas comes out of solution imperceptibly and is breathed out from the lungs. However, if the ascent is too rapid, the air comes out of solution and forms bubbles in the blood and other tissues, a condition known as *decompression sickness* or *the bends.* The result is painful and, if severe, can cause paralysis or death.

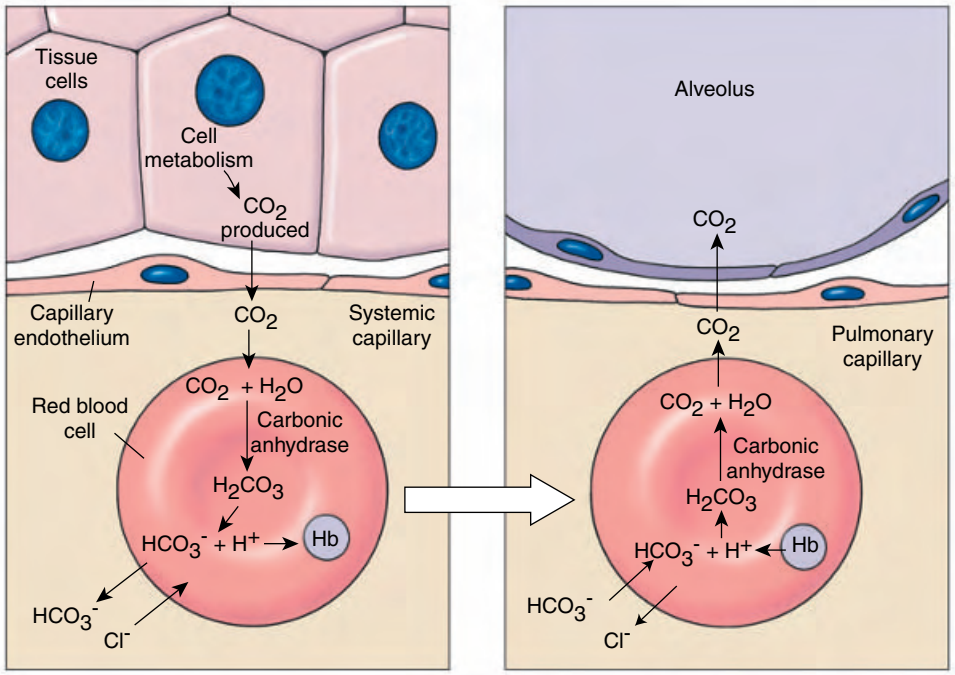
Sickle cell anemia is an up-to-now incurable, inherited condition (p. 99) in which a single amino acid (glutamic acid) in normal hemoglobin (HbA) is replaced by a valine in sickle cell hemoglobin (HbS). The ability of HbS to carry oxygen is severely impaired, and erythrocytes tend to crumple during periods of oxygen stress (for example, during exercise). Capillaries become clogged with misshapen red cells; the affected area is very painful, and the tissue may die. About 1 in 10 black Americans carry the trait (heterozygous). Heterozygotes do not have sickle cell anemia and live normal lives, but if both parents are heterozygous, each of their offspring has a 25% chance of inheriting the disease.

The most widespread respiratory pigment in the animal kingdom is **hemoglobin,** a red, iron-containing protein present in all vertebrates and many invertebrates. Each molecule of hemoglobin is 5% **heme,** an iron-containing compound giving the red color to blood, and 95% **globin,** a colorless protein. The heme portion of hemoglobin has a great affinity for oxygen; each gram of hemoglobin can carry a maximum of approximately 1.3 ml of oxygen. Because there are approximately 15 g of hemoglobin in each 100 ml of blood, fully oxygenated blood contains approximately 20 ml of oxygen per 100 ml. Of course, for hemoglobin to be of value to the body it must hold oxygen in a loose, reversible chemical combination so that it can be released to tissues. The actual amount of oxygen that combines with hemoglobin depends on the shape or conformation of the hemoglobin molecule, which is affected by several factors, including the concentration of oxygen itself. When the oxygen concentration is high, as it is in the capillaries of the lung alveoli, hemoglobin loads up with oxygen; in tissues where the prevailing oxygen partial pressure is low, hemoglobin releases its stored oxygen reserves (Figure 33-26).

Although hemoglobin is the only vertebrate respiratory pigment, several other respiratory pigments are known among invertebrates. *Hemocyanin,* a blue, copper-containing protein, occurs in crustaceans and most molluscs. Among other pigments is *chlorocruorin* (klor-a-cru′-o-rin), a green-colored, iron-containing pigment found in four families of polychaete tube worms. Its structure and oxygen-carrying capacity are very similar to those of hemoglobin, but it is carried free in the plasma rather than being enclosed in blood corpuscles. *Hemerythrin* is a red pigment found in some polychaete worms. Although it contains iron, this metal is not present in a heme group (despite the name of the pigment!), and its oxygen-carrying capacity is poor compared to hemoglobin.

Figure 33-27

Transport of carbon dioxide in the blood. **A,** Carbon dioxide produced by metabolic oxidation of glucose diffuses from the tissues into plasma and red blood cells. Carbonic anhydrase in red blood cells catalyzes conversion of carbon dioxide into carbonic acid, then bicarbonate and hydrogen ions. Part of the bicarbonate diffuses out of the cells, and diffusion inward of chloride ions maintains electrical balance. Hydrogen ions mostly associate with hemoglobin. **B,** The lower partial pressure of carbon dioxide in the alveoli of the lungs favors reversal of these reactions.



Unfortunately for humans and many other animals, hemoglobin has an affinity for carbon monoxide that is about 200 times greater than its affinity for oxygen. Consequently, even when carbon monoxide is present in the atmosphere at lower concentrations than oxygen, it tends to displace oxygen from hemoglobin to form a stable compound called carboxyhemoglobin. Air containing only 0.2% carbon monoxide may be fatal. Because of their higher respiratory rate, children and small animals are poisoned more rapidly than adults. Carbon monoxide is becoming an atmospheric contaminant of ever-increasing proportions as the world's population and industrialization continue to increase rapidly.

We can express the relationship of carrying capacity to surrounding oxygen concentration as **hemoglobin saturation curves** (also called oxygen dissociation curves [Figure 33-26]). As these curves show, the lower the surrounding oxygen tension, the greater the quantity of oxygen released. This important characteristic of hemoglobin allows more oxygen to be released to those tissues which need it most (those having the lowest partial pressure of oxygen).

Another factor that affects conformation of hemoglobin and therefore its release of oxygen to tissues is the sensitivity of oxyhemoglobin (hemoglobin with bound oxygen) to carbon dioxide. Carbon dioxide shifts the hemoglobin saturation curve to the right (Figure 33-26B), a phenomenon called the **Bohr effect** after the Danish scientist who first described it. As carbon dioxide enters the blood from respiring tissues, it causes hemoglobin to unload more oxygen. The opposite event occurs in the lungs; as carbon dioxide diffuses from venous blood into alveolar space, the hemoglobin saturation curve shifts back to the left, allowing more oxygen to be loaded onto hemoglobin.

The same blood that transports oxygen to the tissues from the lungs must carry carbon dioxide back to the lungs on its return trip. However, unlike oxygen that is transported almost exclusively in combination with hemoglobin, carbon dioxide is transported in three different forms. A small fraction of the blood-borne carbon dioxide, only about 7%, is carried as gas physically dissolved in the plasma. The remainder diffuses into red blood cells. In red blood cells, most carbon dioxide, approximately 70%, becomes carbonic acid through action of the enzyme carbonic anhydrase. Carbonic acid immediately dissociates into hydrogen ion and bicarbonate ion. We can summarize the entire reaction as follows:

$$CO_2 + H_2O \underset{\text{carbonic anhydrase}}{\rightleftharpoons} H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$

Several systems buffer the hydrogen-ion concentration in blood, thus preventing a severe decrease in blood pH. Bicarbonate ions remain in solution in plasma and red blood cells since, unlike carbon dioxide, bicarbonate is extremely soluble (Figure 33-27).

Another fraction of the carbon dioxide, approximately 23%, combines reversibly with hemoglobin. Carbon dioxide does not combine with the heme group but with amino groups of several amino acids to form a compound called carbaminohemoglobin.

All of these reactions are reversible. When the venous blood reaches the lungs, carbon dioxide diffuses from red blood cells into alveolar air.

Summary

Fluid in the body, whether intracellular, plasma, or interstitial, is mostly water, but contains many dissolved substances, including electrolytes and proteins. Vertebrate blood consists of fluid plasma and formed elements, including red and white blood cells and platelets. Plasma has many dissolved solids, as well as dissolved gases. Mammalian red blood cells lose their nucleus during development and contain the oxygen-carrying pigment, hemoglobin. White blood cells are important defensive elements. Platelets are vital in the process of clotting, necessary to prevent excess blood loss when a blood vessel is damaged. Platelets release a series of factors that activate prothrombin to thrombin, an enzyme that causes fibrinogen to change to the gel form, fibrin.

In open circulatory systems, such as those of arthropods and most molluscs, blood escapes from arteries into a hemocoel, which is a primary body cavity derived from the blastocoel. In closed circulatory systems, such as those of annelids, vertebrates, and cephalopod molluscs, the heart pumps blood into arteries, then into arterioles of smaller diameter, through a bed of fine capillaries, through venules, and finally through veins, which lead back to the heart. In fishes, which have a two-chambered heart with a single atrium and a single ventricle, blood is pumped to gills and then directly to systemic capillaries throughout the body without first returning to the heart. With evolution of lungs, vertebrates developed a double circulation consisting of a systemic circuit serving the body, and a pulmonary circuit serving the lungs. To be fully efficient, this change required partitioning of both atrium and ventricle to form a double pump; partial partitioning occurs in lungfishes and amphibians which have two atria but an undivided ventricle, and is complete in birds and mammals, which have four-chambered hearts.

One-way flow of blood during the heart's contraction (ventricular systole) and relaxation (ventricular diastole) is assured by valves between the atria and ventricles and between the ventricles and pulmonary arteries and aorta. Although the heart can beat spontaneously, its rate is controlled by nerves from the central nervous system. Heart muscle uses a great deal of oxygen and has a well-developed coronary blood circulation. The walls of arteries are thicker than those of veins, and the connective tissue in the walls of arteries allows them to expand during ventricular systole and contract during ventricular diastole. Normal arterial blood pressure (hydrostatic) of humans in systole is 120 mm Hg and in diastole, 80 mm Hg. Because capillary walls are permeable to water, a protein-free filtrate crosses capillary walls, its movement determined by a balance between opposing forces of hydrostatic and protein osmotic pressure. Tissue fluid (lymph) that does not reenter the capillary system is collected by the lymphatic system and returned to blood by lymph ducts.

Very small animals can depend on diffusion between the external environment and their tissues or cytoplasm for transport of respiratory gases, but larger animals require specialized organs, such as gills, tracheae, or lungs, for this function. Gills and lungs provide an increased surface area for exchange of respiratory gases between blood and environment. Many animals have special respiratory pigments and other mechanisms to help transport oxygen and carbon dioxide in blood. The most widespread respiratory pigment in the animal kingdom, hemoglobin, has a high affinity for oxygen at high oxygen concentrations but releases it at lower concentrations. Vertebrate hemoglobin, which is packaged in red blood cells, combines readily with oxygen in gills or lungs, then releases it in respiring body tissues where the oxygen partial pressure is low. Blood carries carbon dioxide from the tissues to the lungs as bicarbonate ion, in combination with hemoglobin, and as dissolved gas.

Review Questions

1. Name the chief intracellular electrolytes and the chief extracellular electrolytes.
2. What is the fate of spent erythrocytes in the body?
3. Outline or briefly describe the sequence of events that leads to blood coagulation.
4. Two distinctly different styles of circulatory systems have evolved among animals: open and closed. What is "open" about an open circulatory system? Closed systems sometimes are cited as adaptive for actively moving animals with (at least at times) high metabolic demand. Can you suggest possible reasons for this assertion?
5. Place the following in correct order to describe the circuit of blood through the vascular system of a fish: ventricle, gill capillaries, sinus venosus, body tissue capillaries, atrium, dorsal aorta.
6. Trace the flow of blood through the heart of a mammal, naming the four chambers, their valves, and explaining where the blood entering each atrium comes from and where blood leaving each ventricle goes. When the ventricles contract, what prevents blood from reentering the atria?
7. Explain the origin and conduction of the excitation that leads to a heart contraction. Why is the vertebrate heart said to be a myogenic heart? If the heart is myogenic, how do you account for alterations in rate of the heartbeat?
8. Define the terms systole and diastole. Distinguish atrial and ventricular systole and diastole.
9. Explain the movement of fluid across the walls of capillaries. How does balance of hydrostatic pressure and colloid osmotic pressure determine direction of net fluid flow?
10. Hydrostatic pressure at the arterial end of capillaries is about 40 mm Hg in humans. If hydrostatic pressure at the venous end is about 15 mm Hg, and colloid osmotic pressure is 25 mm Hg throughout, what is the net effect on fluid movement between capillaries and tissue spaces?
11. Provide a brief description of the lymphatic system. What are its principal functions? Why is movement of lymph through the lymphatic system very slow?
12. What is an advantage of a fish's gills for breathing in water and a disadvantage for breathing on land?

13. Describe the tracheal system of insects. What is the advantage of such a system for a small animal?
14. Trace the route of inspired air in humans from the nostrils to the smallest chamber of the lungs. What is the "dead air space" of a mammalian lung and how does it affect the partial pressure of oxygen reaching the alveoli?
15. The amount of time that scuba divers can spend underwater is limited by several factors, including time required to deplete the air supply in their tanks. To make their air last longer novice divers may be instructed to breathe slowly and exhale as much as possible on each breath. Can you suggest a reason why this behavior would lengthen a diver's air supply?
16. How does a frog ventilate its lungs? Contrast an amphibian's positive-pressure breathing with a mammal's negative-pressure breathing.
17. What is the role of carbon dioxide in the control of rate and depth of mammalian breathing of a mammal?
18. The air pressure supplied to a scuba diver must equal that exerted by the surrounding seawater, and for each 10 m increase in depth, pressure of the surrounding seawater increases one full atmosphere. Assuming the partial pressure of oxygen in air at sea level (one atmosphere) is 0.209 × 760 mm Hg (= 159 mm Hg), what partial pressure of oxygen would a diver be breathing at a depth of 30 m?
19. Explain how oxygen is carried in blood, including specifically the role of hemoglobin. Answer the same question with regard to carbon dioxide transport.
20. The ability of hemoglobin to bind oxygen decreases with decreasing oxygen concentration and also decreases with increasing carbon dioxide concentration. What effect do these phenomena have on the delivery of oxygen to tissues?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

National Heart Lung, and Blood Institute Home Page. Information and many links to resources on the circulatory and respiratory systems.

Heart Disease, Hypertension, Cholesterol, Treatment and Prevention. Mayo Clinic informational site on heart health. Reference articles, information, references, links, and quizzes.

Cholesterol Counts for Everyone. More information on cholesterol and heart disease from the National Heart, Lung, and Blood Institute.

The Heart: An Online Exploration. A variety of heart-related topics.

Cardiovascular Physiology Class Notes from Kings College in London.

Blood: Outline. An introduction to blood.

Lymphatic System. Graphics, much information on the lymphatic system from the University of Luton, England.

CHAPTER

34

Digestion and Nutrition

Topi and zebras on the African savannah.

A Consuming Cornucopia

Sir Walter Raleigh observed that the difference between a rich man and a poor man is that the former eats when he pleases while the latter eats when he can get it. In today's crowded world, with nearly 80 million people added each year to the world's population of 6 billion, the separation between the well-fed affluent and the hungry and malnourished poor reminds us that time has not diminished the shrewdness of Sir Walter's remark. Unlike the affluent for whom food acquisition requires only the selection of prepackaged foods at a well-stocked supermarket, the world's poor can appreciate that for them, as for the rest of the animal kingdom, procuring food is fundamental to survival. For most animals, eating is the main business of living.

Potential food is everywhere and little remains unexploited. Animals bite, chew, nibble, crush, graze, browse, shred, rasp, filter, engulf, enmesh, suck, and soak up foods of incredible variety. What an animal eats and how it eats profoundly affect an animal's feeding specialization, its behavior, its physiology, and its internal and external anatomy—in short, both its body form and its role in the web of life. The endless evolutionary jostling between predator and prey has provided compromise adaptations for eating and adaptations for avoiding being eaten. By whatever means food may be secured, there is far less variation among animals in the subsequent digestive simplification of foods. Vertebrates and invertebrates alike use similar digestive enzymes. Even more uniform are the final biochemical pathways for nutrient use and energy transformation. The nourishment of animals is like a cornucopia in which the food flows in rather than out. A great diversity of foods procured by countless feeding adaptations streams into the mouth of the horn, is simplified, and finally applied to the common purpose of survival and reproduction. ■

All organisms require energy to maintain their highly ordered and complex structure. This energy is chemical bond energy that is released by transforming complex compounds acquired from the organism's environment into simpler ones.

The ultimate source of energy for life on earth is the sun. Sunlight is captured by chlorophyll molecules in green plants, which transform a portion of this energy into chemical bond energy (food energy). Green plants are **autotrophic** organisms; they require only inorganic compounds absorbed from their surroundings to provide the raw material for synthesis and growth. Most autotrophic organisms are the chlorophyll-bearing **phototrophs,** although some, the chemosynthetic bacteria, are **chemotrophs;** they gain energy from inorganic chemical reactions.

Almost all animals are **heterotrophic organisms** that depend on already synthesized organic compounds of plants and other animals to obtain the materials they will use for growth, maintenance, and reproduction of their kind. Since the food of animals, normally the complex tissues of other organisms, is usually too bulky to be absorbed directly by cells, it must be broken down, or digested, into soluble molecules that are small enough to be used.

Animals may be divided into a number of categories on the basis of dietary habits. **Herbivorous** animals feed mainly on plant life. **Carnivorous** animals feed mainly on herbivores and other carnivores. **Omnivorous** forms eat both plants and animals. **Saprophagous** animals feed on decaying organic matter.

The ingestion of foods and their simplification by digestion are only initial steps in nutrition. Foods reduced by digestion to soluble, molecular form are **absorbed** into the circulatory system and **transported** to the body's tissues. There they are **assimilated** into the structure of cells. Oxygen is also transported by blood to the tissues, where food products are **oxidized,** or burned to yield energy and heat. Food not immediately used is **stored** for future use. Wastes produced by oxidation must be **excreted.** Food products unsuitable for digestion are **egested** in the form of feces.

In this chapter we first examine the feeding adaptations of animals. Next we discuss digestion and absorption of food. We close with a consideration of nutritional requirements of animals.

Feeding Mechanisms

Few animals can absorb nutrients directly from their external environments. Exceptions are some blood parasites (p. 230), certain intestinal protozoan parasites (p. 227), and tapeworms and acanthocephalans, (p. 294) that nourish themselves on primary organic molecules absorbed directly across their body surfaces. Most animals, however, must work for their meals. They are active feeders that have evolved numerous specializations for obtaining food. With food procurement as one of the most potent driving forces in animal evolution, natural selection has placed a high priority on adaptations for exploiting new sources of food and the means of food capture and intake. In this brief discussion we consider some of the major food-gathering devices.

Feeding on Particulate Matter

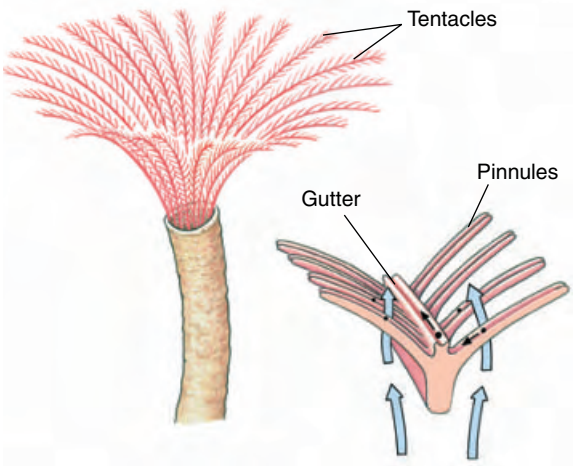
Drifting microscopic particles are found in the upper hundred meters of the ocean. Most of this multitude is **plankton,** organisms too small to do anything but drift with the ocean's currents. The rest is organic debris, the disintegrating remains of dead plants and animals. Although this oceanic swarm of plankton forms a rich life domain, it is unevenly distributed. The heaviest plankton growth occurs in estuaries and areas of upwelling, where there is an abundant nutrient supply. It is consumed by numerous larger animals, invertebrates and vertebrates, using a variety of feeding mechanisms.

One of the most important and widely employed methods for feeding is **suspension feeding** (Figure 34-1). The majority of suspension feeders use ciliated surfaces to produce currents that draw drifting food particles into their mouths. Most suspension-feeding invertebrates, such as tube-dwelling polychaete worms, bivalve molluscs, hemichordates, and most protochordates, entrap particulate food on mucous sheets that convey the food into the digestive tract. Others, such as fairy shrimps, water fleas, and barnacles, use sweeping movements of their setae-fringed legs to create water currents and entrap food, which is transferred to the mouth. In freshwater developmental stages of certain insect orders, the organisms use fanlike arrangements of setae or spin silk nets to entrap food.

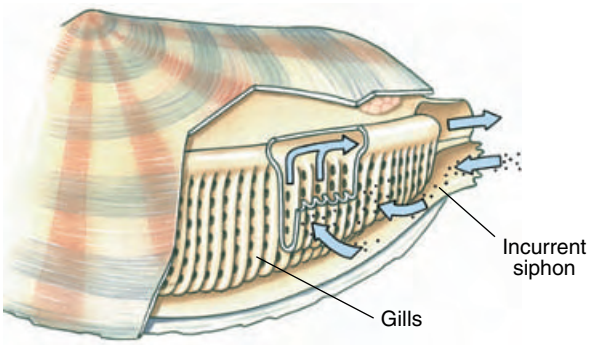
One form of suspension feeding, often called **filter feeding,** has evolved frequently as a secondary modification among representatives of groups that are primarily selective feeders. Examples are many of the microcrustaceans, fishes such as herring, menhaden, and basking sharks, certain birds such as flamingos, and the largest of all animals, baleen (whalebone) whales. The vital importance of one component of plankton, the diatoms, in supporting a great pyramid of suspension-feeding animals is stressed by N. J. Berrill:*

> A humpback whale . . . needs a ton of herring in its stomach to feel comfortably full—as many as five thousand individual fish. Each herring, in turn, may well have 6000 or 7000 small crustaceans in its own stomach, each of which contains as many as 130,000 diatoms. In other words, some 400 billion yellow-green diatoms sustain a single medium-sized whale for a few hours at most.

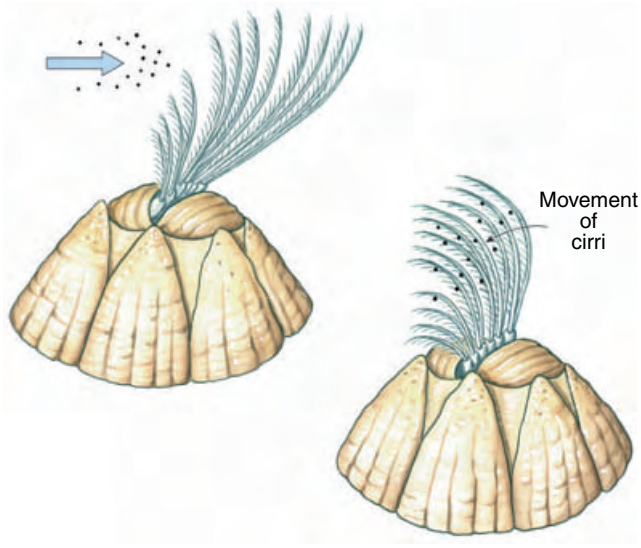
*Berrill, N. J. 1958. You and the universe. New York, Dodd, Mead & Co.



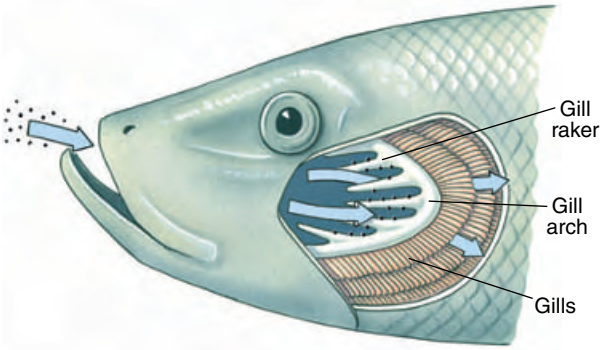
A, Marine fan worms (class Polychaeta, phylum Annelida) have a crown of tentacles. Numerous cilia on the edges of the tentacles draw water (*solid arrows*) between pinnules where food particles are entrapped in mucus; particles are then carried down a "gutter" in the center of the tentacle to the mouth (*broken arrows*).



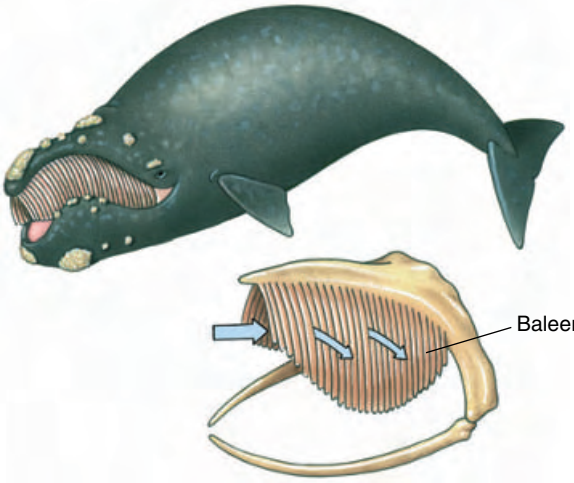
B, Bivalve molluscs (class Bivalvia, phylum Mollusca) use their gills as feeding devices, as well as for respiration. Water currents created by cilia on the gills carry food particles into the current siphon and between slits in the gills where they are entangled in a mucous sheet covering the gill surface. Ciliated food grooves then transport the particles to the mouth (not shown). Arrows indicate direction of water movement.



C, Barnacles sweep their thoracic appendages (cirri) through the water to trap plankton and other organic particles on fine bristles that fringe the cirri. Food is transferred to the barnacle's mouth by the first, short cirri. Class Malacostraca, subphylum Crustacea, phylum Arthropoda.



D, Herring and other suspension-feeding fishes (class Osteichthyes, phylum Chordata) use gill rakers that project forward from the gill arches into the pharyngeal cavity to strain plankton. Herring swim almost constantly, forcing water and suspended food into the mouth; food is strained out by the gill rakers, and the water passes through the gill openings.



E, Whalebone whales (class Mammalia, phylum Chordata) filter out plankton, principally large crustaceans called krill, with whalebone, or baleen. Water enters the swimming whale's open mouth by the force of the animal's forward motion and is strained out through the more than 300 horny baleen plates that hang like a curtain from the roof of the mouth. Krill and other plankton caught in the baleen are periodically collected by the huge tongue and swallowed.

Figure 34-1
Some suspension feeders and their feeding mechanisms.

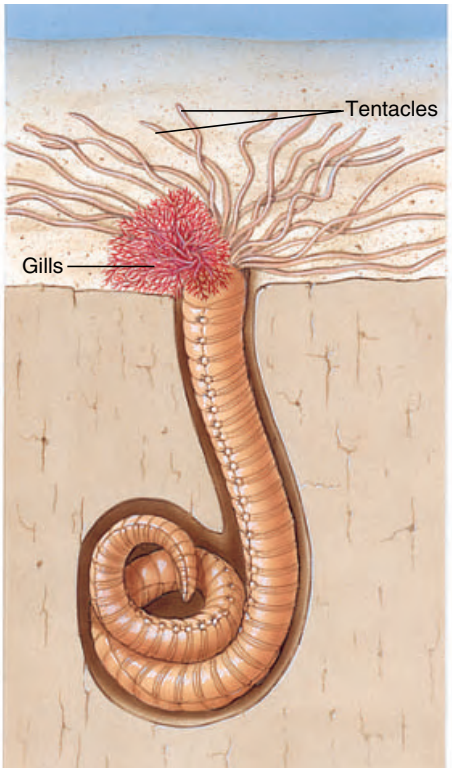


Figure 34-2
The annelid *Amphitrite* is a deposit feeder that lives in a mucus-lined burrow and extends long feeding tentacles in all directions across the surface. Food trapped on mucus is conveyed along the tentacles to the mouth.

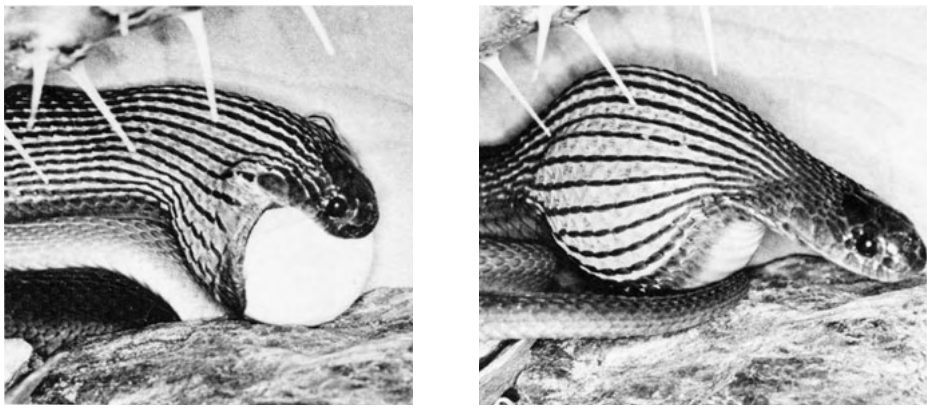


Figure 34-3
This African egg-eating snake, *Dasypeltis,* subsists entirely on hard-shelled birds' eggs, which it swallows whole. Its special adaptations are reduced size and number of teeth, enormously expansible jaw provided with elastic ligaments, and teethlike vertebral spurs that puncture the shell. Shortly after the second photograph was taken, the snake punctured and collapsed the egg, swallowed its contents, and regurgitated the crushed shell.

Another type of particulate feeding exploits deposits of disintegrated organic material (detritus) that accumulates on and in the substratum; this type is called **deposit feeding.** Some deposit feeders, such as many annelids and some hemichordates, simply pass the substrate through their bodies, removing from it whatever provides nourishment. Others, such as scaphopod molluscs, certain bivalve molluscs, and some sedentary and tube-dwelling polychaete worms, use appendages to gather organic deposits some distance from the body and move them toward the mouth (Figure 34-2).

Feeding on Food Masses

Among the most interesting animal adaptations are those that have evolved for procuring and manipulating solid food. Such adaptations and the animals bearing them are largely shaped by what the animal eats.

Predators must be able to locate, capture, hold, and swallow prey. Most carnivorous animals simply seize food and swallow it intact, although some employ toxins that paralyze or kill prey at time of capture. Although no true teeth appear among invertebrates, many have beaks or toothlike structures for biting and holding. A familiar example is the carnivorous polychaete *Nereis,* which possesses a muscular pharynx armed with chitinous jaws that can be everted with great speed to seize prey (Figure 17-3A, p. 360). Once a capture is made, the pharynx is retracted and the prey swallowed. Fish, amphibians, and reptiles use their teeth principally to grip the prey and prevent its escape until they can swallow it whole. Snakes and some fishes can swallow enormous meals. Gripping of prey, together with absence of limbs, is associated with some striking feeding adaptations in these groups: recurved teeth for seizing and holding prey and distensible jaws and stomachs to accommodate their large and infrequent meals (Figure 34-3). Birds lack teeth, but their bills are often provided with serrated edges or the upper bill is hooked for seizing and tearing prey (see Figure 29-11, p. 592).

Many invertebrates are able to reduce food size by shredding devices (such as the shredding mouthparts of many crustaceans) or by tearing devices (such as the beaklike jaws of the cephalopod molluscs). Insects have three pairs of appendages on their heads that serve variously as jaws, chitinous teeth, chisels, tongues, or sucking tubes. Usually the first pair serves as crushing teeth; the second as grasping jaws; and the third, as a probing and tasting tongue.

True mastication, the chewing of food as opposed to tearing or crushing, is found only among mammals. Mammals usually have four different types of teeth, each adapted for specific functions. **Incisors** are designed for biting, cutting, and stripping; **canines** are for seizing, piercing and tearing; **premolars** and **molars,** at the back of the jaw, are for grinding and crushing (Figure 34-4). This basic pattern is often greatly modified in animals having specialized food habits (Figure 34-5; see also Figure 30-10, p. 618). Herbivores have suppressed canines but well-developed molars with enamel ridges for grinding. The well-developed, self-sharpening incisors of rodents grow throughout life and must be worn away by gnawing to keep pace with growth. Some teeth have become so highly modified that they are no longer useful for biting or chewing food. An elephant's tusk (Figure 34-6) is a modified upper incisor used for defense, attack, and rooting,

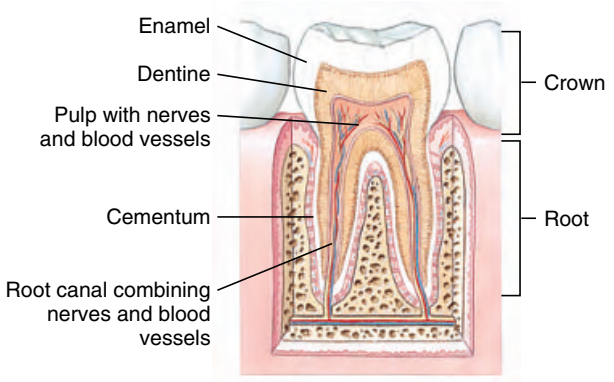


Figure 34-4
Structure of human molar tooth. The tooth is built of three layers of calcified tissue covering: enamel, which is 98% mineral and the hardest material in the body; dentine, which composes the mass of the tooth and is approximately 75% mineral; and cementum, which forms a thin covering over the dentine in the root of the tooth and is very similar to dense bone in composition. The pulp cavity contains loose connective tissue, blood vessels, nerves, and tooth-building cells.

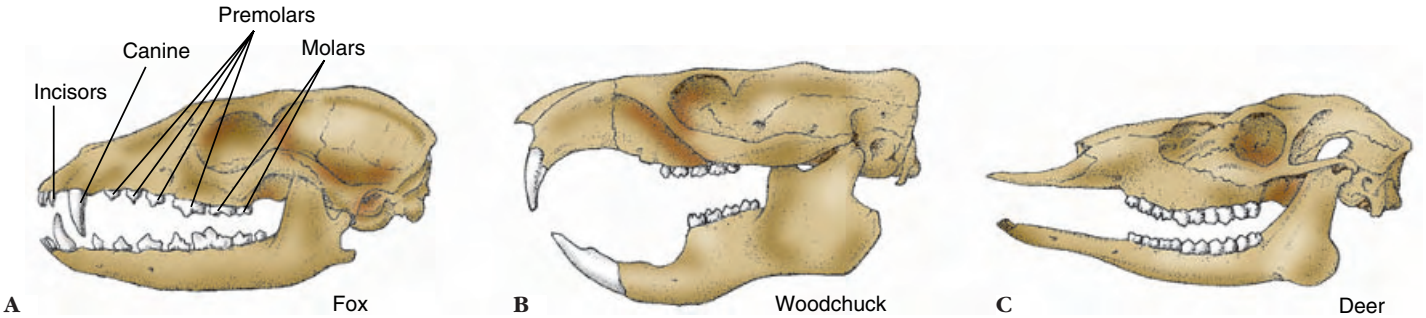


Figure 34-5
Mammalian dentition. **A,** Teeth of gray fox, a carnivore, showing the four types of teeth; **B,** Woodchuck, a rodent, has chisel-like incisors that continue to grow throughout life to replace wear; **C,** White-tailed deer, a browsing ungulate, with flat molars bearing complex ridges suited for grinding.

and the male wild boar has modified canines that are used as weapons. Many feeding specializations of mammals are described on pp. 618–621.

Herbivorous, or plant-eating, animals have evolved special devices for crushing and cutting plant material. Some invertebrates have scraping mouthparts, such as the radula of snails (Figure 16-3, p. 328). Insects such as locusts have grinding and cutting mandibles; herbivorous mammals such as horses and cattle use wide, corrugated molars for grinding. All these mechanisms disrupt the tough cellulose cell wall to accelerate its digestion by intestinal microorganisms, as well as to release cell contents for direct enzymatic breakdown. Thus herbivores are able to digest food that carnivores cannot, and in doing so, convert plant material into protein for consumption by carnivores and omnivores.

Feeding on Fluids

Fluid feeding is especially characteristic of parasites, but it is practiced among many free-living forms as well. Some internal parasites (endoparasites) simply absorb the nutrient surrounding them, unwittingly provided by the host. Others bite and rasp host tissue, suck blood, and feed on the contents of the host's intestine. External parasites (ectoparasites) such as leeches, lampreys, parasitic crustaceans, and insects use a variety of efficient piercing and sucking mouthparts to feed on blood or other body fluid. There are numerous arthropods that feed on fluids, for example, fleas, mosquitoes, sucking lice, bedbugs, ticks and mites, to name some of the more troublesome that assault humans as well as other vertebrate hosts. Many are vectors of serious diseases of humankind and thus qualify as far more than pesky annoyances.

Unfortunately for humans and other warm-blooded animals, the ubiquitous mosquito excels in its blood-sucking habit. Alighting gently, the mosquito sets about puncturing its prey with an array of six needlelike mouthparts (Figure 20-18B, p. 422). One of these is used to inject an anticoagulant saliva (responsible for the irritating itch that follows the "bite" and serving as a vector for microorganisms causing malaria, yellow fever, encephalitis, and other diseases); another mouthpart is a channel through which the blood is sucked. It is of little comfort that only the female dines on blood to obtain nutrients necessary for formation of her eggs.

Digestion

In the process of digestion, which means literally "carrying asunder," organic foods are mechanically and chemically broken into small units for absorption. Although food solids consist principally of carbohydrates, proteins, and fats, the very components

Figure 34-6
An African elephant loosening soil from a salt lick with its tusk. Elephants use their powerful modified incisors in many ways in the search for food and water: plowing the ground for roots, prying apart branches to reach the edible cambium, and drilling into dry riverbeds for water.

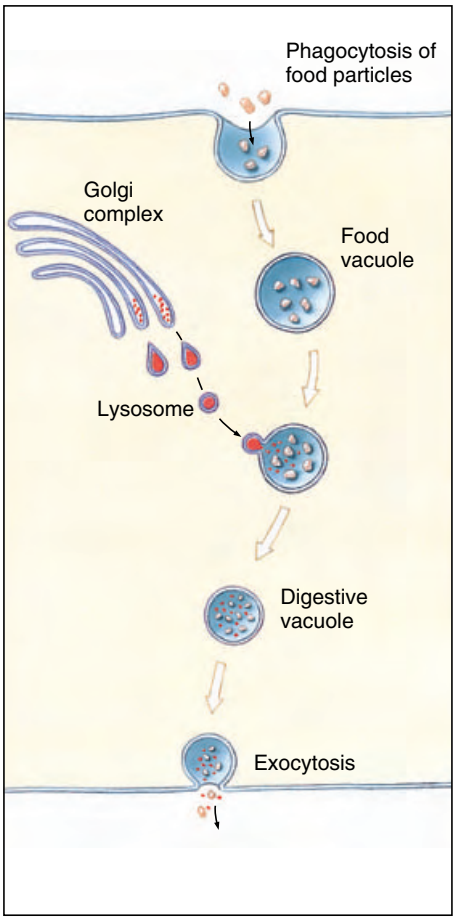


Figure 34-7
Intracellular digestion. Lysosomes containing digestive enzymes (lysozymes) are produced within the cell, possibly by the Golgi complex. Lysosomes fuse with food vacuoles and release enzymes that digest the enclosed food. Usable products of digestion are absorbed into the cytoplasm, and indigestible wastes are expelled.

that make up the body of the consumer, these components must first be reduced to their simplest molecular units and dissolved before they can be assimilated. Each animal reassembles some of these digested and absorbed units into organic compounds of the animal's own unique pattern. Cannibalism confers no special metabolic benefit; victims of an animal's own kind are digested just as thoroughly as food composed of another species.

In protozoa and sponges digestion is entirely **intracellular** (Figure 34-7). A food particle is enclosed within a food vacuole by phagocytosis (see p. 50). Digestive enzymes are added and the products of digestion, the simple sugars, amino acids, and other molecules, are absorbed into the cell cytoplasm where they may be used directly or, in the case of multicellular animals, may be transferred to other cells. Food wastes are simply extruded from the cell.

There are important limitations to intracellular digestion. Only particles small enough to be phagocytized can be accepted, and every cell must be capable of secreting all of the necessary enzymes, and of absorbing the products into the cytoplasm. These limitations were resolved with the evolution of an **alimentary system** in which **extracellular** digestion of large food masses could take place. In extracellular digestion certain cells lining the **lumen** (cavity) of the alimentary canal specialize in forming various digestive secretions, whereas other function largely, or entirely, in absorption. Many simpler metazoans, such as radiates, turbellarian flatworms, and ribbon worms (nemerteans), practice both intracellular and extracellular digestion. With evolution of greater complexity and appearance of complete mouth-to-anus alimentary systems, extracellular digestion became emphasized, together with increasing regional specialization of the digestive tract. For arthropods and vertebrates, digestion is almost entirely extracellular. Ingested food is exposed to various mechanical, chemical, and bacterial treatments, to different acidic and alkaline phases, and to digestive juices that are added at appropriate stages as the food passes through the alimentary canal.

Action of Digestive Enzymes

Mechanical processes of cutting and grinding by teeth and muscular mixing by the intestinal tract are important in digestion. However, reduction of foods to small, absorbable units relies principally on chemical breakdown by **enzymes**, discussed in Chapter 4 (p. 59-62). Digestive enzymes are **hydrolytic** enzymes, or **hydrolases**, so called because food molecules are split by the process of **hydrolysis**, breaking of a chemical bond by adding the components of water across it:

$$R{-}R + H_2O \xrightarrow[\text{enzyme}]{\text{digestive}} R{-}OH + H{-}R$$

In this general enzymatic reaction, R—R represents a food molecule that is split into two products, R—OH and R—H. Usually these reaction products must in turn be split repeatedly before the original molecule is reduced to its numerous subunits. Proteins, for example, are composed of hundreds, or even thousands, of interlinked amino acids, which must be completely separated before the individual amino acids can be absorbed. Similarly, carbohydrates must be reduced to simple sugars. Fats (lipids) are reduced to molecules of glycerol, fatty acids, and monoglycerides, although some fats, unlike proteins and carbohydrates, may be absorbed without first being completely hydrolyzed. There are specific enzymes for each class of organic compounds. These enzymes are located in specific regions of the alimentary canal in an "enzyme chain," in which one enzyme may complete what another has started. The product then moves posteriorly for still further hydrolysis.

Motility in the Alimentary Canal

Food is moved through the digestive tract by **cilia** or by specialized **musculature,** and often by both. Movement is usually by cilia in the acoelomate and pseudocoelomate metazoa that lack the mesodermally derived gut musculature of true coelomates. Cilia move intestinal fluids and materials also in some eucoelomates, such as most molluscs, in which the coelom is weakly developed. In animals with well-developed coeloms, the gut is usually lined with two opposing layers of smooth muscle: a longitudinal layer, in which the smooth muscle fibers run parallel with the length of the gut, and a circular layer, in which the muscle fibers embrace the circumference of the gut. The most characteristic gut movement is **segmentation,** the alternate constriction of rings of smooth muscle of the intestine that constantly divide and squeeze the contents back and forth (Figure 34-8A). Walter B. Cannon of homeostasis fame (p. 664), while still a medical student at Harvard in 1900, was the first to use X rays to watch segmentation in experimental animals that had been fed suspensions of barium sulfate. Segmentation serves to mix food but does not move it through the gut. Another kind of muscular action, called **peristalsis,** sweeps the food down the gut with waves of contraction of circular muscle (Figure 34-8B).

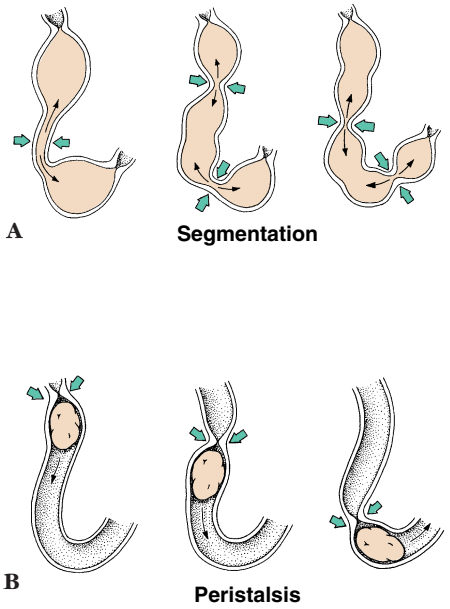


Figure 34-8
Movement of intestinal contents by segmentation and peristalsis. **A,** Segmentational movements of food showing how constrictions squeeze the food back and forth, mixing it with enzymes. The sequential mixing movements occur at about 1-second intervals. **B,** Peristaltic movement, showing how food is propelled forward by a traveling wave of contraction.

Organization and Regional Function of the Alimentary Canal

The metazoan alimentary canal can be divided into five major regions: (1) reception, (2) conduction and storage, (3) grinding and early digestion, (4) terminal digestion and absorption, and (5) water absorption and concentration of solids. Food progresses from one region to the next, allowing digestion to proceed in sequential stages (Figures 34-9 and 34-10).

Receiving Region

The first region of the alimentary canal consists of devices for feeding and swallowing. These include **mouthparts** (for example, mandibles, jaws, teeth, radula, bills), **buccal cavity** and muscular **pharynx.** Most metazoans other than suspension feeders have **salivary glands** (buccal glands) that produce lubricating secretions containing mucus to assist swallowing (Figure 34-9). Salivary glands often have other specialized functions such as secretion of toxic enzymes for quieting struggling prey and secretion of salivary enzymes to begin digestion. The salivary secretion of the leech, for example, is a complex mixture containing an anesthetic substance (making its bite nearly painless) and several en-zymes that prevent blood coagulation and increase blood flow by dilating veins and dissolving the tissue cement that binds cells together.

Salivary **amylase** is a carbohydrate-splitting enzyme that begins hydrolysis of plant and animal starches. It is found only in certain herbivorous molluscs, some insects, and in primate mammals, including humans. Starches are long polymers of glucose. Salivary amylase does not completely hydrolyze starch, but breaks it down mostly into two-glucose fragments called **maltose.** Some free glucose and longer fragments of starch are also produced. When the food mass (bolus) is swallowed, salivary amylase continues to act for some time, digesting perhaps half of the starch before the enzyme is inactivated by the acidic environment of the stomach. Further starch digestion resumes beyond the stomach in the intestine.

The tongue is a vertebrate innovation, usually attached to the floor of the mouth, that assists in food manipulation and swallowing. It may be used for other purposes, however, such as food capture (for example, chameleons, woodpeckers, anteaters) or as an olfactory sensor (many lizards and snakes).

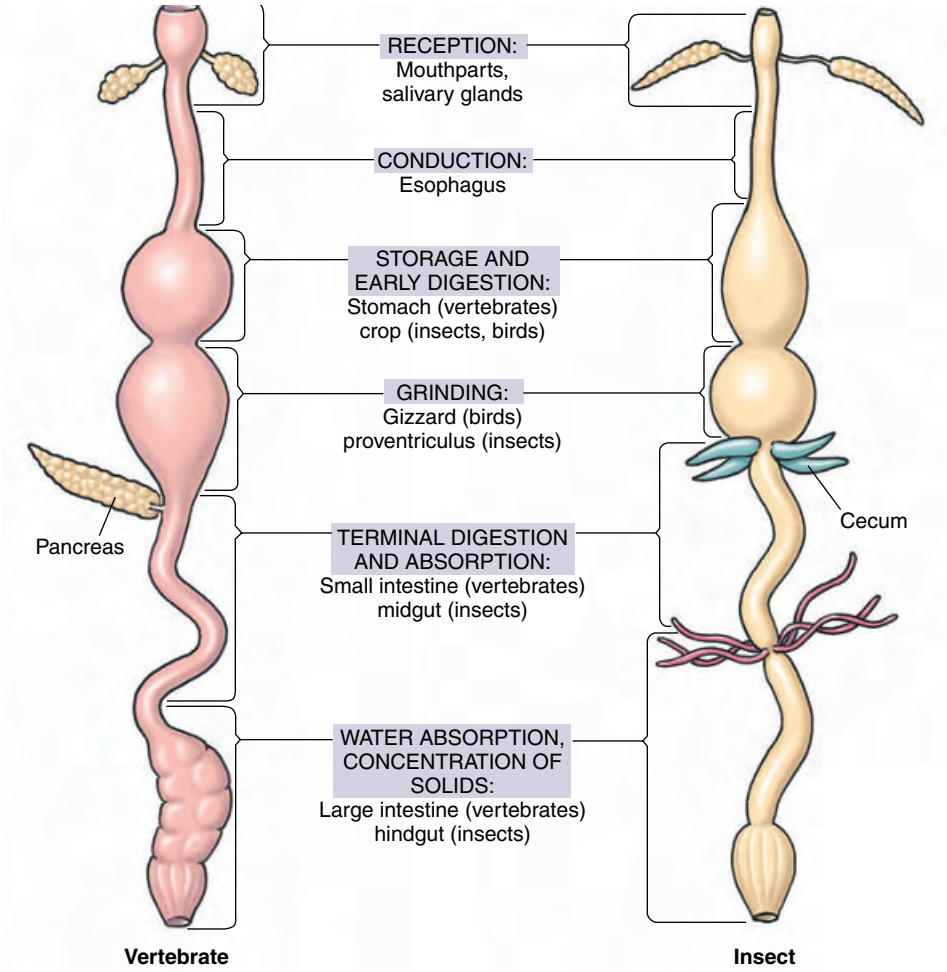


Figure 34-9

Generalized digestive tracts of a vertebrate and an insect, showing the major functional regions of the metazoan digestive system.

In humans, swallowing begins with the tongue pushing moistened food toward the pharynx. The nasal cavity closes reflexively by raising the soft palate. As the food slides into the pharynx, the epiglottis tips down over the trachea, nearly closing it (Figure 34-10). Some particles of food may enter the opening of the trachea but contraction of laryngeal muscles prevents it from going farther. Once food is in the esophagus, peristaltic contraction of esophageal muscles forces it smoothly toward the stomach.

Conduction and Storage Region

The **esophagus** of vertebrates and many invertebrates serves to transfer food to the digestive region. In many invertebrates (annelids, insects, octopods) the esophagus is expanded into a **crop** (Figure 34-9), used for food storage before digestion. Among vertebrates, only birds have a crop. This crop serves to store and soften food (grain, for example) before it passes to the stomach, or to allow mild fermentation of food before it is regurgitated to feed nestlings.

Region of Grinding and Early Digestion

In most vertebrates, and in some invertebrates, the **stomach** provides initial digestion as well as storage and mixing of food with digestive juices. Mechanical breakdown of food, especially plant food with its tough cellulose cell walls, often continues in herbivorous animals by grinding and crushing devices in the stomach. The muscular **gizzard** of terrestrial oligochaete worms and birds is assisted by stones and grit swallowed along with food or, in arthropods, by hardened linings (for example, chitinous teeth of the insect proventriculus [Figure 34-9], and calcareous teeth of the gastric mill of crustaceans).

Digestive diverticula—blind tubules or pouches arising from the main passage—often supplement the stomach of many invertebrates. They are usually lined with a multipurpose epithelium having cells specialized for secreting mucus or digestive enzymes, or absorption or storage. Examples include the ceca of polychaete annelids, digestive glands of bivalve molluscs, hepatopancreas of crustaceans, and pyloric ceca of sea stars.

Herbivorous vertebrates have evolved several strategies for exploiting cellulose-splitting microorganisms to derive maximal nutrition from plant food. Despite its abundance on earth, the woody cellulose that encloses plant cells can be broken down only by an enzyme, **cellulase,** that has limited distribution in the living world. No metazoan animals can produce intestinal cellulase for the direct digestion of cellulose. However many herbivorous metazoans harbor microorganisms (bacteria and protozoa) in their gut that do produce cellulase. These microorganisms ferment cellulose under the anaerobic conditions of the gut, producing fatty acids and sugars that the herbivore can use. While the ultimate fermentation machine is the multichambered stomach of the cud-chewing ruminants described on p. 620, many other animals harbor microorganisms in other parts of the gut, such as the intestine proper or the cecum.

The stomach of carnivorous and omnivorous vertebrates is typically a U-shaped muscular tube provided with glands that produce proteolytic enzymes and strong acids, the latter an adaptation that probably arose for killing prey and halting bacterial activity. When food arrives at the stomach,

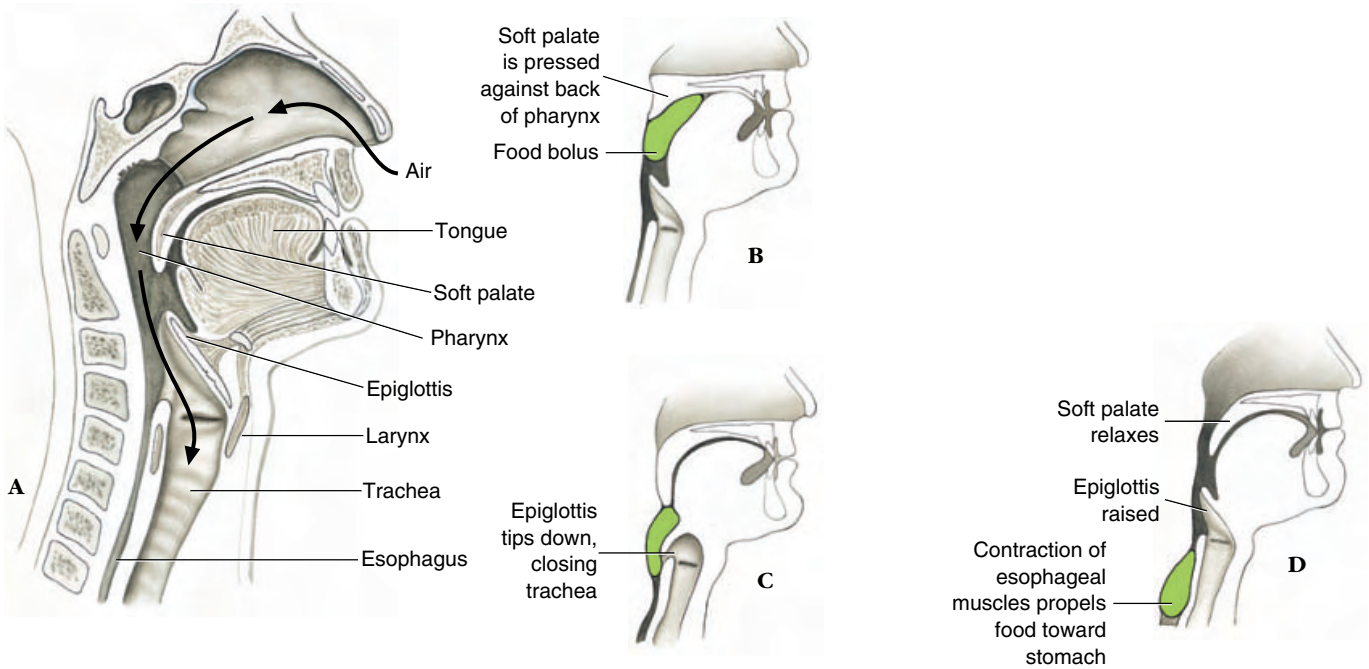


Figure 34-10
Oral cavity and throat in humans in sagittal section **(A),** and sequence of swallowing **(B** to **D).**

the **cardiac sphincter** opens reflexively to allow the food to enter, then closes to prevent regurgitation back into the esophagus. In humans, gentle peristaltic waves pass over the filled stomach at the rate of approximately three each minute. Churning is most vigorous at the intestinal end where food is steadily released into the **duodenum,** first region of the small intestine. A **pyloric sphincter** regulates the flow of food into the intestine and prevents regurgitation in the stomach. Deep tubular glands in the stomach wall secrete **gastric juice,** in humans approximately 2 liters each day. Two types of cells line these glands: **chief cells,** which secrete **pepsin,** and **parietal cells,** which secrete **hydrochloric acid.** Pepsin is a **protease** (protein-splitting enzyme) that acts only in an acid medium (pH 1.6 to 2.4). This highly specific enzyme splits large proteins by preferentially breaking down certain peptide bonds scattered along the peptide chain of the protein molecule. Although pepsin, because of its specificity, cannot completely degrade proteins, it effectively hydrolyzes them into smaller polypeptides. Other proteases that together can split all peptide bonds complete digestion of protein in the intestine. Pepsin is present in the stomachs of nearly all vertebrates.

That the stomach mucosa is not digested by its own powerful acid secretions results from another gastric secretion, mucin, a highly viscous organic compound that coats and protects the mucosa from both chemical and mechanical injury. We should note that despite the popular misconception that an "acid stomach" is unhealthy, a notion nourished in advertising, stomach acidity is normal and essential. Sometimes, however, the protective mucous coating fails. This failure is often associated with an infection from a bacterium (*Helicobacter pylori*) that secretes toxins causing inflammation of the stomach's lining. This inflammation may lead to a stomach ulcer.

Rennin (not to be confused with renin, an enzyme produced by the kidney, p. 674) is a milk-curdling enzyme found in the stomach of ruminant mammals. It probably occurs in many other mammals. By clotting and precipitating milk proteins, it slows the movement of milk through the stomach. Rennin extracted from stomachs of calves is used in making cheese. Human infants, lacking rennin, digest milk proteins with acidic pepsin, just as adults do.

The secretion of gastric juices is intermittent. Although a small volume of gastric juice is secreted continuously, even during prolonged periods of starvation, secretion normally increases when stimulated by the sight and smell of food, by presence of food in the stomach, and by emotional states such as anxiety and anger.

A most unusual and classic investigation in the field of digestion was made by U.S. Army surgeon William Beaumont during the years 1825 to 1833. His subject was a young, hard-living French-Canadian voyageur named Alexis St. Martin, who in 1822 accidentally shot himself in the abdomen with a musket, the blast "blowing off integuments and muscles of the size of a man's hand, fracturing and carrying away the anterior half of the sixth rib, fracturing the fifth, lacerating the lower portion of the left lobe of the lungs, the diaphragm, and perforating the stomach." Miraculously the wound healed, but a permanent opening, or fistula, formed that permitted Beaumont to see directly into the stomach

Figure 34-11
Dr. William Beaumont at Fort Mackinac, Michigan Territory, collecting gastric juice from Alexis St. Martin.

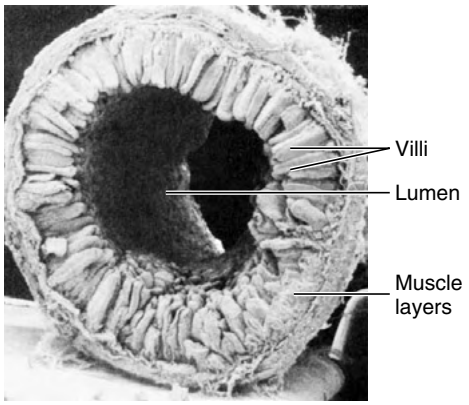


Figure 34-12
Scanning electron micrograph of a rat intestine showing the numerous fingerlike villi that project into the lumen and vastly increase the effective absorptive and secretory surface of the intestine. (×21)

(Figure 34-11). St. Martin became a permanent, although temperamental, patient in Beaumont's care, which included food and housing. Over a period of 8 years, Beaumont was able to observe and record how the lining of the stomach changed under different psychological and physiological conditions, how foods changed during digestion, the effect of emotional states on stomach motility, and many other facts about the digestive process of his famous patient.

Region of Terminal Digestion and Absorption: The Intestine

The importance of the intestine varies widely among animal groups. In invertebrates that have extensive digestive diverticula in which food is broken down and phagocytized, the intestine may serve only as a pathway for conducting wastes out of the body. In other invertebrates with simple stomachs, and in all vertebrates, the intestine is equipped for both digestion and absorption.

Devices for increasing the internal surface area of the intestine are highly developed in vertebrates, but are generally absent among invertebrates. Perhaps the most direct way to increase the absorptive surface of the gut is to increase its length. Coiling of the intestine is common among all vertebrate groups and reaches its highest development in mammals, in which the length of the intestine may exceed eight times the length of the body. Although a coiled intestine is rare among invertebrates, other strategies for increasing surface sometimes occur. For example, the **typhlosole** of terrestrial oligochaete worms (see Figure 17-12, p. 364), an inward folding of the dorsal intestinal wall that runs the full length of the intestine, effectively increases internal surface area of the gut in a narrow body lacking space for a coiled intestine.

Lampreys and sharks have longitudinal or spiral folds in their intestine. Other vertebrates have developed elaborate folds (amphibians and reptiles) and minute fingerlike projections called **villi** (birds and mammals), which give the inner surface of fresh intestinal tissue the appearance of velvet (Figure 34-12). The electron microscope reveals that each cell lining the intestinal cavity additionally is bordered by hundreds of short, delicate processes called **microvilli** (Figure 34-13C and D). These processes, together with larger villi and intestinal folds, may increase the internal surface area of the intestine more than a million times as compared to a smooth cylinder of the same diameter. This elaborate surface greatly facilitates the absorption of food molecules.

Digestion in the Vertebrate Small Intestine

Food is released into the small intestine through the **pyloric sphincter,** which relaxes at intervals to allow entry of acidic stomach contents into the initial segment of the small intestine, the **duodenum.** Two secretions pour into this region: **pancreatic juice** and **bile** (Figure 34-14). Both of these secretions have a high bicarbonate content, especially pancreatic juice, which effectively neutralizes gastric acid, raising the pH of the liquefied food mass, now called **chyme,** from 1.5 to 7 as it enters the duodenum. This change in pH is essential because all intestinal enzymes are effective only in a neutral or slightly alkaline medium.

Cells of the intestinal mucosa, like those of the stomach mucosa, are subjected to considerable wear and are constantly undergoing replacement. Cells deep in the crypt between adjacent villi divide rapidly and migrate up the villus. In mammals the cells reach the tip of the villus in about two

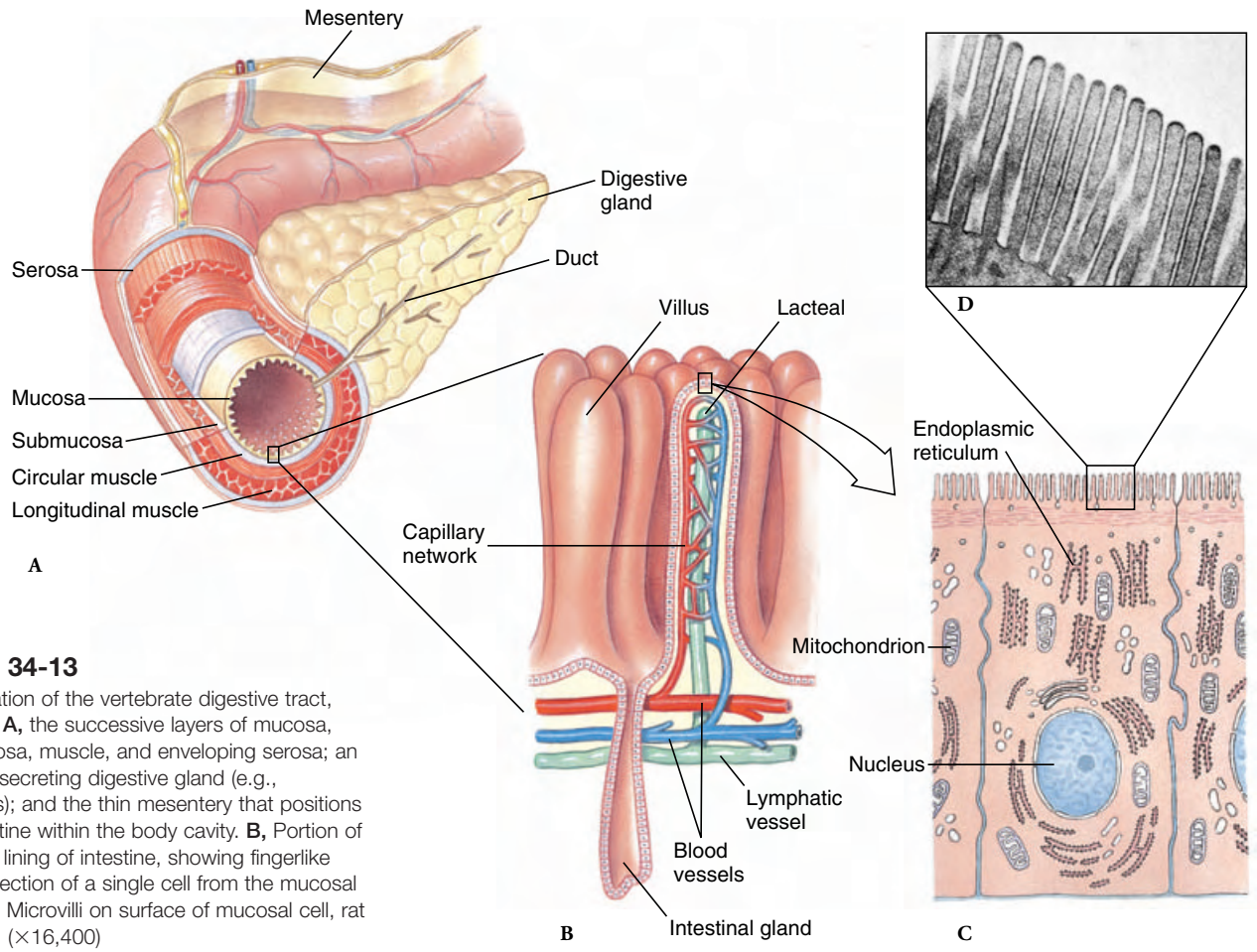
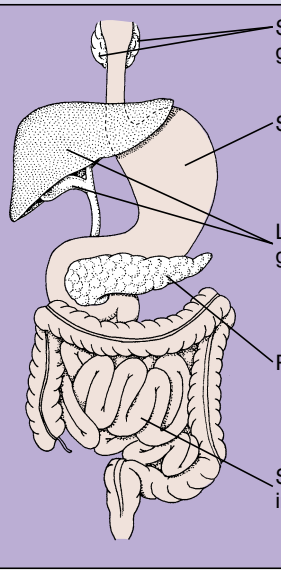


Figure 34-13
Organization of the vertebrate digestive tract, showing **A,** the successive layers of mucosa, submucosa, muscle, and enveloping serosa; an enzyme-secreting digestive gland (e.g., pancreas); and the thin mesentery that positions the intestine within the body cavity. **B,** Portion of mucosal lining of intestine, showing fingerlike villi. **C,** Section of a single cell from the mucosal lining. **D,** Microvilli on surface of mucosal cell, rat intestine. (×16,400)

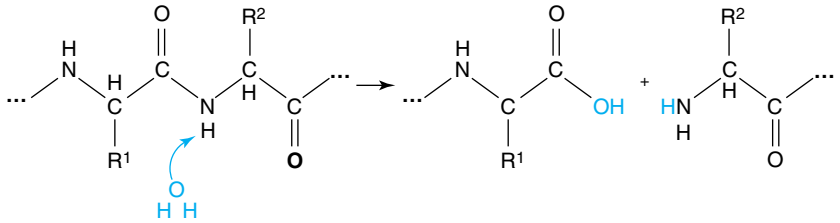


REGION	SECRETION	pH	COMPOSITION
	Saliva	6.5	Amylase Bicarbonate
	Gastric juice	1.5	Pepsin HCl Rennin in ruminant mammals
	Bile	7–8	Bile salts and pigments Cholesterol
	Pancreatic juice	7–8	Trypsin, Chymotrypsin, Carboxypeptidase, Lipase, Amylase, Nucleases Bicarbonate
	Membrane enzymes	7–8	Aminopeptidase Maltase Lactase Sucrase Alkaline Phosphatase

Figure 34-14
Secretions of the mammalian alimentary canal with the principal components and the pH of each secretion.

days. There they are shed, along with their membrane enzymes, into the lumen at the rate of some 17 billion a day along the length of the human intestine. Before they are shed, however, these cells differentiate into absorptive cells that transport nutrients into the network of blood and lymph vessels, once digestion is complete.

Pancreatic Enzymes The pancreatic secretion of vertebrates contains several enzymes of major importance in digestion (Figure 34-14). Two powerful proteases, **trypsin** and **chymotrypsin,** continue enzymatic digestion of proteins begun by pepsin, which is now inactivated by the alkalinity of the intestine. Trypsin and chymotrypsin, like pepsin, are highly specific proteases that split apart peptide bonds deep inside the protein molecule. The hydrolysis of a peptide linkage may be shown as:



Pancreatic juice also contains **carboxypeptidase,** which removes amino acids from the carboxyl ends of polypeptides; **pancreatic lipase,** which hydrolyzes fats into fatty acids and glycerol; **pancreatic amylase,** a starch-splitting enzyme identical to salivary amylase in its action; and **nucleases,** which degrade RNA and DNA to nucleotides.

Membrane Enzymes The cells lining the intestine have digestive enzymes embedded in their surface membrane that continue digestion of carbohydrates, proteins, and phosphate compounds (Figure 34-14). These enzymes of the microvillus membrane (Figure 34-13D) include **aminopeptidase** that splits terminal amino acids from the amino end of short peptides, and several **disaccharidases,** enzymes that split 12-carbon sugar molecules into 6-carbon units. The disaccharidases include **maltase,** which splits maltose into two molecules of glucose; **sucrase,** which splits sucrose to fructose and glucose; and **lactase,** which breaks lactose (milk sugar) into glucose and galactose. Also present is **alkaline phosphatase,** an enzyme that attacks a variety of phosphate compounds.

Although milk is the universal food of newborn mammals and one of the most complete human foods, many adult humans cannot digest milk because they are deficient in lactase, the enzyme that hydrolyzes lactose (milk sugar). Lactose intolerance is genetically determined. It is characterized by abdominal bloating, cramps, flatulence, and watery diarrhea, all appearing within 30 to 90 minutes after ingesting milk or its unfermented by-products. (Fermented dairy products, such as yogurt and cheese, create no intolerance problems.)

Northern Europeans and their descendants, which include the majority of North American whites, are most tolerant of milk. Many other ethnic groups are generally intolerant to lactose, including the Japanese, Chinese, Jews in Israel, Eskimos, South American Indians, and most African blacks. Only about 30% of North American blacks are tolerant; those who are tolerant are mostly descendants of slaves brought from east and central Africa where dairying is traditional and tolerance to lactose is high.

Bile The liver secretes bile into the **bile duct,** which drains into the upper intestine (duodenum). Between meals bile collects in the **gallbladder,** an expansible storage sac that releases bile when stimulated by the presence of fatty food in the duodenum. Bile contains water, bile salts, and pigments, but no enzymes. **Bile salts** (mainly sodium taurocholate and sodium glycocholate) are essential for digestion of fats. Fats, because of their tendency to remain in large, water-insoluble globules, are especially resistant to enzymatic digestion. Bile salts reduce surface tension of fat globules, allowing the churning action of the intestine to break fats into tiny droplets (emulsification). With total surface exposure of fat particles greatly increased, fat-splitting lipases are able to reach and hydrolyze the triglyceride molecules. The yellow-green color of bile is produced by **bile pigments,** breakdown products of hemoglobin from worn-out red blood cells. Bile pigments also give the feces its characteristic color.

Bile production is only one of the liver's many functions. This highly versatile organ is a storehouse for glycogen, production center for plasma proteins, site of protein synthesis and detoxification of protein wastes, site for destruction of worn-out red blood cells, and center for metabolism of fat, amino acids, and carbohydrates.

Absorption

Little food is absorbed in the stomach because digestion is still incomplete and because of limited absorptive surface area. However, some materials, such as drugs and alcohol, are absorbed mostly there, which contributes to their rapid action. Most digested food is absorbed from the small intestine where the numerous finger-shaped villi provide an enormous surface area through which materials can pass from the intestinal lumen into the circulation.

Carbohydrates are absorbed almost exclusively as simple sugars (monosaccharides, for example, glucose, fructose, and galactose) because the intestine is virtually impermeable to polysaccharides. Proteins are absorbed principally as their amino acid subunits, although a limited amount of small proteins or peptide fragments sometimes may be absorbed. Both active and passive processes transfer simple sugars and amino acids across the intestinal epithelium.

Immediately after a meal these materials are in such high concentration in the gut that they readily diffuse into the blood, where their concentration is initially lower. However, if absorption were passive only, we would expect transfer to cease as soon as concentrations of a substance became equal on both sides of the intestinal epithelium. Passive transfer alone would permit valuable nutrients to be lost in the feces. In fact, very little is lost because passive transfer is supplemented by an **active transport** mechanism located in the epithelial cells that transfers food molecules into the blood. Materials thus are moved *against* their concentration gradient, a process requiring expenditure of energy. Although not all food products are actively transported, those that are, such as glucose, galactose, and most amino acids, are handled by transport mechanisms that are specific for each kind of molecule.

As mentioned previously, fat droplets are emulsified by bile salts and then digested by pancreatic lipase. Triglycerides are broken into fatty acids and monoglycerides, which complex with bile salts to form minute droplets called **micelles.** When micelles contact the microvilli of the intestinal epithelium, the fatty acids and monoglycerides are absorbed by simple diffusion. They then enter the endoplasmic reticulum of the absorptive cells, where they are resynthesized into triglycerides before passing into **lacteals** (Figure 34-13B). From the lacteals, fat droplets enter the lymph system (Figure 33-18, p. 696) and eventually pass into the blood circulation through the thoracic duct. After a fatty meal, even a peanut butter sandwich, the presence of numerous fat droplets in the blood imparts a milky appearance to the blood plasma.

Region of Water Absorption and Concentration of Solids

The large intestine consolidates the indigestible remnants of digestion by reabsorption of water to form solid or semisolid feces for removal from the body by **defecation.** Reabsorption of water is of special significance in insects, especially those living in dry environments, which must (and do) conserve nearly all water entering the rectum. Specialized **rectal glands** absorb water and ions as needed, leaving behind fecal pellets that are almost completely dry. In reptiles and birds, which also produce nearly dry feces, most of the water is reabsorbed in the cloaca. A white pastelike feces is formed containing both indigestible food wastes and uric acid.

The colon of humans contains enormous numbers of bacteria, which first enter the sterile colon of the newborn infant with its food. In adults approximately one-third of the dry weight of feces is bacteria; these include harmless bacteria as well as bacteria that can cause serious illness should they escape into the abdomen or bloodstream. Normally the body's defenses prevent invasion of such bacteria. Bacteria degrade organic wastes in the feces and provide some nutritional benefit by synthesizing certain vitamins (vitamin K and small quantities of some of the B vitamins), which are absorbed by the body.

Regulation of Food Intake

Most animals unconsciously adjust intake of food to balance energy expenditure. If energy expenditure is increased by greater physical activity, more food is consumed. Most vertebrates, from fish to mammals, eat for calories rather than bulk because, if the diet is diluted with fiber, they respond by eating more. Similarly, intake is adjusted downward following a period of several days when caloric intake is too high.

A **hunger center** located in the hypothalamus of the brain regulates the intake of food. A drop in the blood glucose level stimulates a craving for food. While most animals seem able to stabilize their weight at normal levels with ease, many humans cannot. Obesity is rising throughout the industrial world and is a major health problem in many countries today. According to recent surveys some 60% of the adult population in the United States meets the current definition of clinical obesity. (Assessment of overweight relies on body mass index [weight in kilograms divided by the square of height in meters], waist circumference, and risk factor for diseases associated with obesity.)

It is becoming clear that many obese people do not eat significantly more food than thin people, but rather they have an inherited genetic predisposition to gain weight on a high-fat diet. Many obese people have a reduced capacity to burn excess calories by "nonshivering thermogenesis" (p. 680). Placental mammals are unique in having a dark adipose tissue called **brown fat,** specialized for generation of heat. Newborn mammals, including human infants, have much more brown fat than adults. In human infants brown fat is located in the chest, upper back, and near the kidneys. The abundant mitochondria in brown fat contain a membrane protein called **thermogenin** that acts to uncouple the production of ATP during oxidative phosphorylation (p. 66). In people of average weight, an increased caloric intake induces brown fat to dissipate excess energy as heat through the uncoupling action of thermogenin. We call this process "diet-induced thermogenesis." In many people tending toward obesity, this capacity is diminished.

The body of many mammals contains two kinds of adipose tissue that perform completely different functions. White adipose tissue, which comprises the bulk of body fat, is adapted for the storage of fat derived mainly from surplus fats and carbohydrates in the diet. It is distributed throughout the body, particularly in the deep layers of the skin. Brown adipose tissue is highly specialized for mediating nonshivering thermogenesis rather than for the storage of fat. Brown fat, unique to placental mammals, is especially well developed in hibernating species of bats and rodents, but is present also in many nonhibernating species such as rabbits, artiodactyles, carnivores, and primates (including humans). It is brown because it is packed with mitochondria containing large quantities of iron-bearing cytochrome molecules. In ordinary body cells, ATP is generated by the flow of electrons down the respiratory chain (p. 66). This ATP then powers various cellular processes. In brown fat cells heat is generated instead of ATP. Thermogenesis is activated by the sympathetic nervous system, which responds to signals from the hypothalamus.

There are other reasons for obesity in addition to the fact that many people simply eat too much and get too little exercise. Fat stores are supervised by the hypothalamus, which may be set at a point higher or lower than the norm. A high setting can be lowered somewhat by exercise, but as dieters are painfully aware, the body defends its fat stores with remarkable tenacity. In 1995, a hormone produced by fat cells was discovered that cures obesity in mutant mice lacking the gene that produces the

hormone. The hormone, called **leptin,** appears to operate through a feedback system that tells the hypothalamus how much fat the body carries. If levels are high, release of leptin by fat cells leads to diminished appetite and increased thermogenesis. The discovery of leptin has initiated a flurry of research on obesity and a resurgence of commercial interest in producing a weight-loss drug based on leptin.

Regulation of Digestion

The digestive process is coordinated by a family of hormones (see Chapter 36) produced by the body's most diffuse endocrine tissue, the gastrointestinal tract. These hormones are examples of the many substances produced by the vertebrate body that have hormonal function, yet are not necessarily produced by discrete endocrine glands. Because of their diffuse origins the gastrointestinal (GI) hormones have been difficult to isolate and study and only recently have they been researched in depth.

Among the principal GI hormones are gastrin, cholecystokinin (CCK), and secretin (Figure 34-15). **Gastrin** is a small polypeptide hormone produced by endocrine cells in the pyloric portion of the stomach. Gastrin is secreted in response to stimulation by the parasympathetic nerve endings, and when protein food enters the stomach. Its main actions are to stimulate hydrochloric acid secretion and to increase gastric motility. Gastrin is an unusual hormone in that it exerts its action on the same organ from which it is secreted. **CCK** is also a polypeptide hormone, and it has a striking structural resemblance to gastrin, suggesting that the two arose by duplication of ancestral genes. CCK is secreted by endocrine cells in the walls of the upper small intestine in response to the presence of fatty acids and amino acids in the duodenum. It has at least three distinct functions. It stimulates gallbladder contraction and thus increases the flow of bile salts into the intestine; it stimulates an enzyme-rich secretion from the pancreas; and it acts on the brain to contribute a feeling of satiety after a meal, particularly one rich in fats. The first hormone to be discovered, **secretin** (see the opening essay for Chapter 36 on p. 751), is produced by endocrine cells in the duodenal wall. It is secreted in response to food and strong acid in the stomach and small intestine, and its principal action is to stimulate the release of an alkaline pancreatic fluid that neutralizes stomach acid as it enters the intestine. It also aids fat digestion by inhibiting gastric motility and increasing production of an alkaline bile secretion from the liver.

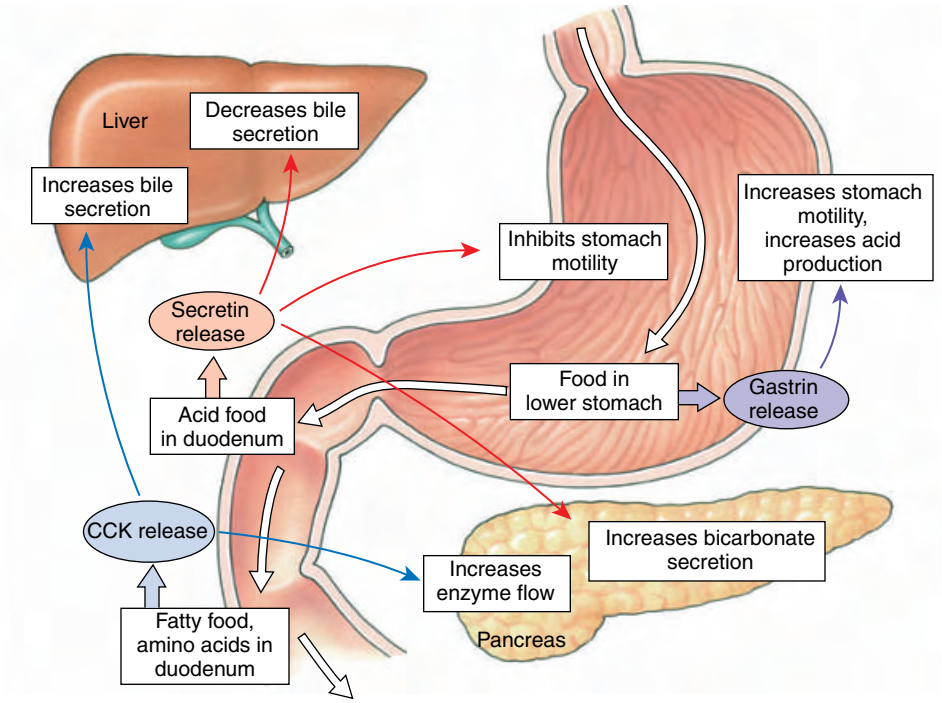


Figure 34-15
Three hormones of digestion. Shown are the principal actions of the hormones gastrin, CCK (cholecystokinin), and secretin.

GI hormones continue to be isolated and their structure determined. So far, all are peptides, and many are present in both the GI tract and in the central nervous system. One of these is CCK, which has been found in high concentrations in the cerebral cortex and hypothalamus of mammals. By providing a feeling of satiety after eating (mentioned above) it may play some role in regulating appetite. Several other GI peptides, for example, vasoactive intestinal peptide (VIP) and gastric inhibitory peptide (GIP) appear to play neurotransmitter roles in the brain. This unexpected versatility has served to broaden our concept of hormones as molecules capable of functioning in several different ways.

Nutritional Requirements

The food of animals must include **carbohydrates, proteins, fats, water, mineral salts,** and **vitamins.** Carbohydrates and fats are required as fuels for energy and for the synthesis of various substances and structures. Proteins (actually the amino acids of which they are composed) are needed for the synthesis of specific proteins and other nitrogen-containing compounds. Water is required as the solvent for body chemistry and as a major component of all fluids of the body. Inorganic salts are required as the anions and cations of body fluids and tissues and form important structural and physiological components throughout the body. Vitamins are accessory factors from food that are often built into the structure of many enzymes.

A **vitamin** is a relatively simple organic compound that is not a carbohydrate, fat, protein, or mineral and that is required in very small amounts in the diet for some specific cellular function. Vitamins are not sources of energy but are often associated with the activity of important enzymes that serve vital metabolic roles. Plants and many microorganisms synthesize all the organic compounds they need; animals, however, have lost certain synthetic abilities during their long evolution and depend ultimately on plants to supply these compounds. Vitamins therefore represent synthetic gaps in the metabolic machinery of animals.

Vitamins are usually classified as fat soluble (soluble in fat solvents such as ether) or water soluble. The **water-soluble vitamins** include the B complex and vitamin C (Table 34-1). Vitamins of the B complex, so grouped because the original B vitamin was subsequently found to consist of several distinct molecules, tend to be found together in nature. Almost all animals, vertebrate and invertebrate, require B vitamins; they are "universal" vitamins. The dietary need for vitamin C and the **fat-soluble vitamins** A, D, E, and K is mostly restricted to vertebrates, although some are required by certain invertebrates. Even within groups of close relationship, requirements for vitamins are relative, not absolute. A rabbit does not require vitamin C, but guinea pigs and humans do. Some songbirds require vitamin A, but others do not.

The recognition years ago that many human diseases and those of domesticated animals were caused by or associated with dietary deficiencies led biologists to search for specific nutrients that would prevent such diseases. These studies eventually yielded a list of **essential nutrients** for human beings and other animal species studied. Essential nutrients are those needed for normal growth and maintenance and that *must* be supplied in the diet. In other words, it is "essential" that these nutrients be in the diet because the animal cannot synthesize them from other dietary constituents. Nearly 30 organic compounds (amino acids and vitamins) and 21 elements are essential for humans (Table 34-1). Considering that the body contains thousands of different organic compounds, the list in Table 34-1 is remarkably short. Animal cells have marvelous powers of synthesis, enabling them to build compounds of enormous variety and complexity from a small, select group of raw materials.

In the average diet of North Americans approximately 50% of the total calories (energy content) comes from carbohydrates and 40% comes from lipids. Proteins, essential as they are for structural needs, supply only a little more than 10% of the total calories of the average diet of North Americans. Carbohydrates are widely consumed because they are more abundant and cheaper than proteins or lipids. Actually humans and many other animals can subsist on diets devoid of carbohydrates, provided sufficient total calories and essential nutrients are present. Eskimos, before the decline of their native culture, lived on a diet that was high in fat and protein and very low in carbohydrate.

Lipids are needed principally to provide energy. However, at least three fatty acids are essential for humans because we cannot synthesize them. Much interest and research have been devoted to lipids in our diets because of the association between fatty diets and the disease **atherosclerosis.** The matter is complex, but evidence suggests that atherosclerosis may occur when the diet is high in saturated lipids (lipids with no double bonds in the carbon chains of the fatty acids) but low in polyunsaturated lipids (two or more double bonds in the carbon chains).

Atherosclerosis (Gr. *atheroma,* tumor containing gruel-like matter, + *sclerosis,* to harden) is a degenerative disease in which fatty substances are deposited in the lining of arteries, resulting in narrowing of the passage and eventual hardening and loss of elasticity.

Proteins are expensive foods and limited in the diet. Proteins, of course, are not themselves the essential nutrients but rather contain essential amino acids. Of the 20 amino acids commonly found in proteins, eight and possibly 10 are essential to humans (Table 34-1). We can synthesize the rest from other amino acids. Generally, animal proteins

TABLE 34.1

Human Nutrient Requirements

Water-Soluble Vitamins	
Thiamine (B_1)	
Riboflavin (B_2)	
Niacin (nicotinic acid)	
Pyridoxine (B_6)	
Pantothenic acid	
Folacin (folic acid)	
Vitamin B_{12} (cobalamin)	
Biotin	
Ascorbic acid (C)	
Fat-Soluble Vitamins	
A, D, E, and K	
Minerals	
Major	*Trace*
Calcium	Iron
Phosphorus	Fluorine
Sulfur	Zinc
Potassium	Copper
Chlorine	Silicon
Sodium	Vanadium
Magnesium	Tin
	Nickel
	Selenium
	Manganese
	Iodine
	Molybdenum
	Chromium
	Cobalt
Amino Acids	
Phenylalanine	
Lysine	
Isoleucine	
Leucine	
Valine	
Methionine	
Tryptophan	
Threonine	
Arginine*	
Histidine*	
Polyunsaturated Fatty Acids	
Arachidonic	
Linoleic	
Linolenic	

*Required for normal growth of children.

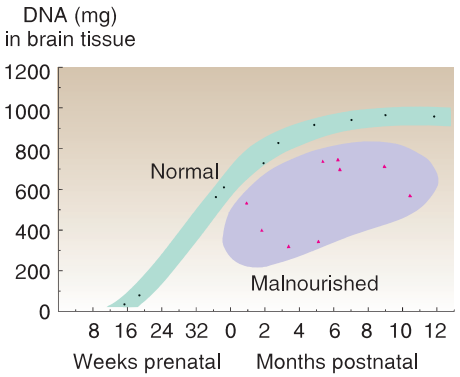


Figure 34-16
Effect of early malnutrition on cell number (measured as total DNA content) in the human brain. This graph shows that malnourished infants (*purple oval*) have far fewer brain cells than do normal infants (*green growth curve*).

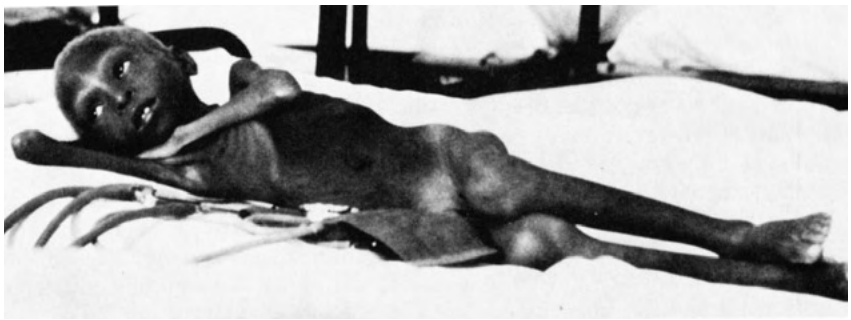


Figure 34-17
Biafran refugee child suffering severe malnutrition.

have more of the essential amino acids than do proteins of plant origin. All eight of the essential amino acids must be present simultaneously in the diet for protein synthesis. If one or more is missing, the use of the other amino acids will be reduced proportionately; they cannot be stored and are broken down for energy. Thus heavy reliance on a single plant source as a diet will inevitably lead to protein deficiency. This problem can be corrected if two kinds of plant proteins having complementary strengths in essential amino acids are ingested together. For example, a balanced protein diet can be prepared by mixing wheat flour, which is deficient only in lysine, with a legume (peas or beans), which is a good source of lysine but deficient in methionine and cysteine. Each plant complements the other by having adequate amounts of those amino acids that are deficient in the other.

Because animal proteins are rich in essential amino acids, they are in great demand in all countries. North Americans eat far more animal proteins than do Asians and Africans. In 1989 the annual per capita consumption of red meat was 76 kg in the United States, 27 kg in Japan, 12 kg in Egypt, and 1 kg in India.* Seventy percent of the protein in the diet of Americans comes from animal products and 30% from plants. By comparison, in China only 11% comes from animal sources and 89% from plants. North Americans consume approximately one-quarter of all beef produced in the world. The high consumption of meat in North America and Europe carries the price of a high death rate from so-called diseases of affluence: heart disease, stroke, and certain kinds of cancer.

Undernourishment and malnourishment rank as two of the world's oldest problems and remain major health problems today, afflicting an eighth of the human population. Growing children and pregnant and lactating women are especially vulnerable to the devastating effects of malnutrition. Cell proliferation and growth in the human brain are most rapid in the terminal months of gestation and the first year after birth. Adequate protein for neuron development is a requirement during this critical time to prevent neurological dysfunction. The brains of children who die of protein malnutrition during the first year of life have 15% to 20% fewer brain cells than those of normal children (Figure 34-16). Malnourished children who survive this period suffer permanent brain damage and cannot be helped by later corrective treatment (Figure 34-17). Recent studies suggest that poverty, with attendant lack of educational and medical resources, and lowered expectations, exacerbates the effects of malnutrition by delaying intellectual development.†

Two different types of severe food deficiency are recognized: marasmus, general undernourishment from a diet low in both calories and protein, and kwashiorkor, protein malnourishment from a diet adequate in calories but deficient in protein. Marasmus (Gr. *marasmos,* to waste away) is common in infants weaned too early and placed on low-calorie–low-protein diets; these children are listless, and their bodies waste away. Kwashiorkor is a West African word describing a disease a child gets when displaced from the breast by a newborn sibling. This disease is characterized by retarded growth, anemia, weak muscles, a bloated body with typical pot belly, acute diarrhea, susceptibility to infection, and high mortality.

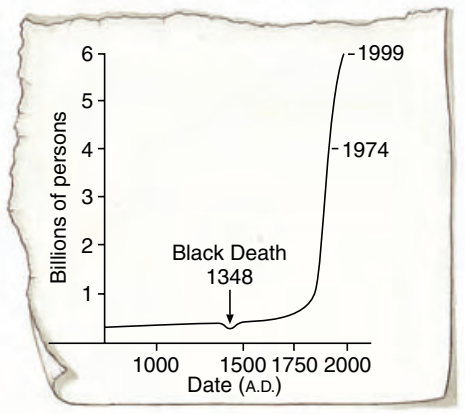


Figure 34-18
Portion of a graph for human population growth since A.D. 800, as it appeared in the 1979 edition of this book when the earth's population had passed 4 billion five years earlier, and updated to show the 1999 figure of 6 billion.

*Brown, L. R. 1991. State of the World 1991. New York, Worldwatch Institute/W.W. Norton & Company, p. 159.

†Brown, J. L, and E. Pollitt. 1996. Malnutrition, poverty and intellectual development. Sci. Am. **274:**38–43 (Feb.).

The world's precarious food supply is threatened by rapid population growth. The world population was 2 billion in 1927, reached 4 billion in 1974, passed 6 billion in October of 1999 (Figure 34-18), and is expected to reach 8.9 billion by the year 2030, several years ahead of earlier estimates. Approximately 78 million people are added each year. The equivalent of the total 1999 United States population of 274 million people is added to the world every 42 months. Yet today, as the demand for food increases, the world per capita production of grain and the world fish catch are in decline‡. Furthermore, the world each year loses billions of tons of topsoil and trillions of gallons of groundwater needed to grow food crops. In the view of many, the exploding human population is a major force driving the global environmental crisis.

‡According to State of the World 1996, Worldwatch Institute, the world grain harvest has not grown at all since 1990, and 13 of the 15 leading oceanic fisheries are in decline. See also: Safina, C. 1995. The world's imperiled fish. Sci. Am. **273:**46–53 (Nov.).

Summary

Autotrophic organisms (mostly green plants), using inorganic compounds as raw materials, capture the energy of sunlight through photosynthesis and produce complex organic molecules. Heterotrophic organisms (bacteria, fungi, and animals) use the organic compounds synthesized by plants, and chemical bond energy stored therein for their own nutritional and energy needs.

A large group of animals with very different levels of complexity feed by filtering out minute organisms and other particulate matter suspended in water. Others feed on organic detritus deposited in the substrate. Selective feeders, on the other hand, have evolved mechanisms for manipulating larger food masses, including various devices for seizing, scraping, boring, tearing, biting, and chewing. Fluid feeding is characteristic of endoparasites, which may absorb food across the general body surface, and of ectoparasites, herbivores, and predators that have developed specialized mouthparts for piercing and sucking.

Digestion is the process of breaking down food mechanically and chemically into molecular subunits for absorption. Digestion is intracellular in protozoan groups and sponges. In more complex metazoans it is supplemented, and finally replaced entirely, by extracellular digestion, which takes place in sequential stages in a tubular cavity, the alimentary canal. The mouth receives food, mixes it with lubricating saliva, then passes it down the esophagus to regions where the food may be stored (crop), or ground (gizzard), or acidified and subjected to early digestion (vertebrate stomach). Among vertebrates, most digestion occurs in the small intestine. Enzymes from the pancreas and intestinal mucosa hydrolyze proteins, carbohydrates, fats, nucleic acids, and various phosphate compounds. The liver secretes bile, containing salts that emulsify fats. Once foods are digested, their products are absorbed as molecular subunits (monosaccharides, amino acids, and fatty acids) into the blood or lymph vessels of the villi of the small intestine. The large intestine (colon) serves mainly to absorb water and minerals from the food wastes as they pass through it. It also contains symbiotic bacteria that produce certain vitamins.

Most animals balance food intake with energy expenditure. Food intake is regulated primarily by a hunger center located in the hypothalamus. In mammals, should caloric intake exceed requirements for energy, the excess calories normally are dissipated as heat in specialized brown fat tissue. A deficiency in this response is one cause of human obesity.

Several gastrointestinal hormones coordinate digestive functions. They include gastrin, which stimulates acid secretion by the stomach; CCK, which stimulates gallbladder and pancreatic secretion; and secretin, which stimulates bicarbonate secretion from the pancreas and inhibits gastric motility.

All animals require a balanced diet containing both fuels (mainly carbohydrates and lipids) and structural and functional components (proteins, minerals, and vitamins). For every multicellular animal, certain amino acids, lipids, vitamins, and minerals are "essential" dietary factors that cannot be produced by the animal's own synthetic machinery. Animal proteins are better-balanced sources of amino acids than are plant proteins, which tend to lack one or more essential amino acids. Undernourishment and protein malnourishment are among the world's major health problems, afflicting millions of people.

Review Questions

1. Distinguish between the following pairs of terms: autotrophic and heterotrophic; phototrophic and chemotrophic; herbivores and carnivores; omnivores and insectivores.
2. Suspension feeding is one of the most important methods of feeding among animals. Explain the characteristics, advantages, and limitations of suspension feeding, and name three different groups of animals that are suspension feeders.
3. An animal's feeding adaptations are an integral part of an animal's behavior and usually shape the appearance of the animal itself. Discuss the contrasting feeding adaptations of carnivores and herbivores.
4. Explain how food is propelled through the digestive tract.
5. Compare intracellular with extracellular digestion and suggest why there

has been a phylogenetic trend in some animals from intracellular to extracellular digestion.

6. Which structural modifications vastly increase the internal surface area of the intestine (both invertebrate and vertebrate), and why is this large surface area important?
7. Trace the digestion and final absorption of a carbohydrate (starch) in the vertebrate gut, naming the carbohydrate-splitting enzymes, where they are found, the breakdown products of starch digestion, and in what form they are finally absorbed.
8. As in question 7, trace the digestion and final absorption of a protein.
9. Explain how fats are emulsified and digested in the vertebrate gut. Explain how bile aids the digestive process even though it contains no enzymes. Provide an explanation for the following observation: fats are broken down to fatty acids and monoglycerides in the intestinal lumen, but appear later in the blood as fat droplets.
10. Explain the phrase "diet-induced thermogenesis" and relate it to the problem of obesity in some people.
11. Name three hormones of the gastrointestinal tract and explain how they assist in the coordination of gastrointestinal function.
12. Name the basic classes of foods that serve mainly as (1) fuels and as (2) structural and functional components.
13. If vitamins are neither biochemically similar compounds nor sources of energy, what characteristics distinguish vitamins as a distinct group of nutrients? What are the water-soluble and the fat-soluble vitamins?
14. Why are some nutrients considered "essential" and others "nonessential" even though both types of nutrients are used in growth and tissue repair?
15. Explain the difference between saturated and unsaturated lipids, and comment on the current interest in these compounds as they relate to human health.
16. What is meant by "protein complementarity" among plant foods?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Anatomy of the Stomach. The anatomy of the stomach.

Hepatitis C. New CDC site has information on hepatitis C.

Colorectal Cancer Information Links. A wealth of links provided by the CDC.

The Digestive System. Hypertextbook on the pathophysiology of the digestive tract. In-depth tutorials investigate the parts of the digestive tube, and the accessory organs.

The Digestive Physiology of Herbivores. Describes various strategies employed by herbivores, including digestive anatomy and physiology of ruminants.

OLC Student Center Website

CHAPTER

35

Nervous Coordination

Nervous System and Sense Organs

Wood tick on a grass stem awaits its host.

The Private World of the Senses

By any measure, people enjoy a rich sensory world. We are continually assailed by information from the senses of vision, hearing, taste, olfaction, and touch. These classic five senses are supplemented by sensory inputs of cold, warmth, vibration, and pain, as well as by information from numerous internal sensory receptors that operate silently and automatically to keep our interior domain working smoothly. The world our senses perceive is uniquely human. We share this exclusive world with no other animal, nor can we venture into the sensory world of any other animal except as an abstraction through our imagination.

The idea that each animal enjoys an unshared sensory world was first conceived by Jakob von Uexküll, a seldom cited German biologist of the early part of this century. Von Uexküll asks us to try to enter the world of a tick through our imagination, supplemented by what we know of tick biology. It is a world of temperature, of light and dark, and of the odor of butyric acid, a chemical common to all mammals. Insensible to all other stimuli, the tick climbs up a blade of grass to wait, for years if necessary, for cues that will betray the presence of a potential host. Later, swollen with blood, she drops to the earth, lays her eggs, and dies. The tick's impoverished sensory world, devoid of sensory luxuries and fine-tuned by natural selection for the world she will encounter, has ensured her single goal, reproduction.

A bird and a bat may share for a moment precisely the same environment. The worlds of their perceptions, however, are vastly different, structured by the limitations of the sensory windows each employs and by the brain that garners and processes what it needs for survival. For one it is a world dominated by vision; for the other, echolocation. The world of each is alien to the other, just as their worlds are to us. ■

The nervous system originated in a fundamental property of life: **irritability,** the ability to respond to environmental stimuli (Chapter 1, p. 10). The response may be simple, such as a protozoan moving to avoid a noxious substance, or quite complex, such as a vertebrate animal responding to elaborate signals of courtship. A protistan receives and responds to a stimulus, all within the confines of a single cell. Evolution of multicellularity and more complex levels of animal organization required increasingly complex mechanisms for communication between cells and organs. Relatively rapid communication is by **neural mechanisms** and involves propagated electrochemical changes in cell membranes. The basic plan of a nervous system is to code information and to transmit and process it for appropriate action. These functions are examined in this chapter. Relatively less rapid or long-term adjustments in animals are governed by **hormonal mechanisms,** subject of the next chapter.

Neurons: Functional Units of Nervous Systems

A **neuron,** or nerve cell, may assume many shapes, depending on its function and location; a typical kind is shown diagrammatically in Figure 35-1. From the nucleated cell body extend cytoplasmic processes of two types: one or more **dendrites,** in all but the simplest neuron, and a single **axon.** As the name dendrite suggests (Gr. *dendron,* tree), these neurons are often profusely branched. They, and the entire cell body surface, are the nerve cell's receptive apparatus, often receiving information from several different sources at once. Some of these inputs are excitatory, others inhibitory.

The single axon (Gr. *axon*, axle), often a long fiber (meters in length in the largest mammals), is relatively uniform in diameter, and typically carries impulses away from the cell body. In vertebrates and some complex invertebrates, the axon is often covered with an insulating sheath of **myelin.**

Neurons are commonly classified as **afferent,** or sensory; **efferent,** or motor; and **interneurons,** which are neither sensory nor motor but connect neurons with other neurons. Afferent and efferent neurons lie mostly outside the central nervous system (brain and nerve cord) while interneurons, which in humans make up 99% of all neurons in the body, lie entirely within the central nervous system. Afferent neurons are connected to **receptors.** Receptors function to convert environmental stimuli into nerve impulses, which are carried by the afferent neurons into the central nervous system. Here impulses may be perceived as conscious sensation. Impulses also move to efferent neurons, which carry them via the peripheral system to **effectors,** such as muscles or glands.

In vertebrates, nerve processes (usually axons) are often bundled together in a well-formed wrapping of connective tissue to form a **nerve** (Figure 35-2). Cell bodies of these nerve processes are located either in the central nervous system or in **ganglia,** which are discrete bundles of nerve cell bodies located outside the central nervous system.

Surrounding neurons are nonnervous **neuroglial cells** (often simply called **"glial"** cells) that have a special relationship to neurons. Glial cells are extremely numerous in the vertebrate brain, where they outnumber neurons 10 to 1 and may form almost half the volume of the brain. Some glial cells form intimate insulating sheaths of lipid-containing **myelin** around nerve fibers. Vertebrate nerves are often enclosed by myelin, an insulating sheath laid down in concentric rings by special glial cells called **Schwann cells** (Figure 35-3) in the peripheral nervous system, and **oligodendrocytes** in the central nervous system. Certain glial cells, called **astrocytes,** because of their radiating, starlike shape, serve as nutrient and ion reservoirs for neurons, as well as a scaffold during brain development, enabling migrating neurons to find their destinations from points of origin. Astrocytes, and smaller **microglial** cells, are essential for the regenerative process that follows brain injury. Unfortunately, astrocytes also participate in several diseases of the nervous system, including Parkinsonism and multiple sclerosis. Other functional roles of glial cells are still being determined.

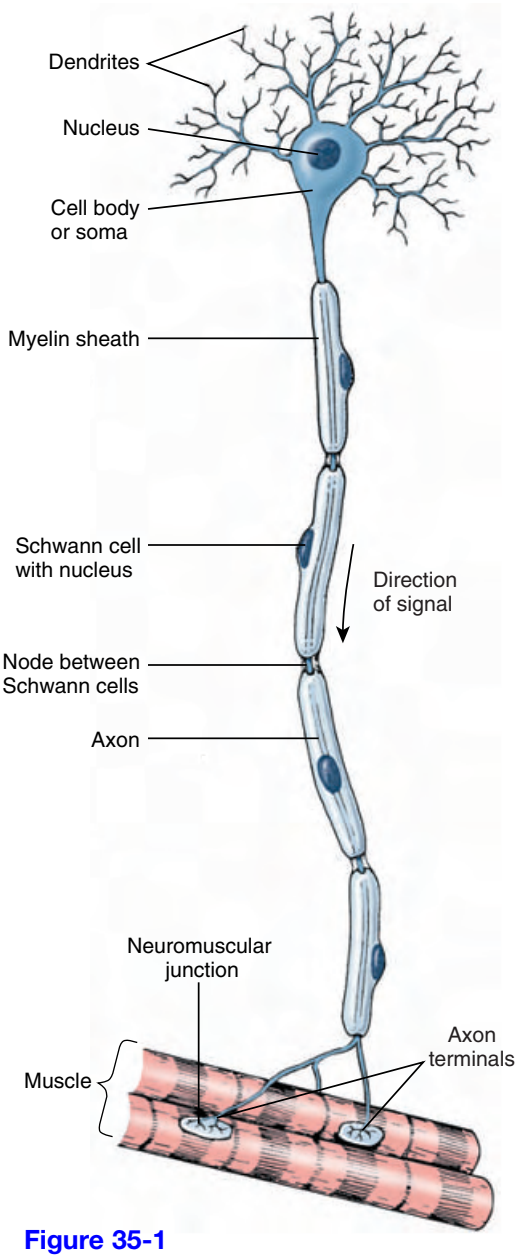


Figure 35-1
Structure of a motor (efferent) neuron.

Nature of a Nerve Impulse

A **nerve** impulse is an electro-chemical message of neurons, the common functional denominator of all nervous

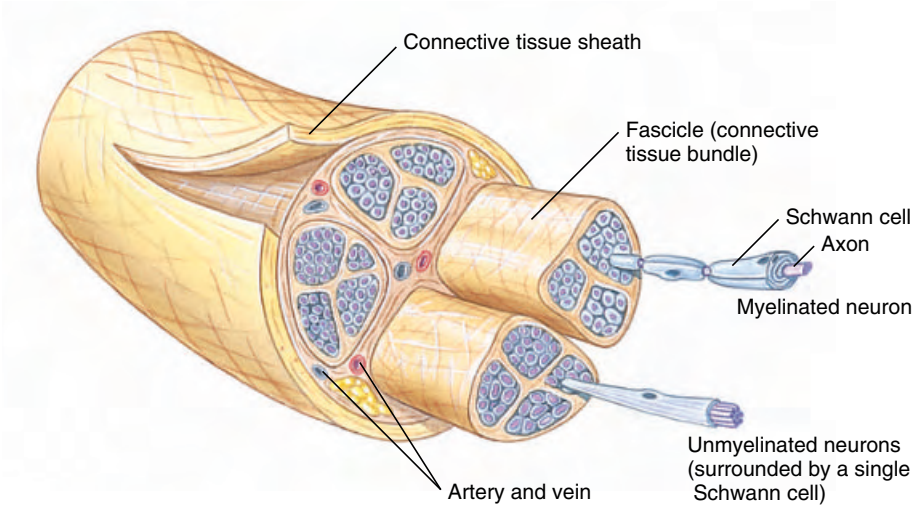


Figure 35-2
Structure of a nerve showing nerve fibers surrounded by various layers of connective tissue. A nerve may contain thousands of both efferent and afferent fibers.

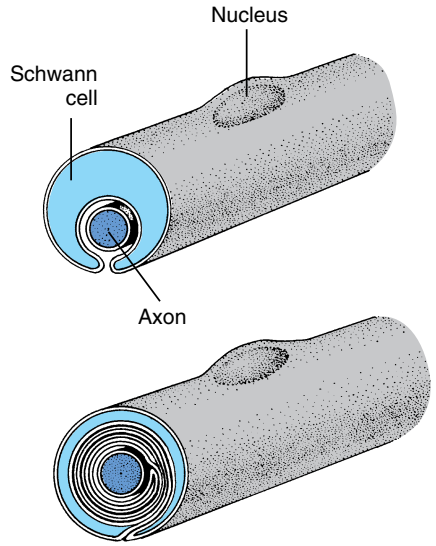


Figure 35-3
Development of the myelin sheath in the peripheral nervous system. The whole Schwann cell grows around an axon, then rotates around it, enclosing the axon in a tight, multilayered sheath. The myelin sheath insulates a nerve axon and facilitates transmission of nerve impulses.

system activity. Despite the incredible complexity of the nervous system of many animals, nerve impulses are basically alike in all neurons and in all animals. An impulse is an "all-or-none" phenomenon; either the fiber is conducting an impulse, or it is not. Because all impulses are alike, the only way a nerve fiber can vary its signal is by changing the frequency of impulse conduction. Frequency change is the language of a nerve fiber. A fiber may conduct no impulses at all or very few per second up to a maximum approaching 1000 per second. The higher the frequency (or rate) of conduction, the greater is the level of excitation.

Resting Membrane Potential

Membranes of neurons, like all cellular membranes, have a special permeability that creates ionic imbalances. The interstitial fluid surrounding neurons contains relatively high concentrations of sodium (Na^+) and chloride (Cl^-) ions, but a low concentration of potassium ions (K^+) and large impermeable anions with negative charge. Inside the neuron, the ratio is reversed: the K^+ and impermeable anion concentration is high, but the Na^+ and Cl^- concentrations are low (Figure 35-4; see also Figure 33-1B, p. 685) These differences are pronounced; there is approximately 10 times more Na^+ outside than in and 25 to 30 times more K^+ inside than out.

When at rest, the membrane of a neuron is selectively permeable to K^+, which can traverse the membrane through special potassium channels. The permeability to Na^+ is nearly zero because the Na^+ channels are closed in a resting membrane. Potassium ions tend to diffuse outward through the membrane, following the gradient of potassium concentration. Very quickly the positive charge outside reaches a level that prevents any more K^+ from diffusing out of the axon (because like charges repel each other), and because the large anions cannot pass through the membrane, the positively charged potassium ions are drawn back into the cell. Now the resting membrane is at equilibrium, with an electrical gradient that exactly balances the concentration gradient. This **resting membrane potential** is usually −70 mV (millivolts), with the inside of the membrane negative with respect to the outside.

Action Potential

A nerve impulse is a rapidly moving change in electrical membrane potential called an **action potential** (Figure 35-5). It is a very rapid and brief depolarization of the membrane of the nerve fiber. In most nerve fibers, the action potential does not simply return the membrane potential to zero, but instead overshoots zero. In other words, the membrane potential reverses for an instant so that the outside becomes negative compared with the inside. Then, as the action potential moves ahead, the membrane returns to its normal resting membrane potential, ready to conduct another impulse. The entire event occupies approximately a millisecond. Perhaps the most significant property of the nerve impulse is that it is **self-propagating;** once started the impulse moves ahead automatically, much like the burning of a fuse.

What causes the reversal of polarity in the cell membrane during passage of an action potential? We have seen that the resting membrane potential depends on the high membrane permeability (leakiness) to K^+, some 50 to 70 times greater than the permeability to Na^+. When the action potential arrives at a given point, Na^+ channels suddenly open, permitting a flood of Na^+ to diffuse into the axon from the outside, moving down the concentration gradient for Na^+. Actually only a very minute amount of

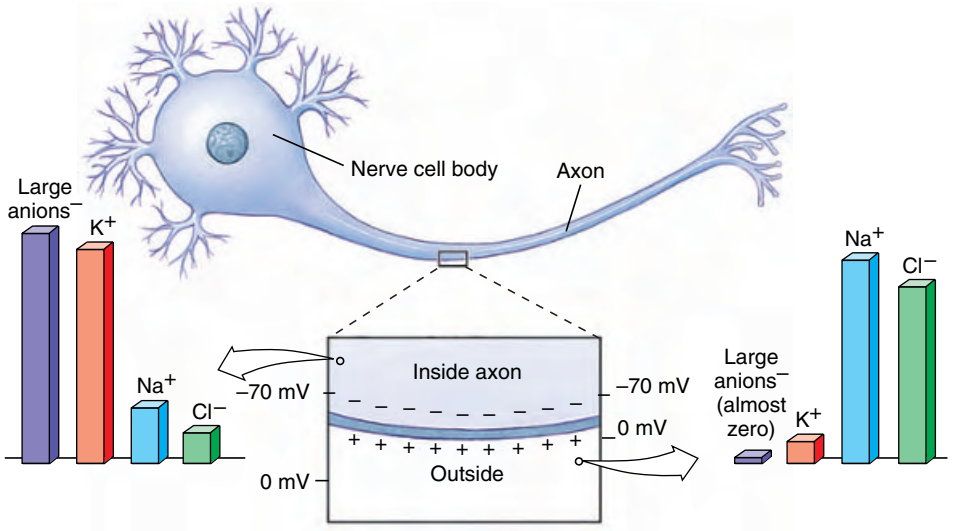


Figure 35-4

Ionic composition inside and outside a resting nerve cell. An active sodium-potassium exchange pump located in the cell membrane drives sodium to the outside, keeping its concentration low inside. Potassium concentration is high inside. Although the membrane is "leaky" to potassium, this ion is held inside by the repelling positive charge outside the membrane, and its attraction to large negatively charged anions inside the membrane, which cannot leave the cell.

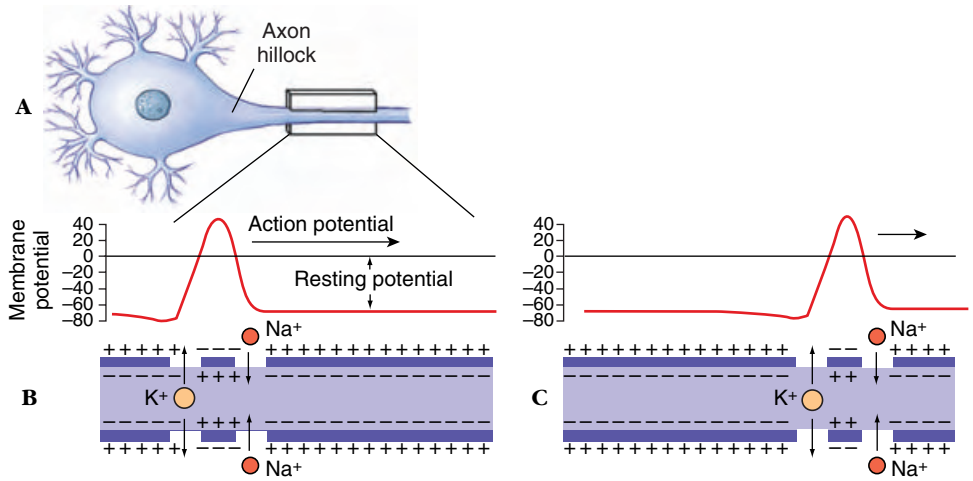


Figure 35-5

Conduction of action potential of a nerve impulse. The action potential originates in the axon hillock of the neuron **(A)** and moves toward the right. **B** and **C** show the electrical event and associated changes in localized membrane permeability to sodium and potassium. The position of the action potential in **C** is shown about 4 milliseconds after **B.** When the impulse arrives at a point, sodium channels open, allowing sodium ions to enter. Sodium inflow reverses the membrane polarity, making the inner surface of the axon positive and the outside negative. Sodium channels then close and potassium channels open. Potassium ions can now restore the normal resting potential.

Na^+ moves across the membrane—less than one-millionth of the Na^+ outside—but this sudden rush of positive ions cancels the local resting membrane potential. The membrane is **depolarized,** creating a minute electrical "hole." Potassium ions, finding their electrical barrier gone, begin to move outside the cell. Then, as the action potential passes, the membrane quickly regains its resting properties. It becomes once again practically impermeable to Na^+ and the outward movement of K^+ is checked.

Thus, the rising phase of the action potential is associated with rapid influx (inward movement) of Na^+ (Figure 35-5). When the action potential reaches its peak, Na^+ permeability is restored to normal, and K^+ permeability briefly increases above the resting level. Increased potassium permeability causes the action potential to drop rapidly toward the resting membrane level, during the **repolarization** phase. The membrane is now ready to transmit another nerve impulse.

Sodium Pump

A resting cell membrane has a very low permeability to Na^+. Nevertheless some Na^+ leaks through it, even in the resting condition. When the axon is active, during an action potential, Na^+ flows inward with each passing impulse. If not removed, the accumulation of Na^+ inside the axon would cause the resting membrane potential of the fiber to decay. This decay is prevented by **sodium pumps,** each a complex of protein subunits embedded in the plasma membrane of the axon (see Figure 3-19, p. 50). Each sodium pump uses energy in ATP to transport sodium from the inside to the outside of the membrane. The sodium pump in nerve axons, as in many other cell membranes, also moves K^+ into the axon while it is moving Na^+ out. Thus, it is a **sodium-potassium exchange pump** that helps to restore the ion gradients of both Na^+ and K^+. The astrocytes (mentioned earlier) help to maintain the correct balance of ions surrounding neurons by sweeping away excess potassium produced during neuronal activity.

High-Speed Conduction

Although the ionic and electrical events associated with action potentials are much the same throughout the animal kingdom, conduction velocities vary enormously from nerve to nerve and from animal to animal—from as slow as 0.1 m/sec in sea anemones to as fast as 120 m/sec in some mammalian motor axons. The speed of

conduction is closely related to the diameter of the axon. Small axons conduct slowly because internal resistance to current flow is high. In most invertebrates, where fast conduction velocities are important for quick response, such as in locomotion to capture prey or to avoid capture, axon diameters are larger. The giant axon of squids is nearly 1 mm in diameter and carries impulses 10 times faster than ordinary fibers in the same animal. A squid's giant axon innervates the animal's mantle musculature and is used for powerful mantle contractions when the animal swims by jet propulsion. Similar giant axons enable earthworms, which are normally slow-moving animals, to withdraw almost instantaneously into their burrows when startled.

Some invertebrates, including prawns and insects, also have fast fibers invested with multiple layers of a myelin-like substance that is interrupted at intervals much like myelinated fibers of vertebrates. Conduction rates, though not as fast as vertebrate saltatory conduction, are much faster than unmyelinated fibers of the same diameter in other invertebrates.

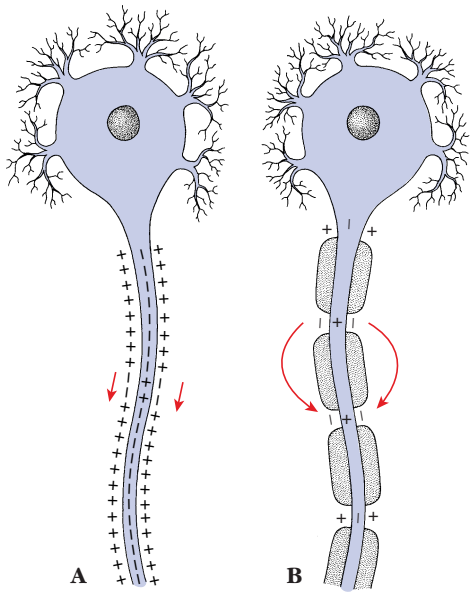


Figure 35-6
Impulse conduction in unmyelinated and myelinated fibers. In unmyelinated fibers **(A),** the action potential spreads continuously along the entire length of the axon. In myelinated fibers **(B),** the action potential leaps from node to node, bypassing the insulated portions of the fiber. This is saltatory conduction, which is much faster than continuous conduction.

Vertebrates do not possess giant axons, but they can achieve high-conduction velocities in another way, by a cooperative relationship between axons and the investing layers of myelin laid down by the Schwann cells or oligodendrocytes described earlier. Insulating myelin sheaths are interrupted at intervals by nodes (called **nodes of Ranvier**) where the surface of the axon is exposed to fluid surrounding the nerve. In these **myelinated fibers** the action potential depolarizes the axon membrane only at the nodes because the myelin sheath prevents depolarization elsewhere (Figure 35-6). The ion pumps and channels that move ions across the membrane are concentrated in each node. Once an action potential starts down an axon, depolarization of the first node initiates an electrical current that stretches out to the neighboring node, causing it to depolarize and trigger an action potential. Thus the action potential leaps from node to node, a kind of conduction called **saltatory** (L. *salto,* to dance, leap). The gain in efficiency as compared with nonmyelinated fibers is impressive. For example, a frog myelinated axon only 12 μm in diameter conducts nerve impulses at the same speed as a squid axon 350 μm in diameter.

Synapses: Junctions Between Nerves

When an action potential passes down an axon to its terminal, it must cross a small gap, the **synapse** (Gr. *synapsis,* contact, union), separating it from another neuron or an effector organ. Two distinct kinds of synapses are known: electrical and chemical.

Electrical synapses, although much less common than chemical synapses, have been demonstrated in both invertebrate and vertebrate groups. Electrical synapses are points at which ionic currents flow directly across a narrow gap junction (see Figure 3-15, p. 47) from one neuron to another. Electrical synapses show no time lag and consequently are important for escape reactions. They also have been observed in other excitable cell types, and form an important method of communication between cardiac muscle cells of the heart (p. 692) and smooth muscle cells (for example, the uterus, p. 151).

Much more complex than electrical synapses are **chemical synapses,** which contain packets of specialized chemicals called **neurotransmitters.** Neurons bringing impulses toward chemical synapses are called **presynaptic neurons;** those carrying impulses away are **postsynaptic neurons.** At a synapse, membranes are separated by a narrow gap, the **synaptic cleft,** having a width of approximately 20 nm.

The axon of most neurons divides at its end into many branches, each of which bears a synaptic knob that sits on the dendrites or cell body of the next neuron (Figure 35-7A). Because a single impulse coming down a nerve axon is transmitted along these many branches and synaptic endings on the next neuron, many impulses converge on the cell body at one instant. In addition, the axon terminations of many neurons may almost cover a nerve cell body and its dendrites with thousands of synapses.

The 20 nm fluid-filled gap between presynaptic and postsynaptic membranes prevents action potentials from spreading directly to the postsynaptic neuron. Instead the synaptic knobs secrete a specific neurotransmitter that communicates chemically with the postsynaptic cell. One of the most common neurotransmitters of the peripheral nervous system is **acetylcholine,** which illustrates typical synaptic transmission. Inside the synaptic knobs are numerous tiny **synaptic vesicles,** each containing several thousand molecules of acetylcholine. Evidence suggests that when an impulse arrives at a terminal knob a sequence of events occurs as portrayed in Figure 35-8. The

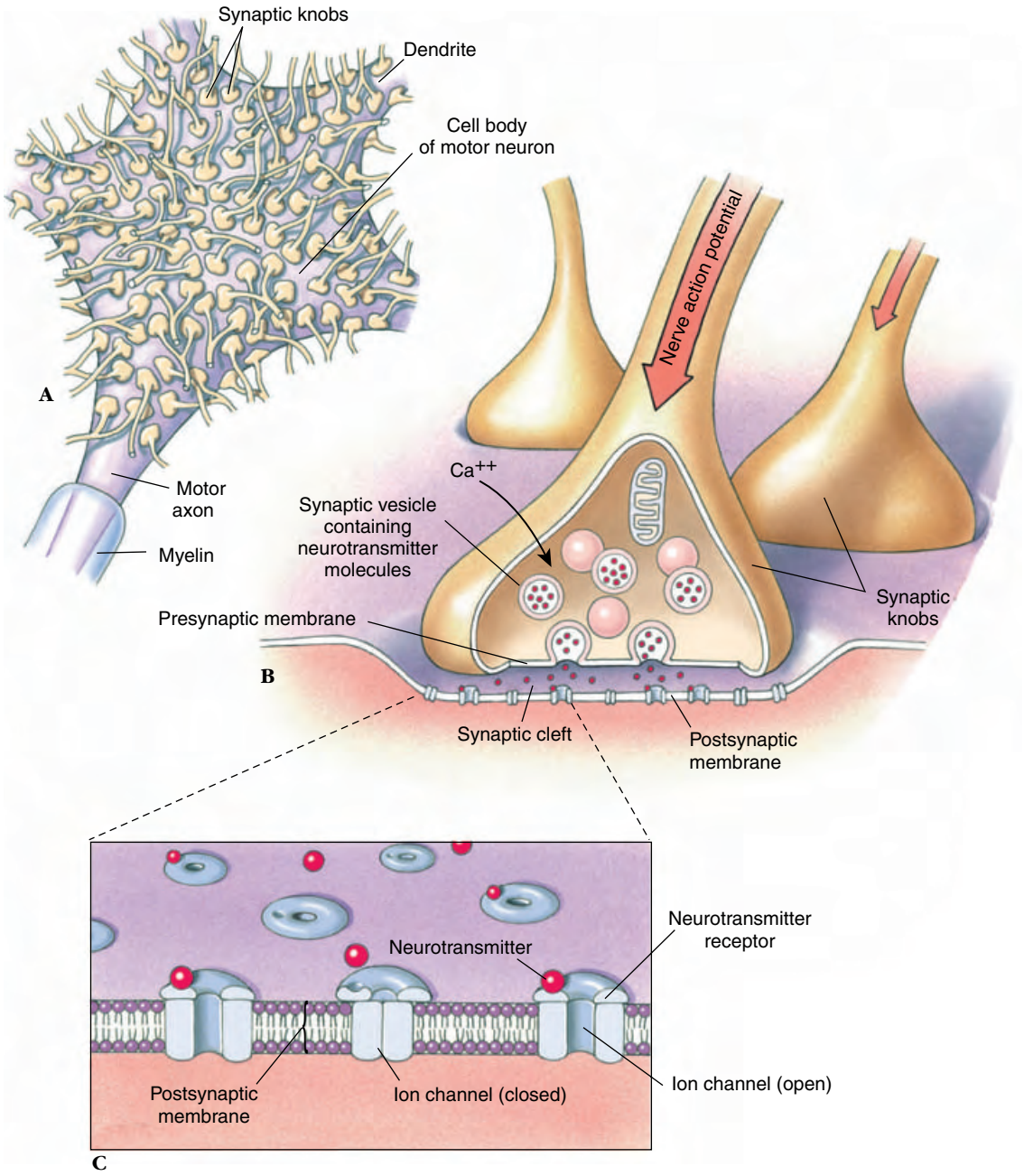


Figure 35-7
Transmission of impulses across nerve synapses. **A,** A cell body of a motor nerve is shown with the terminations of interneurons. Each termination ends in a synaptic knob; thousands of synaptic knobs may rest on a single nerve cell body and its dendrites. **B,** A synaptic knob enlarged 60 times more than in **A.** An impulse traveling down the axon causes movement of synaptic vesicles to the presynaptic membrane where exocytosis occurs, releasing neurotransmitter molecules into the cleft. **C,** Diagram of a synaptic cleft at the ultrastructural level. Upon vesicular exocytosis, neurotransmitter molecules move rapidly across the gap to bind briefly with receptor molecules in the postsynaptic membrane. Binding of neurotransmitter to receptor produces a change in the potential of the postsynaptic membrane.

action potential causes an inward movement of calcium (Ca^+) ions through channels in the synaptic knob membrane and this induces exocytosis of some neurotransmitter-filled synaptic vesicles. Acetylcholine molecules diffuse across the gap in a fraction of a millisecond and bind briefly to receptor molecules on ion channels in the postsynaptic membrane. This creates a voltage change in the postsynaptic membrane. Whether the voltage change is large enough to trigger a postsynaptic potential depends on how many acetylcholine molecules are released and how many channels are opened. Acetylcholine is rapidly destroyed by the enzyme **acetylcholinesterase,** which converts acetylcholine into acetate and choline. If not inactivated in this way, the neurotransmitter would continue to stimulate indefinitely. Organophosphate insecticides (such as malathion) and certain military nerve gases are poisonous for precisely this reason; they block acetylcholinesterase. The final step in the sequence is reabsorption of choline into the presynaptic terminal, resynthesis of acetylcholine and its storage in synaptic vesicles, ready to respond to another impulse.

Many different chemical neurotransmitters have been identified in both vertebrate and invertebrate nervous systems. Some, such as acetylcholine, norepinephrine, and glutamate, depolarize postsynaptic membranes; they are released at **excitatory synapses.** Other neurotransmitters,

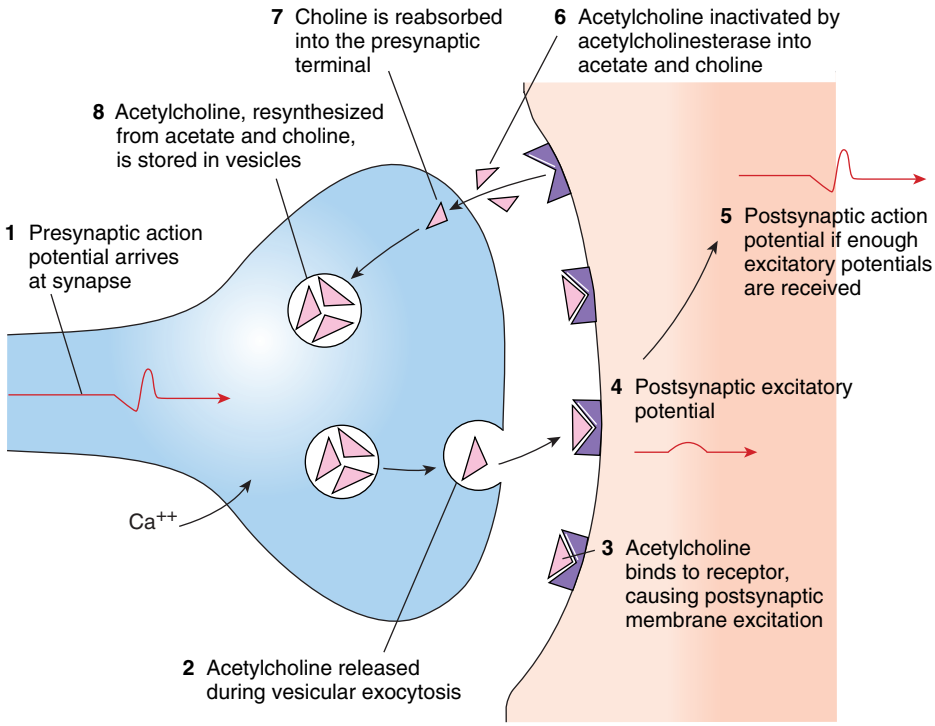


Figure 35-8
Sequence of events in synaptic transmission.

such as gamma aminobutyric acid (GABA), hyperpolarize postsynaptic membranes; thereby stabilizing them against depolarization. These neurotransmitters are released at **inhibitory synapses.** Neurons in the central nervous system have both excitatory and inhibitory synapses among the hundreds or thousands of synaptic knobs on the dendrites and cell body of each neuron.

The net balance of all excitatory and inhibitory inputs received by a postsynaptic cell determines whether it generates an action potential (Figure 35-8). If many excitatory impulses are received at one time, they can reduce the resting membrane potential enough in the postsynaptic membrane to elicit an action potential. Inhibitory impulses, however, stabilize the postsynaptic membrane, making it less likely that an action potential will be generated. The synapse is a crucial part of the decision-making equipment of the central nervous system, modulating flow of information from one neuron to the next.

Evolution of Nervous Systems

Invertebrates: Development of Centralized Nervous Systems

Various metazoan phyla reveal a progressive increase in complexity of nervous systems that probably reflects in a general way the stages in evolution of nervous systems. The simplest pattern of invertebrate nervous systems is the nerve net of radiate animals, such as sea anemones, jellyfishes, hydras, and comb jellies (Figure 35-9A). A nerve net is a quantum leap in complexity beyond sensory systems of the unicellular forms, which lack nerves. A nerve net forms an extensive network in and under the epidermis over all the body. An impulse starting in one part of this net spreads in all directions, since synapses in most radiates do not restrict transmission to one-way movement, as occurs in more complex animals. There are no differentiated sensory, motor, or connector components in the strict meaning of those terms. Branches of a nerve net connect to receptors in the epidermis and to epithelial cells that have contractile properties, and there is evidence of organization into reflex arcs (p. 731). Although most responses tend to be generalized, many are astonishingly complex for so simple a nervous system. This type of nervous system is found among vertebrates in nerve plexuses located, for example, in the intestinal wall; such nerve plexuses govern generalized intestinal movements such as peristalsis and segmentation (p. 712).

Bilateral nervous systems, the simplest of which occur in flatworms, represent a distinct increase in complexity over the nerve net of radiate animals. Flatworms have two anterior ganglia, composed of groups of nerve cell bodies from which two main nerve trunks run posteriorly, with lateral branches extending throughout the body (Figure 35-9B). This is the simplest nervous system showing differentiation into a **peripheral nervous system** (a communication network extending to all parts of the body) and a **central nervous system** (a concentration of nerve cell bodies), which coordinates everything. More complex invertebrates exhibit a more centralized nervous system (brain), with two longitudinal fused nerve cords and many ganglia. The elaborate nervous systems of annelids contain a bilobed brain, a double nerve cord with segmental ganglia, and distinctive **afferent** (sensory) and **efferent** (motor) neurons (Figure 35-9C). Segmental ganglia are relay stations for coordinating regional activity.

The basic plan of molluscan nervous systems is a series of three pairs of well-defined ganglia, but in cephalopods (such as octopus and squid), the ganglia have burgeoned into textured nervous centers of great complexity; those of the octopus contain more than 160 million cells. Sense organs, too, are highly developed. Consequently, cephalopod behavior far outstrips that of any other invertebrate.

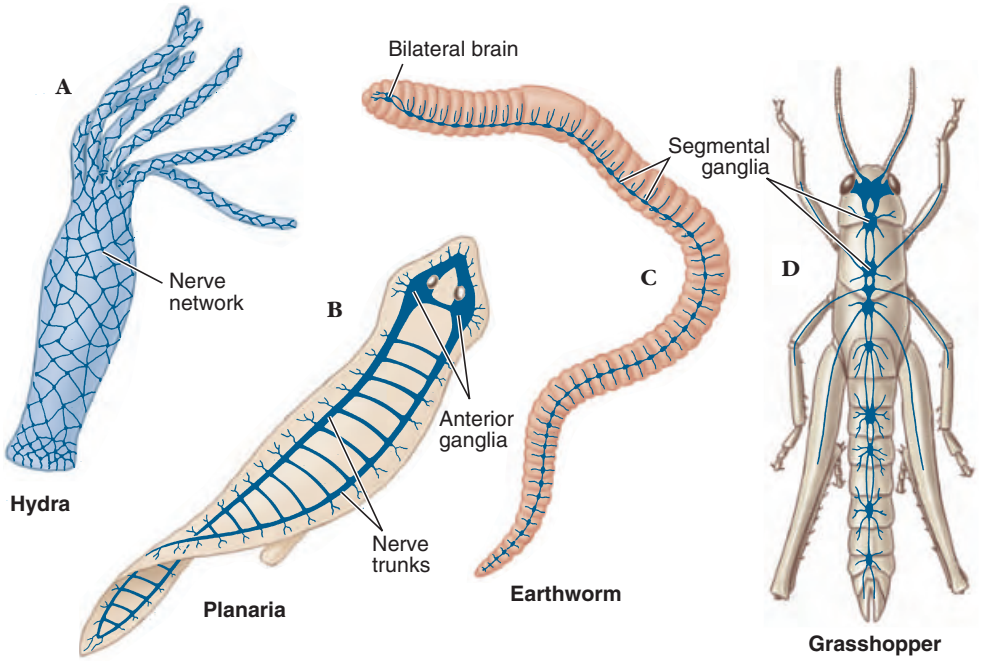


Figure 35-9

Invertebrate nervous systems. **A,** Nerve net of radiates, the simplest neural organization. **B,** Flatworm system, the simplest linear-type nervous system of two nerves connected to a complex neuronal network. **C,** Annelid nervous system, organized into a bilobed brain and ventral cord with segmental ganglia. **D,** Arthropod nervous system with large ganglia and more elaborate sense organs.

The basic plan of arthropod nervous systems (Figure 35-9D) resembles that of annelids, but ganglia are larger and sense organs are much better developed. Social behavior is often elaborate, particularly in hymenopteran insects (bees, wasps, and ants), and most arthropods are capable of considerable manipulation of their environment. Despite the complexity of much insect behavior, insects are nevertheless reflex-bound animals incapable of involved learned behavior principally because of their small size.

Vertebrates: Fruition of Encephalization

The basic plan of the vertebrate nervous system is a hollow, *dorsal* nerve cord terminating anteriorly in a large ganglionic mass, the brain. This pattern contrasts with the nerve cord of bilateral invertebrates, which is solid and ventral to the alimentary canal. By far the most important trend in the evolution of vertebrate nervous systems is the great elaboration of size, configuration, and functional capacity of the brain, a process called **encephalization.** Vertebrate encephalization has brought to full fruition several functional capabilities including fast responses, great capacity for storage of information, and enhanced complexity and flexibility of behavior. Another consequence of encephalization is the ability to form associations between past, present, and (at least in humans) future events.

The Spinal Cord

The **brain** and **spinal cord** compose the central nervous system. During early embryonic development, the spinal cord and brain begin as an ectodermal neural groove, which by folding and enlarging becomes a long, hollow neural tube (Figure 8-12, p. 166). The cephalic end enlarges to form brain vesicles, and the rest becomes the spinal cord. Unlike any invertebrate nerve cord, the segmental nerves of the spinal cord (31 pairs in humans) are separated into dorsal sensory roots and ventral motor roots. The sensory nerve cell bodies are gathered together into dorsal root (spinal) ganglia. Both dorsal (sensory) and ventral (motor) roots meet beyond the spinal cord to form a mixed spinal nerve (Figure 35-10).

The spinal cord is enclosed by the central spinal canal and is additionally wrapped in three layers of membranes called **meninges** (men-in′jeez; Gr. *meningos,* membrane). In cross section the cord shows two zones (Figure 35-10). An inner zone of gray matter, resembling in shape the wings of a butterfly, contains the cell bodies of motor neurons and interconnecting interneurons (described in the following text). An outer zone of white matter contains bundles of axons and dendrites linking different levels of the cord with each other and with the brain.

Reflex Arc

Many neurons work in groups called **reflex arcs.** There must be at least two neurons in a reflex arc, but usually there are more. The parts of a typical reflex arc are (1) a **receptor,** a sense organ in skin, muscle, or another organ; (2) an **afferent,** or sensory, neuron, which carries impulses toward the central nervous system; (3) the **central nervous system,** where synaptic connections are made between sensory neurons and interneurons; (4) an **efferent,** or motor, neuron, which makes a synaptic connection with the interneuron and carries impulses from the central nervous system; and (5) an **effector,** by which the animal responds to environmental changes. Examples of effectors are muscles, glands, ciliated cells, nematocysts of radiate animals, electric organs of fish, and certain pigmented cells called chromatophores.

A reflex arc in its simplest form contains only two neurons—a sensory (afferent) neuron and a motor (efferent) neuron (for example, the "knee-jerk" or stretch reflex, Figure 35-11). Usually, however, interneurons are interposed between sensory and motor neurons (Figure 35-11). An interneuron may connect afferent and efferent neurons on the same side of the spinal cord or on opposite sides, or it may

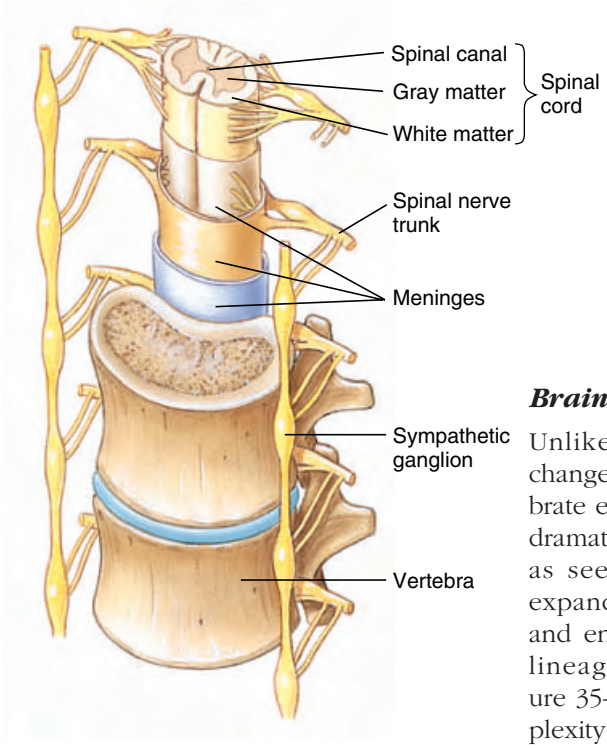


Figure 35-10
Human spinal cord and its protection. Two vertebrae show position of the spinal cord, emerging spinal nerves, and the sympathetic trunk. The cord is wrapped by three layers of membrane (meninges) between two of which lies a protective bath of cerebrospinal fluid.

connect them on different levels of the spinal cord, either on the same or opposite sides.

A **reflex act** is a response to a stimulus acting over a reflex arc. It is involuntary, meaning that it is often not under the control of the will. For example, many vital processes of the body, such as control of breathing, heartbeat, diameter of blood vessels, and sweat gland secretion are reflex acts. Some reflex acts are innate; others are acquired through learning.

In almost any reflex act, a number of reflex arcs are involved. For instance, a single afferent neuron may make synaptic connections with many efferent neurons. In a similar way an efferent neuron may receive impulses from many afferent neurons. Afferent neurons also make connections with ascending sensory neurons, which travel in the white matter of the spinal cord, bringing information about peripheral reflexes to the brain. Reflex activity may then be modified by descending motor neurons, which impinge on the final efferent motor neurons before they leave the spinal cord for the periphery.

Brain

Unlike the spinal cord, which has changed little in structure during vertebrate evolution, the brain has changed dramatically. A primitive linear brain, as seen in fishes and amphibians, expanded to form a deeply fissured and enormously intricate brain in the lineage leading to mammals (Figure 35-12). It reaches its greatest complexity in the human brain, which contains some 35 billion nerve cells, each of which may receive information from tens of thousands of synapses at one time. The ratio between weight of the brain and that of the spinal cord affords a fair criterion of an animal's intelligence. In fish and amphibians this ratio is approximately 1:1; in humans the ratio is 55:1—in other words, the brain is 55 times heavier than the spinal cord. Although the human brain is not the largest (the sperm whale's brain is seven times heavier) nor the most convoluted (that of the porpoise is even more folded), it is by all odds the best in overall performance. This "great ravelled knot," as the British physiologist Sir Charles Sherrington called the human brain, in fact may be so complex that it will never be able to understand its own function!

Although the large size of their brain undoubtedly makes humans the wisest of animals, it is apparent that they can do without much of it and still remain wise. Brain scans of persons with hydrocephalus (enlargement of the head as a result of pressure disturbances that cause the brain ventricles to enlarge many times their normal size) show that although many of them are functionally disabled, others are nearly normal. The cranium of one person with hydrocephalus was nearly filled with cerebrospinal fluid and the only remaining cerebral cortex was a thin layer of tissue, 1 mm thick, pressed against the cranium. Yet this young man, with only 5% of his brain, had achieved first-class honors in mathematics at a British university and was socially normal. This and other similarly dramatic observations suggest that there is enormous redundancy and spare capacity in corticocerebral function. It also suggests that the deep structures of the brain, which are relatively spared in hydrocephalus, may peform functions once believed to be performed solely by the cortex.

Brains of early vertebrates had three principal divisions: a forebrain, or **prosencephalon;** a midbrain, or **mesencephalon;** and a hindbrain, or **rhombencephalon** (Figure 35-13). Each part was concerned with one or more special senses: the forebrain with smell, the midbrain with vision, and the hindbrain with hearing and balance. These primitive but very fundamental concerns of the brain have been in some instances amplified and in others reduced or overshadowed during continued evolution as sensory priorities were shaped by an animal's habitat and way of life.

Hindbrain The **medulla,** the most posterior division of the brain, is really a conical continuation of the spinal cord. The medulla, together with the more anterior midbrain, constitutes the "brain stem," an area that controls numerous vital and largely subconscious activities such as heartbeat, respiration, vascular tone, gastric secretions, and swallowing. The **pons,** also a part of the hindbrain, contains a thick bundle of fibers that carry impulses from one side of the cerebellum to the other, and also connects both medulla and cerebellum to other brain regions.

The **cerebellum,** lying dorsal to the medulla, controls equilibrium, posture, and movement (Figure 35-14). Its development is directly correlated with the animal's mode of locomotion, agility of limb movement, and balance. It is usually weakly developed in amphibians and reptiles, forms that live close to

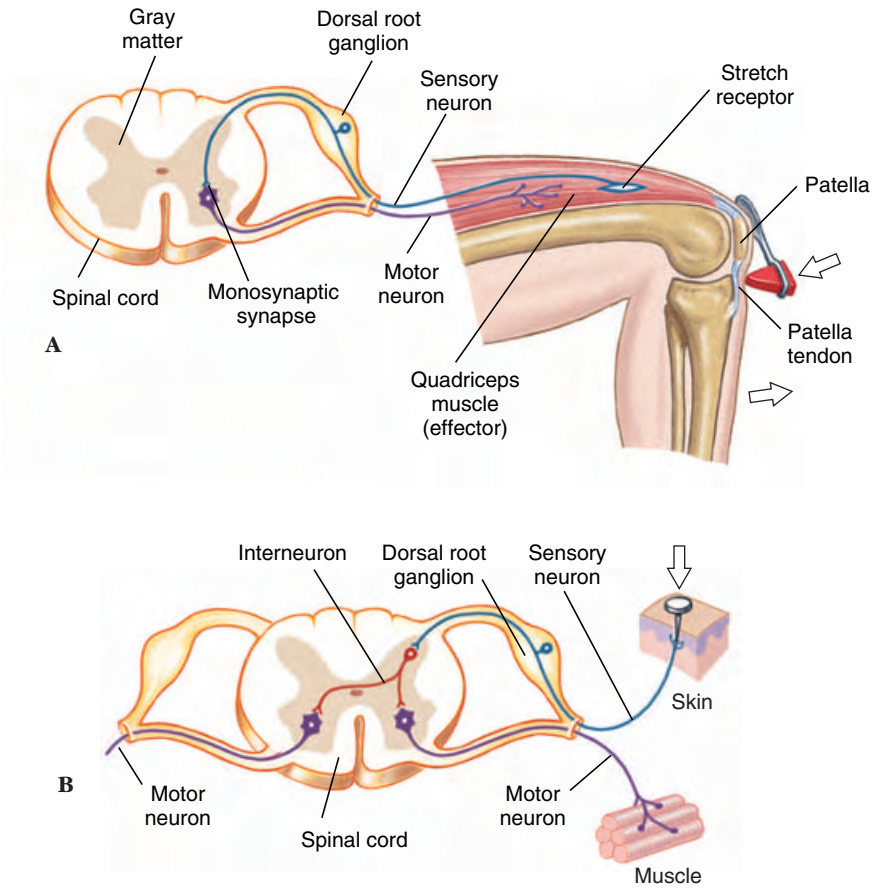


Figure 35-11

The reflex arc. **A,** The "knee-jerk" or stretch reflex, a simple reflex arc. Sudden pressure on the patellar ligament stretches muscles in the upper leg. Impulses generated in stretch receptors are conducted along afferent (sensory) neurons to the spinal cord and relayed directly to an efferent (motor) nerve cell body. Impulses pass along efferent neurons to leg muscles (effectors), stimulating them to contract. **B,** Multisynaptic relfex arc. A more common reflex arc includes interneurons between the sensory and motor neuron. Tack puncture is sensed by pain receptors in the skin and the signal is conducted along afferent fibers to the spinal cord where synaptic connections are made with interneurons. Here, an interneuron is shown making connections with motor neurons on both sides of the spinal cord, such that stimulation of muscle fibers in more than one part of the body (both legs, or example) allows coordination of muscle responses to the tack puncture.

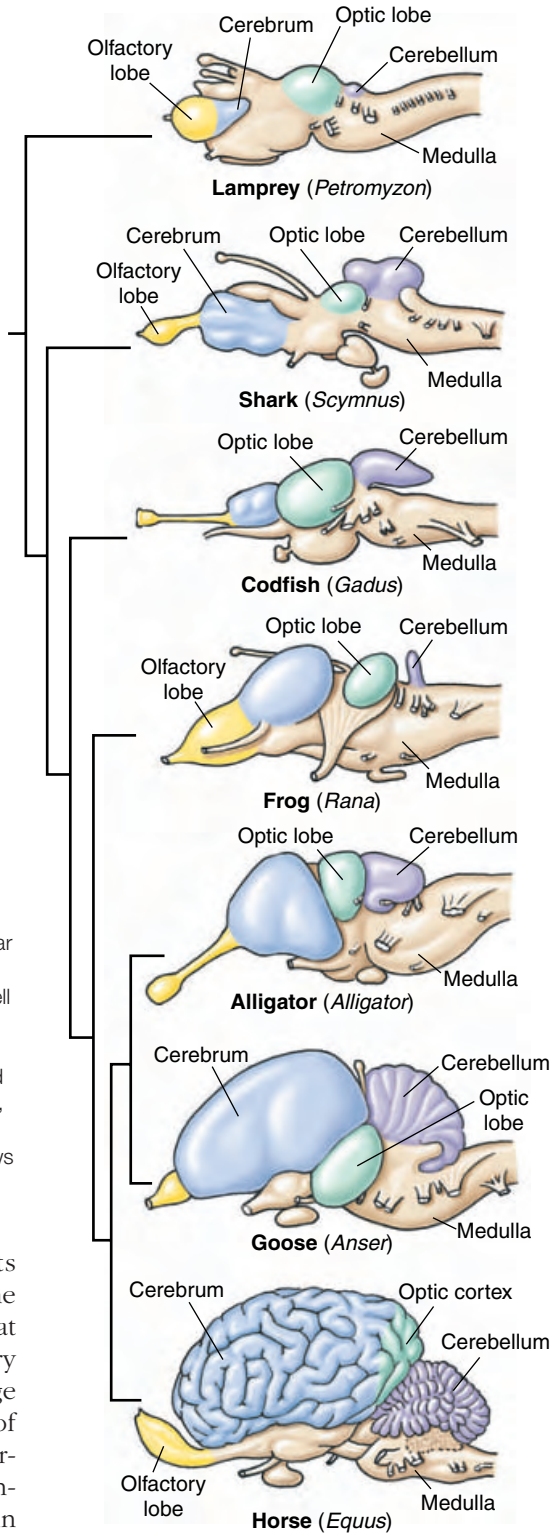
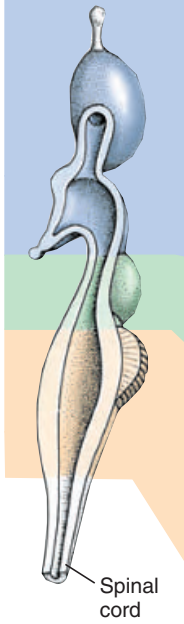


Figure 35-12

Evolution of the vertebrate brain. Note the progressive increase in size of the cerebrum. The cerebellum, concerned with equilibrium and motor coordination, is largest in animals whose balance and precise motor movements are well developed (fishes, birds, and mammals).

the ground, and well developed in the more agile bony fishes. It reaches its apogee in birds and mammals in which it is greatly expanded and folded. The cerebellum does not initiate movement but operates as a precision error-control center, or servomechanism, that programs a movement initiated somewhere else, such as the motor cortex of the cerebrum (Figure 35-14). Primates and especially humans, who possess a manual dexterity far surpassing that of other animals, have the most complex cerebellum. Movements of hands and fingers may involve cerebellar coordination of simultaneous contraction and relaxation of hundreds of individual muscles.

Midbrain The midbrain consists mainly of the **tectum** (including the optic lobes), which contains nuclei that serve as centers for visual and auditory reflexes. (In neurophysiological usage a *nucleus* is a small aggregation of nerve cell bodies within the central nervous system.) The midbrain has undergone little evolutionary change in structure among vertebrates but has changed markedly in function. It mediates the most complex behavior of fishes and amphibians, integrating visual, tactile, and auditory information. Such functions have been gradually assumed by the forebrain in amniotes. In mammals, the midbrain is mainly a



Embryonic vesicle		Main components in adults	Function
Early embryo	Late embryo		
Forebrain (Prosencephalon)	Telencephalon	Cerebrum	Motor area controls voluntary muscle movements; sensory cortex is center of conscious perception of touch, pressure, vibration, pain, temperature, and taste; association areas integrate and process sensory data
	Diencephalon	Thalamus	Part of limbic system; integrates sensory information arriving at thalamus, projects to cerebral frontal lobes
		Hypothalamus	Controls autonomic functions; sets appetitive drives (thirst, hunger, sexual desire) and reproductive behavior; participates in emotional responses; secretes ADH, oxytocin; secretes releasing hormones for anterior pituitary regulation
Midbrain (Mesencephalon)	Mesencephalon	Optic lobes (tectum)	Integrates visual information with other sensory inputs; relays auditory information
		Midbrain nuclei	Involuntary control of muscle tone; processing of incoming sensations and outgoing motor commands
Hindbrain (Rhombencephalon)	Metencephalon	Cerebellum	Involuntary coordination and control of outgoing movements for equilibrium, muscle tone, posture
		Pons	Links cerebellum with other brain centers and with medulla and spinal cord; modifies output of respiratory centers in medulla
	Myelencephalon	Medulla oblongata	Regulates heart rate and force of contraction; vasomotor control; sets rate of respiration; relays information to the cerebellum

Figure 35-13
Divisions of the vertebrate brain.

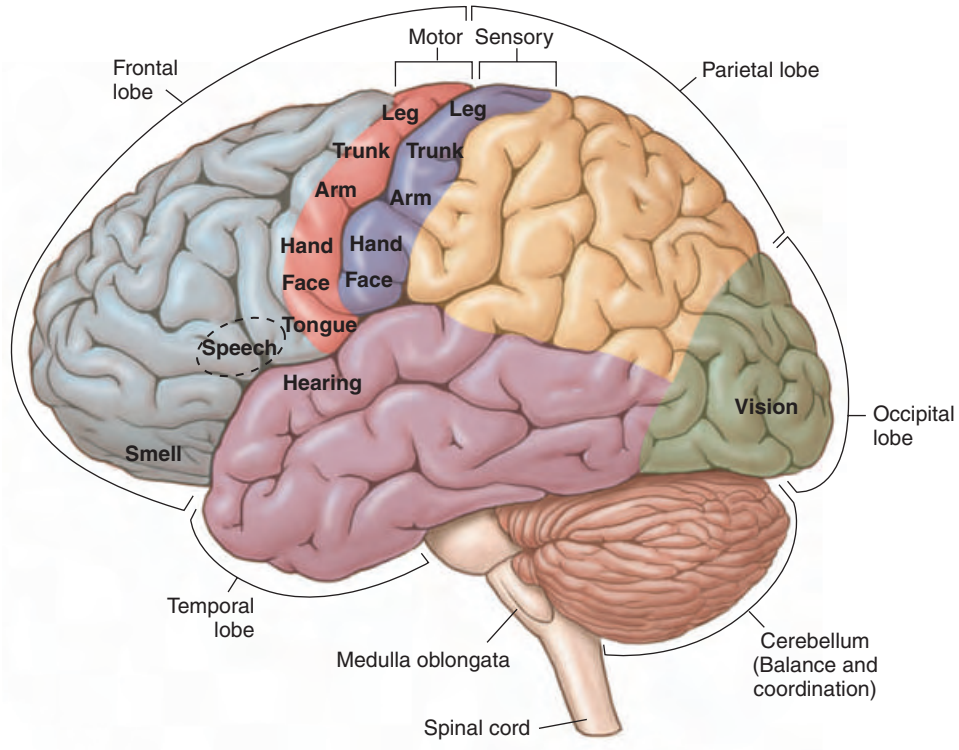


Figure 35-14
External view of the human brain, showing lobes of the cerebrum and localization of major function of the cerebrum and cerebellum.

relay center for information on its way to higher brain centers.

Forebrain Just anterior to the midbrain lie the **thalamus** and **hypothalamus,** the most posterior elements of the forebrain. The egg-shaped thalamus is a major relay station that analyzes and passes sensory information to higher brain centers. In the hypothalamus are several "housekeeping" centers that regulate body temperature, water balance, appetite, and thirst—all functions concerned with maintenance of internal constancy (homeostasis). Neurosecretory cells located in the hypothalamus produce several neurohormones (described in Chapter 36). The hypothalamus also contains centers for regulating reproductive function and sexual behavior, and it participates in emotional behaviors.

The anterior portion of the forebrain, the **cerebrum** (Figure 35-14), can be divided into two anatomically distinct areas, the **paleocortex** and **neocortex.** Originally concerned with

smell, it became well developed in advanced fishes and early terrestrial vertebrates, which depend on this special sense. In mammals and especially in primates the paleocortex is a deep-lying area called a rhinencephalon ("nose brain"), because many of its functions depend on olfaction. Better known as the **limbic system,** it mediates several species-specific behaviors that relate to fulfilling needs such as feeding and sex. One region of the limbic system, the **hippocampus,** has been extensively studied as a site involved with spatial learning and memory. Recently, the hippocampus has gained notoriety since its neurons have been shown to divide in the adult, a previously unknown occurrence in neurons.

Although a late arrival in vertebrate evolution, the neocortex completely overshadows the paleocortex and has become so expanded that it envelops much of the forebrain and all of the midbrain (Figure 35-14). Almost all integrative activities primitively assigned to the midbrain were transferred to the neocortex, or **cerebral cortex** as it is usually called.

Functions in the cerebrum have been localized by direct stimulation of exposed brains of people and experimental animals, postmortem examination of persons suffering from various lesions, and surgical removal of specific brain areas in experimental animals. The cortex contains discrete motor and sensory areas (Figures 35-14 and 35-15) as well as large "silent" regions, called **association areas,** concerned with memory, judgment, reasoning, and other integrative functions. These regions are not directly connected to sense organs or muscles.

Thus in mammals, and especially in humans, separate parts of the brain mediate conscious and unconscious functions. The unconscious mind, all of the brain except the cerebral cortex, governs numerous vital functions that are removed from conscious control: respiration, blood pressure, heart rate, hunger, thirst, temperature balance, salt balance, sexual drive, and basic (sometimes irrational) emotions. It is also a complex endocrine gland that regulates and receives feedback from the body's subservient endocrine system. The conscious mind, the cerebral cortex, is the site of higher mental activities (for example, planning and reasoning), memory, and integration of sensory information. Memory appears to transcend all parts of the brain rather than being a property of any particular part of the brain as was once believed.

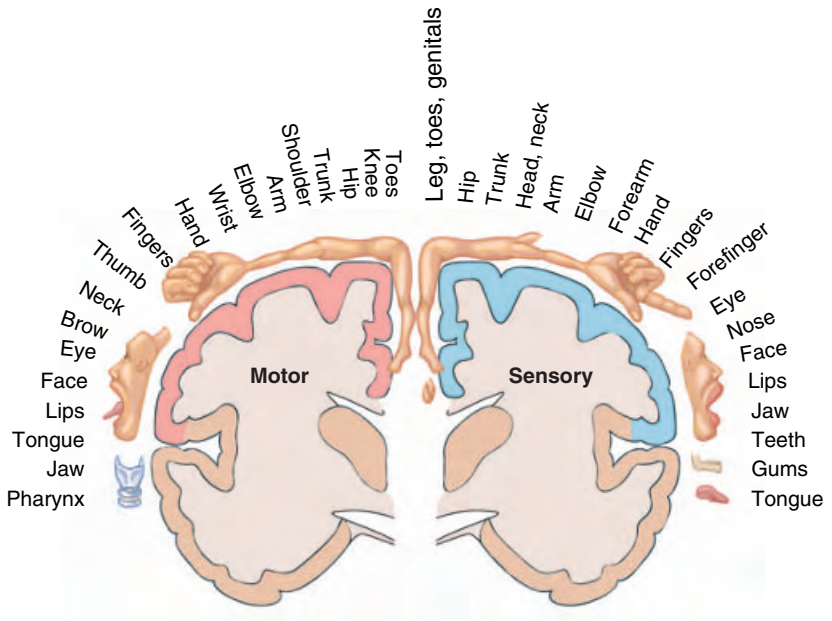


Figure 35-15

Arrangement of sensory and motor cortices. Localizations of sensory terminations from different parts of the body are shown at right; origins of descending motor pathways are shown at left. The motor cortex lies in front of the sensory cortex, so the two are not superimposed. These maps grew out of the 1930s work of Canadian neurosurgeon Wilder Penfield. Recent research shows that the motor cortex is not as orderly as the map suggests; rather correspondence between cortical areas and areas of the body they control is more diffuse.

The right and left hemispheres of the cerebral cortex are bridged through the corpus callosum, a neural connection through which the two hemispheres are able to transfer information and coordinate mental activities. In humans, the two hemispheres of the brain are specialized for entirely different functions: the left hemisphere for language development, mathematical and learning capabilities, and sequential thought processes; and the right hemisphere for spatial, musical, artistic, intuitive, and perceptual activities. Each hemisphere also controls the opposite side of the body. It has been known for a long time that even extensive damage to the right hemisphere may cause varying degrees of left-sided paralysis but has little effect on intellect and speech. Conversely, damage to the left hemisphere usually causes loss of speech and may have disastrous effects on intellect. Since these differences in brain symmetry and function exist at birth, they appear to be inborn rather than the result of developmental or environmental effects as once believed.

Hemispheric specialization has long been considered a unique human trait, but was recently discovered in the brains of songbirds in which one side of the brain is specialized for song production.

Peripheral Nervous System

The peripheral nervous system includes all nervous tissue outside the central nervous system. It consists of two functional divisions: **sensory** or **afferent division,** which brings sensory information to the central nervous system, and **motor** or **efferent division,** which conveys motor commands

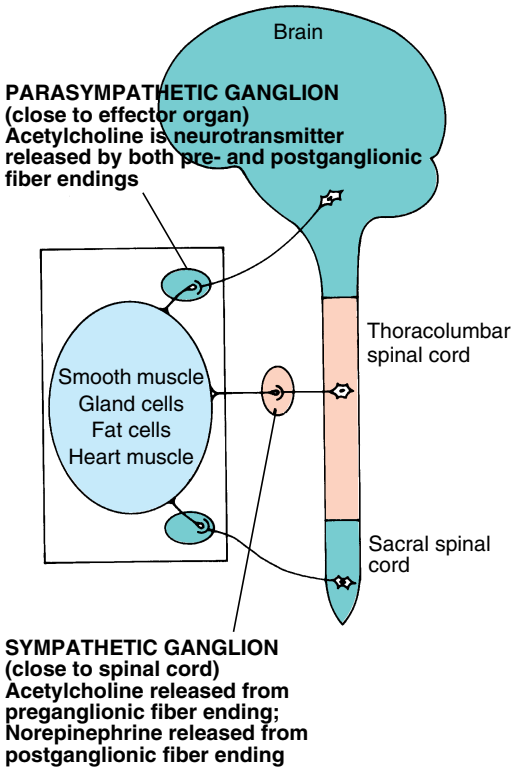


Figure 35-16
General organization of the autonomic nervous system.

to muscles and glands. The efferent division consists of two components: (1) **somatic nervous system,** which innervates skeletal muscle, and (2) **autonomic nervous system,** which innervates smooth muscle, cardiac muscle, and glands.

Autonomic Nervous System The autonomic system governs involuntary, internal functions of the body that do not ordinarily affect consciousness, such as movements of the alimentary canal and heart, contraction of the smooth muscle of blood vessels, urinary bladder, iris of the eye, and others, plus secretions of various glands.

Autonomic nerves originate in the brain or spinal cord as do nerves of the somatic nervous system, but unlike the latter, autonomic fibers consist of not one but two motor neurons. They synapse once after leaving the cord and before arriving at the effector organ. These synapses are located outside the spinal cord in ganglia. Fibers passing from the cord to the ganglia are called preganglionic autonomic fibers; those passing from the ganglia to the effector organs are called postganglionic fibers. These relationships are illustrated in Figure 35-16.

Subdivisions of the autonomic system are the **parasympathetic** and **sympathetic** systems. Most organs in the body are innervated by both sympathetic and parasympathetic fibers, whose actions are antagonistic (Figure 35-17). If one fiber stimulates an activity, the other inhibits it. However, neither kind of nerve is exclusively excitatory or inhibitory. For example, parasympathetic fibers inhibit heartbeat but excite peristaltic movements of the intestine; sympathetic fibers increase heartbeat but inhibit intestinal peristaltic movement.

The parasympathetic system consists of motor neurons, some of which emerge from the brain stem by certain cranial nerves and others of which emerge from the sacral (pelvic) region of the spinal cord (Figures 35-16 and 35-17). In the sympathetic division nerve cell bodies of all the preganglionic fibers are located in the thoracic and upper lumbar areas of the spinal cord. Their fibers exit through the ventral roots of the spinal nerves, separate from these, and go to sympathetic ganglia (Figure 35-17), which are paired and form a chain on each side of the spinal column.

All *preganglionic* fibers, whether sympathetic or parasympathetic, release acetylcholine at the synapse with postganglionic cells. However, parasympathetic *postganglionic* fibers release acetylcholine at their endings, whereas sympathetic *postganglionic* fibers with few exceptions release norepinephrine (also called noradrenaline). This difference is another important characteristic distinguishing the two parts of the autonomic nervous system.

As a general rule the parasympathetic division is associated with nonstressful activities, such as resting, eating, digestion, and urination. The sympathetic division is active under conditions of physical or emotional stress. Under such conditions heart rate increases, blood vessels to the skeletal muscles dilate, blood vessels in the viscera constrict, activity of the intestinal tract decreases, and metabolic rate increases. The importance of these responses in emergency reactions (sometimes called the fright, fight or flight response) are described in the next chapter (p. 764). It should be noted, however, that the sympathetic division is active also during resting conditions in maintaining normal blood pressure and body temperature.

Sense Organs

Animals require a constant inflow of information from the environment to regulate their lives. Sense organs are specialized receptors designed for detecting environmental status and change. An animal's sense organs are its first level of environmental perception; they are channels for bringing information to the brain.

A **stimulus** is some form of energy —electrical, mechanical, chemical, or

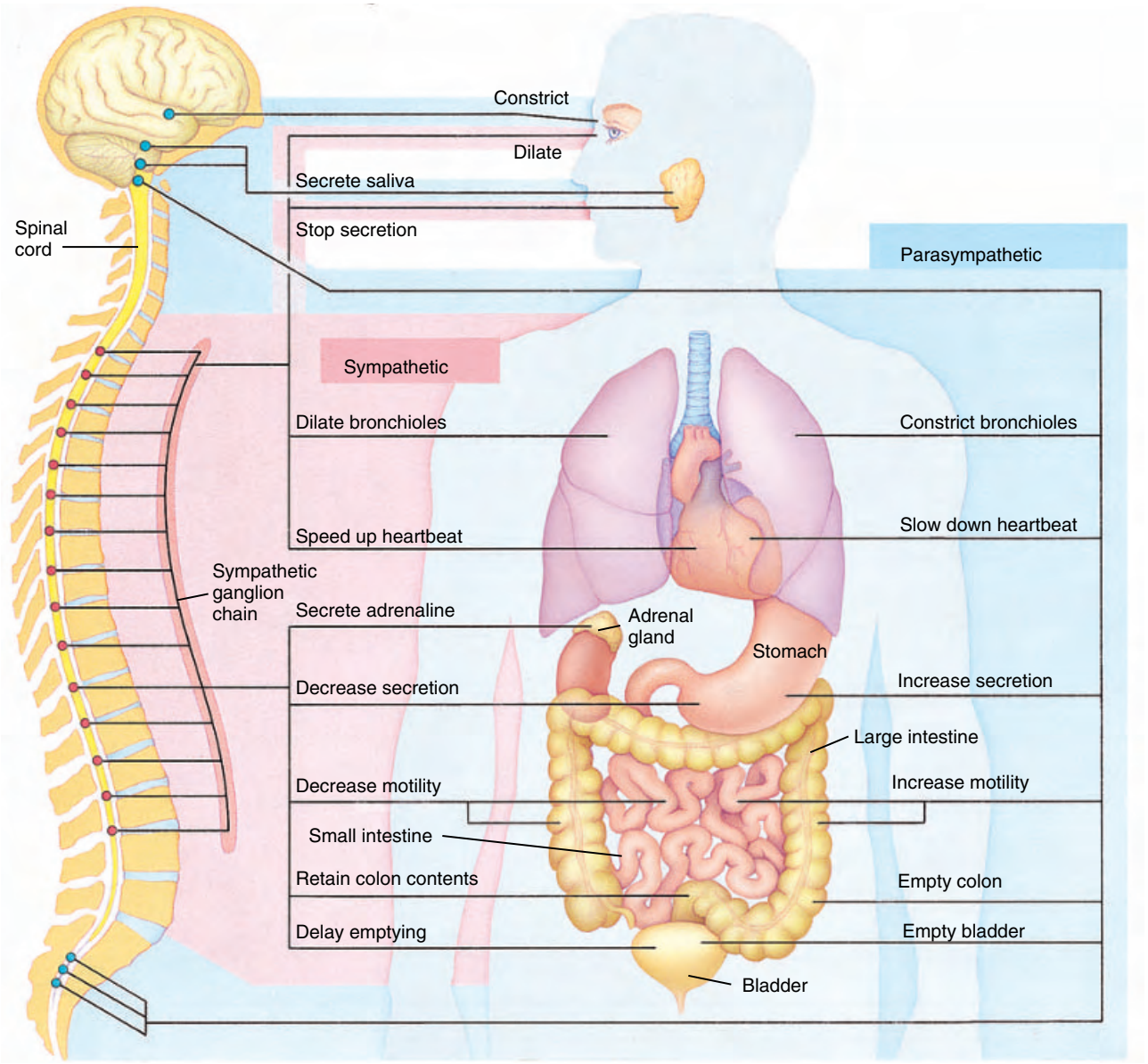


Figure 35-17

Autonomic nervous system in humans. Outflow of autonomic nerves from the central nervous system is shown at left. Sympathetic (*red*) outflow is from the thoracic and lumbar areas of the spinal cord by way of a chain of sympathetic ganglia. Parasympathetic (*blue*) outflow is from the cranial and sacral regions of the central nervous system; parasympathetic ganglia (not shown) are located in or adjacent to the organs innervated. Most organs are innervated by fibers from both sympathetic and parasympathetic divisions.

radiant. A sense organ transforms energy from a stimulus into nerve impulses, the common language of the nervous system. In a very real sense, then, sense organs are biological transducers. A microphone, for example, is a transducer that converts mechanical (sound) energy into electrical energy. Like the microphone, which is sensitive only to sound, sense organs are, as a rule, specific for one kind of stimulus. Thus eyes respond only to light, ears to sound, pressure receptors to pressure, and chemoreceptors to chemical molecules. But again, all forms of energy are converted into nerve impulses.

Since all nerve impulses are qualitatively alike, how do animals perceive and distinguish different sensations of varying stimuli? The answer is that real perception of sensation is done in localized regions of the brain, where each sensory organ has its own hookup. This concept of "labeled lines" of communication to specific brain regions was first described by Johannes Müller in the 1830s, who called this the **law of specific nerve energies.** Impulses arriving at a particular sensory area of the brain can be interpreted in only one way. For example, pressure on the eye causes us to see "stars" or other visual patterns; mechanical distortion of the eye initiates impulses in the optic nerve

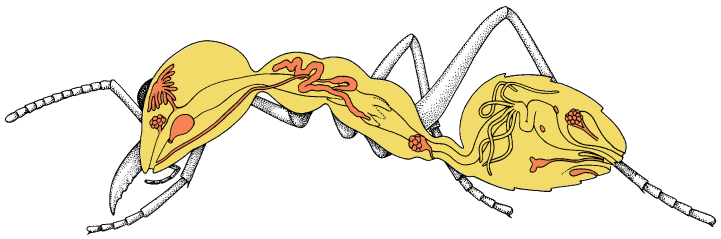


Figure 35-18
Pheromone-producing glands of an ant.

fibers that are perceived as light sensations. Although such an operation probably could never be done, a deliberate surgical switching of optic and auditory nerves would cause the recipient literally to see thunder and hear lightning!

Classification of Receptors

Receptors are traditionally classified by their location. Those near the external surface, called **exteroceptors,** keep the animal informed about the external environment. Internal parts of the body are provided with **interoceptors,** which receive stimuli from internal organs. Muscles, tendons, and joints have **proprioceptors,** which are sensitive to changes in tension of muscles and provide an organism with a sense of body position. Sometimes receptors are classified by the form of energy to which the receptors respond, such as **chemical, mechanical, light,** or **thermal.**

Chemoreception

Chemoreception is the oldest and most universal sense in the animal kingdom. It probably guides behavior of animals more than any other sense. Unicellular forms use **contact chemical receptors** to locate food and adequately oxygenated water and to avoid harmful substances. These receptors elicit an orientation behavior, called **chemotaxis,** toward or away from the chemical source. Most metazoans have specialized **distance chemical receptors,** which are often developed to a remarkable degree of sensitivity. Distance chemoreception, usually called smell or olfaction, guides feeding behavior, location and selection of sexual mates, territorial and trail marking, and alarm reactions of numerous animals.

Social insects and many other animals, including mammals, produce species-specific compounds, called **pheromones,** that constitute a highly developed chemical language. Pheromones are a diverse group of organic compounds that an animal releases to affect the physiology or behavior of another individual of the same species. Ants, for example, are walking batteries of glands (Figure 35-18) that produce numerous chemical signals. These include releaser pheromones, such as alarm and trail pheromones, and primer pheromones, which alter endocrine and reproductive systems of different castes in the colony. Insects bear a variety of chemoreceptors on the surface of the body for sensing specific pheromones, as well as other, nonspecific odors.

In all vertebrates and in insects, the senses of **taste** and **smell** are clearly distinguishable. Although there are similarities between taste and smell receptors, in general taste is more restricted in response and is less sensitive than smell. Central nervous system centers for taste and smell are located in different parts of the brain.

In vertebrates, taste receptors are found in the mouth cavity and especially on the tongue (Figure 35-19), where they provide a means for judging foods before they are swallowed. A **taste bud** consists of a cluster of receptor cells surrounded by supporting cells; it is provided with a small external pore through which the slender tips of the sensory cells project. Chemicals being tasted apparently

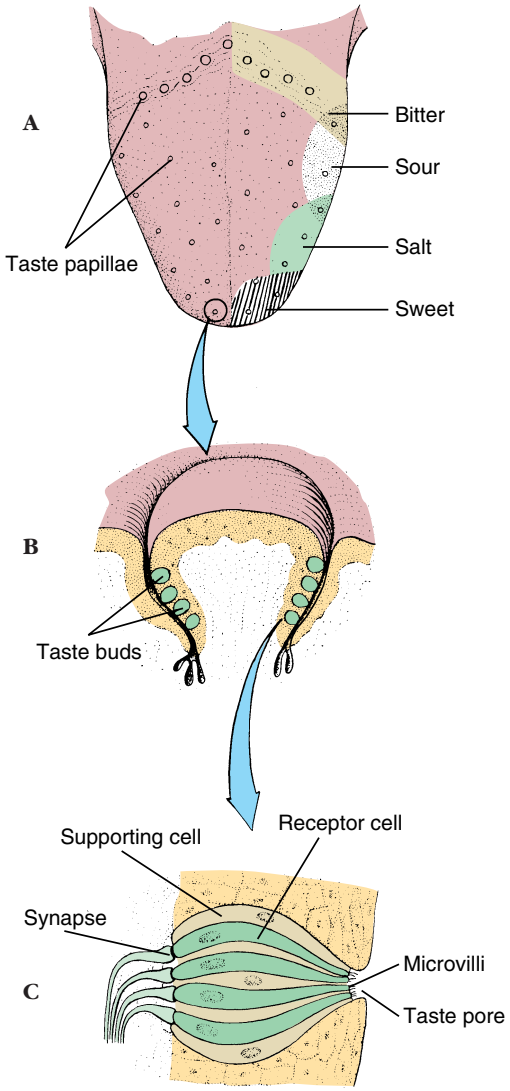


Figure 35-19
Taste receptors. **A,** Surface of human tongue showing regions of maximum sensitivity to the four primary taste sensations. **B,** Position of taste buds on a taste papilla. **C,** Structure of a taste bud.

combine with specific receptor sites on microvilli of the receptor cells. Although the mechanisms are different for each basic taste sensation, receptor cells are depolarized by the specific chemical to which the cell is sensitive and action potentials are generated. These impulses are transmitted across chemical synapses (p. 728) and travel along sensory neurons to specific brains regions. Because receptor cells are subject to wear and tear by abrasive foods, taste buds have a short life (5 to 10 days in mammals) and are continually being replaced.

The four basic taste sensations possessed by humans—sour, salty, bitter, and sweet—are each attributable to a different kind of taste bud. The tastes for salty and sweet are found mainly on the tip, bitter at the base, and sour along the sides of the tongue. Of these, the bitter taste is by far the most sensitive, because it provides early warning against potentially dangerous substances, many of which are bitter.

Smell is more complex than taste, and until very recently odor research has lagged behind other areas of sensory physiology. Although the olfactory sense is a primal sense for many animals, used for identification of food, sexual mates, and predators, olfaction is most highly developed in mammals. Even humans, although a species not celebrated for detecting smells, can discriminate perhaps 20,000 different odors. A human nose can detect 1/25 of one-millionth of 1 mg of mercaptan, the odoriferous substance of skunks. Even so, our olfactory abilities compare poorly with those of other mammals that rely on olfaction for survival. A dog explores new surroundings with its nose much as we do with our eyes. A dog's nose is justifiably renowned; with some odorous sources a dog's nose is at least a million times more sensitive than ours. Dogs are assisted in their proficiency by having a nose located close to the ground where odors from passing creatures tend to linger.

Olfactory endings are located in a special epithelium covered by a thin film of mucus, positioned deep in the nasal cavity (Figure 35-20). Within the epithelium lie millions of olfactory neurons, each with several hairlike cilia protruding from the free end. Odor molecules entering the nose bind to receptor proteins located in the cilia; this binding generates an electrical signal that travels along axons to the olfactory bulb of the brain. From here odor information is sent to the olfactory cortex where odors are analyzed. Odor information is then projected to higher brain centers where they affect emotions, thoughts, and behavior.

Recently, using techniques of gene cloning and molecular hybridization

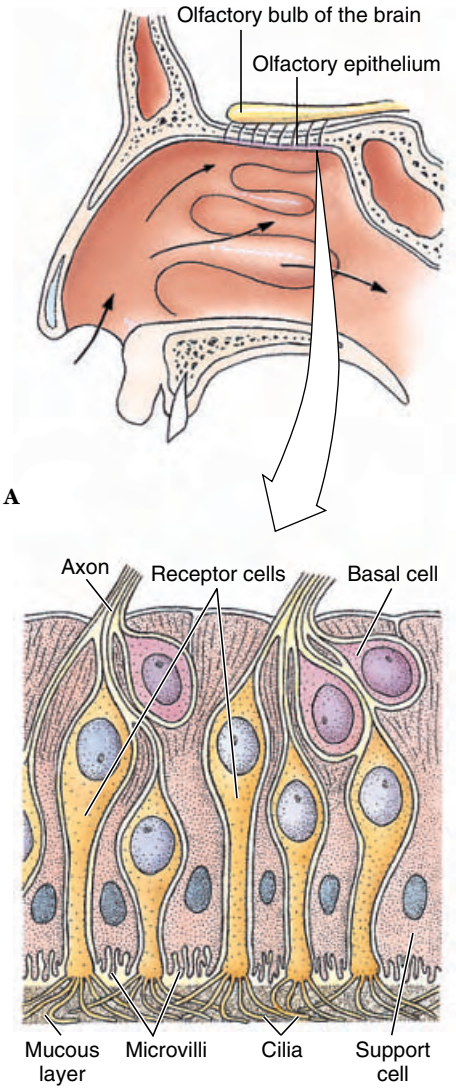


Figure 35-20
Human olfactory epithelium. **A,** The epithelium is a patch of tissue positioned in the roof of the nasal cavity. **B,** It is composed of supporting cells, basal cells, and olfactory receptor cells with cilia protruding from their free ends.

(p. 97), researchers discovered a large family of genes that appears to code for odor reception in mammals (including humans). Each of the 500 to 1000 genes discovered encodes a separate type of odor receptor. Since mammals can detect at least 20,000 different odors, each receptor must respond to several odor molecules, and each odor molecule must bind with several types of receptors, each of which responds to a part of the molecule's structure. Brain mapping techniques have shown that each olfactory neuron projects to a characteristic location on the olfactory bulb, providing a two-dimensional map that identifies which receptors have been activited in the nose. In addition, olfactory neurons expressing the same odor receptor gene converge to a fixed olfactory bulb region, which might provide an explanation for the extremely high sensitivity of smell. Projected to the brain, odor information is recognized as a unique scent.

Because flavor of food depends on odors reaching the olfactory epithelium through the throat passage, taste and smell are easily confused. All "tastes" other than the four basic ones (sweet, sour, bitter, salty) result from flavor molecules reaching the olfactory epithelium in this manner. Food loses its appeal during a common cold because a stuffy nose blocks odors rising from the mouth.

Mechanoreception

Mechanoreceptors are sensitive to quantitative forces such as touch, pressure, stretching, sound, vibration, and gravity—in short, they respond to motion. To interact with their environments, feed themselves, maintain normal postures, and to walk, swim, or fly, animals require a steady flow of information from mechanoreceptors.

Touch

The **pacinian corpuscle,** a relatively large mechanoreceptor that registers deep touch and pressure in mammalian skin, illustrates the general properties of mechanoreceptors. These corpuscles are common in deep layers of skin, connective tissue surrounding muscles and tendons, and the abdominal mesenteries. Each corpuscle consists of a nerve terminus surrounded by a capsule of numerous, concentric, onionlike layers of connective tissue (Figure 35-21). Pressure at any point on the capsule distorts the nerve ending, producing a graded **receptor potential,** a local flow of electric current. Progressively stronger stimuli lead to correspondingly stronger receptor potentials until a **threshold**

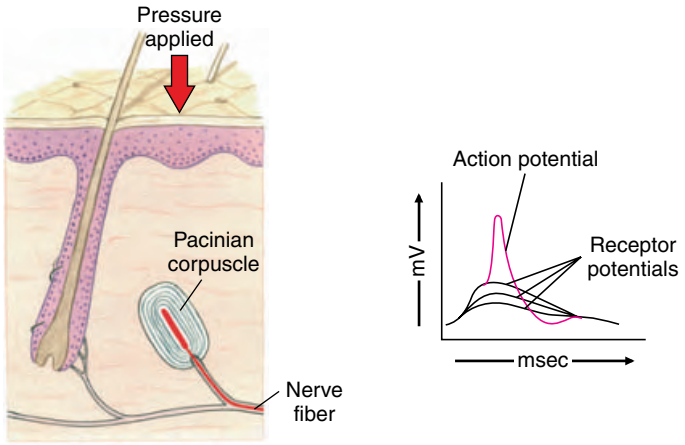


Figure 35-21
Response of pacinian corpuscle to applied pressure. Progressively stronger pressure produces stronger receptor potentials. When the threshold stimulus is reached, an all-or-none action potential is generated in the afferent nerve fiber.

current is produced; this current initiates an action potential in the sensory nerve fiber. Stronger stimuli will produce a burst of action potentials. However, if the pressure is sustained, the corpuscle quickly adjusts to the new shape and no longer responds. This response is called adaptation (not to be confused with the evolutionary meaning of this term [Chapter 6]) and is characteristic of many touch receptors, which are admirably suited to detecting a sudden mechanical change but readily adapt to new conditions. We are aware of new pressures when we put on our shoes in the morning, but we are glad not to be reminded of these pressures all day.

Invertebrates, especially insects, have many kinds of receptors sensitive to touch. Such receptors are well endowed with tactile hairs sensitive to both touch and vibrations. Superficial touch receptors of vertebrates are distributed over the body but tend to be concentrated in areas especially important for exploring and interpreting the environment. In most vertebrates these areas are the face and extremities of limbs. Of the more than half-million separate touch-sensitive spots on the surface of the human body, most are found on the lips, tongue, and fingertips as might be expected based on the large portion of sensory cortex which receives information from these regions (Figure 35-15). The simplest touch receptors are bare nerve-fiber terminals found in skin, but there is an assortment of other kinds of receptors of varying shapes and sizes. Each hair follicle is crowded with receptors that are sensitive to touch.

Pain

Pain receptors are relatively unspecialized nerve fiber endings that respond to a variety of stimuli signaling possible or real damage to tissues. These free nerve endings also respond to other stimuli, such as mechanical movement of the tissue and temperature changes. Pain fibers respond to small peptides, such as substance P and bradykinins, which are released by injured cells. This type of response is termed *slow pain*. *Fast pain* responses (for example, a pin prick, cold or hot stimuli) are a more direct response of the nerve endings to mechanical or thermal stimuli.

Pain is a distress call from the body signaling some noxious stimulus or internal disorder. Although there is no cortical pain center, discrete areas have been located in the brain stem where pain messages from the periphery terminate. These areas contain two kinds of small peptides, endorphins and enkephalins, that have morphinelike or opiumlike activity. When released, they bind with specific opiate receptors in the midbrain. They are the body's own analgesics.

Just as pain is a sign of danger, sensory pleasure is a sign of a stimulus useful to the subject. Pleasure depends on the internal state of an animal and is judged with reference to homeostasis and some physiological set point. Evidence suggests that pleasure and pain states are produced by release of small neuropeptides, called endogenous opioids, within the central nervous system.

Lateral Line System of Fish and Amphibians

A lateral line is a distant touch reception system for detecting wave vibrations and currents in water. Receptor cells, called **neuromasts,** are located on the body surface in aquatic amphibians and some fishes, but in many fishes they are located within canals running beneath the epidermis; these canals open at intervals to the surface (Figure 35-22). Each neuromast is a collection of hair cells with sensory endings, or cilia, embedded in a gelatinous, wedge-shaped mass, the **cupula.** The cupula projects into the center of the lateral line canal so that it bends in response to any disturbance of water on the body surface. The lateral line system is one of the principal sensory systems that guide fishes in their movements and in location of predators, prey, and social partners (p. 516).

Hearing

An ear is a specialized receptor for detecting sound waves in the surrounding environment. Because sound communication and reception are integral to the lives of terrestrial vertebrates, we may be surprised to discover that most invertebrates inhabit a silent world. Only certain arthropod groups—crustaceans, spiders, and insects—have developed true sound-receptor organs. Even among insects, only locusts, cicadas, crickets, grasshoppers, and most moths possess ears, and these are of simple design: a pair of air pockets, each enclosed by a tympanic membrane that passes sound

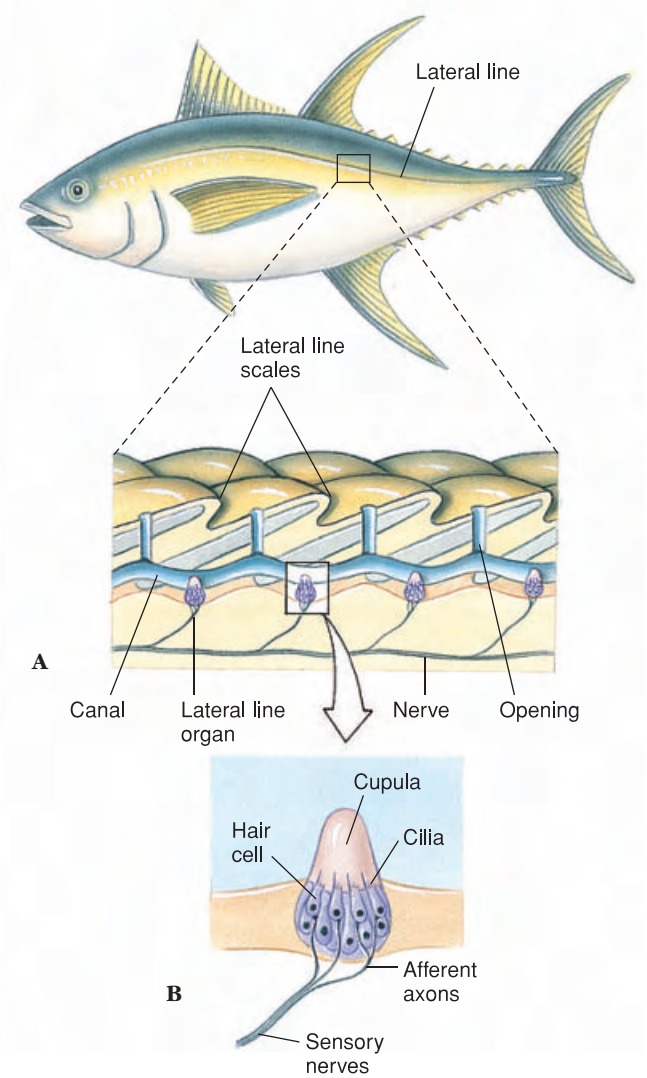


Figure 35-22

Lateral line system. **A,** Lateral line of a bony fish with both exposed and hidden neuromasts. **B,** Structure of a neuromast (lateral line organ).

vibrations to sensory cells. Despite their spartan construction, insect ears are beautifully designed to detect the sound of a potential mate, a rival male, or a predator.

Especially interesting are the ultrasonic detectors of certain nocturnal moths. These have evolved specifically to detect approaching bats and thus lessen the moth's chance of becoming a bat's evening meal (echolocation in bats is described on p. 623). Each moth ear possesses just two sensory receptors, known as A_1 and A_2 (Figure 35-23). The A_1 receptor will respond to ultrasonic cries of a bat that is still too far away to detect the moth. As the bat approaches and its cries increase in intensity, the receptor fires more rapidly, informing the moth that the bat is coming nearer. Since the moth has two ears, its nervous system can determine the bat's position by comparing firing rates from the two ears. The moth's strategy is to fly away before the bat detects it. But if the bat continues its approach, the second (A_2) receptor in each ear, which responds only to high-intensity sounds, will fire. The moth responds immediately with an evasive maneuver, usually making a power dive to a bush or the ground where it is safe because the bat cannot distinguish the moth's echo from those of its surroundings.

In its evolution, the vertebrate ear originated as a balance organ, the **labyrinth.** In all jawed vertebrates, from fishes to mammals, the labyrinth has a similar structure, consisting of two small chambers called the **saccule** and the **utricle,** and three **semicircular canals** (Figure 35-24). In fish the base of the saccule is extended into a tiny pocket (the **lagena**) that, during the evolution of the vertebrates, developed into the hearing receptor of tetrapods. With continued elaboration and elongation in the birds and mammals, the fingerlike lagena was modified go form the **cochlea.**

The human ear (Figure 35-25) is representative of mammalian ears. The outer, or external, ear collects sound waves and funnels them through the **auditory canal** to the eardrum or **tympanic membrane** lying next to the middle ear. The middle ear is an air-filled chamber containing a remarkable chain of three tiny bones, or ossicles, known as the **malleus** (hammer), **incus** (anvil), and **stapes** (stirrup), named because of their fancied resemblance to these objects. These bones conduct sound waves across the middle ear (Figure 35-25B). The bridge of bones is so arranged that the force of sound waves pushing against the tympanic membrane is amplified as much as 90 times where the stapes contacts the **oval window** of the inner ear. Muscles attached to the middle ear bones contract when the ear receives very loud noises, providing the inner ear some protection from damage. The middle ear connects with the pharynx by means of the **eustachian tube,** which permits pressure equalization on both sides of the tympanic membrane.

The origin of the three tiny bones of the mammalian middle ear—the malleus, incus, and stapes—is one of the most extraordinary and well-documented transitions in vertebrate evolution. Amphibians, reptiles, and birds have a single rodlike ear ossicle, the stapes (also called the columella), which originated as a jaw support (the hyomandibular) as seen in fishes (see Figure 25-16, p.504). With evolution of the earliest tetrapods, the braincase became firmly

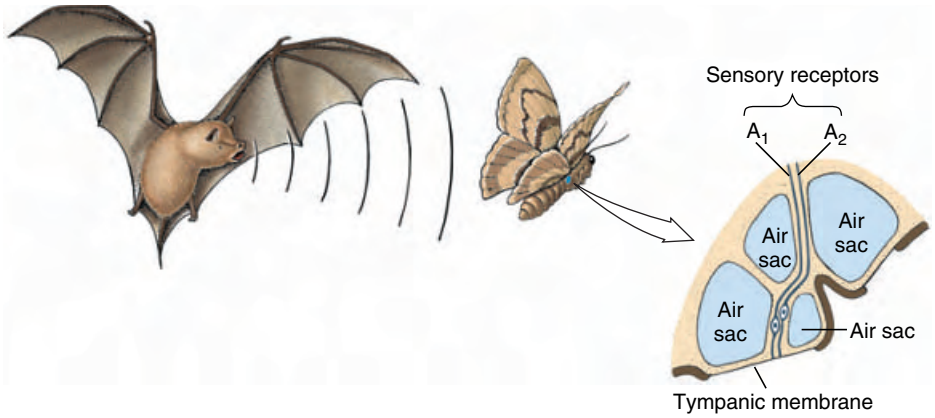


Figure 35-23
Ear of a moth used to detect approaching bats. See text for explanation.

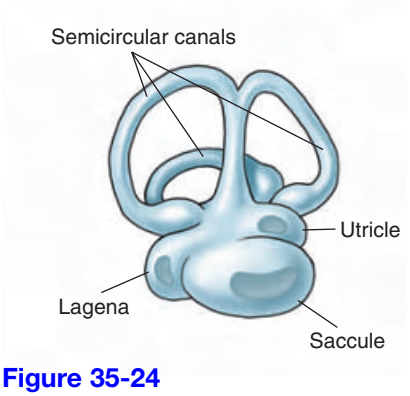


Figure 35-24
Vestibular apparatus of a teleost fish, containing three semicircular canals, which respond to angular acceleration; two balance organs (utricle and saccule), which are static receptors that signal the fish's position in relation to gravity; and a small chamber, the lagena, which is specialized for sound reception.

sutured to the skull, and the hyomandibular, no longer needed to brace the jaw, became converted into the stapes. In a similar way, the two additional ear ossicles of the mammalian middle ear—the malleus and incus—originated from parts of the jaw of early vertebrates. The quadrate bone of the reptilian upper jaw became the incus, and the articular bone of the lower jaw became the malleus. Homology of reptilian jaw bones to mammalian ear bones is clearly documented in the fossil record and in embryological development of mammals.

Within the inner ear is the organ of hearing, the **cochlea** (Gr. *cochlea,* snail's shell), which is coiled in mammals, making two and one half turns in humans (Figure 35-25B). The cochlea is divided longitudinally into three tubular canals running parallel with one another. This relationship is indicated in Figure 35-26. These canals become progressively smaller from the base of the cochlea to the apex. One of these canals is called the **vestibular canal;** its base is closed by the oval window. The **tympanic canal,** which is in communication with the vestibular canal at the tip of the cochlea, has its base closed by the **round window.** Between these two canals is the **cochlear duct,** which contains the **organ of Corti,** the actual sensory apparatus (Figure 35-25C). Within the organ of Corti are fine rows of hair cells that run lengthwise from the base to the tip of the cochlea. At least 24,000 hair cells are present in the human ear. The 80 to 100 "hairs" on each cell are actually microvilli and a single large cilium, which project into the endolymph of the cochlear canal. Each cell is connected with neurons of the auditory nerve. The hair cells rest on the **basilar membrane,** which separates the tympanic canal and cochlear duct, and they are covered by the **tectorial membrane,** lying directly above them (Figure 35-25D).

When a sound wave strikes the ear, its energy is transmitted through the ossicles of the middle ear to the oval window, which oscillates back and forth, driving the fluid of the vestibular and tympanic canals before it. Because these fluids are noncompressible, an inward movement of the oval window produces a corresponding outward movement of the round window. The fluid oscillations also cause the basilar membrane with its hair cells to vibrate simultaneously.

According to the **place hypothesis of pitch discrimination** formulated by Georg von Békésy, different areas of the basilar membrane respond to different frequencies; for every sound frequency, there is a specific "place" on the basilar membrane where the hair cells respond to that frequency. Initial displacement of the basilar membrane starts a wave traveling down the membrane, much as flipping a rope at one end starts a wave moving down the rope (Figure 35-27). The displacement wave increases in amplitude as it moves from the oval window toward the apex of the cochlea, reaching a maximum at the region of the basilar membrane where the natural frequency of the membrane corresponds to the sound frequency. Here, the membrane vibrates with such ease that the energy of the traveling wave is completely dissipated. Hair cells within the organ of Corti in that region are stimulated and the impulses conveyed to the fibers of the auditory nerve. Isolated hair cells have been shown to respond to a particular band of frequencies depending on their location within the cochlea. Thus, impulses that are carried by certain fibers of the auditory nerve are interpreted by the hearing center as particular tones. The **loudness** of a tone depends on the number of hair cells stimulated, whereas the **timbre,** or quality, of a tone is produced by the pattern of hair cells stimulated by sympathetic vibration. This latter characteristic of tone enables us to distinguish between different human voices and different musical instruments, although the notes in each case may be of the same pitch and loudness.

Most recent auditory research has focused on a more active role for the hair cells within the organ of Corti. Experiments have demonstrated that outer hair cells may respond to sound waves by changing their length and thus mechanically altering the position of the basilar and tectorial membranes.

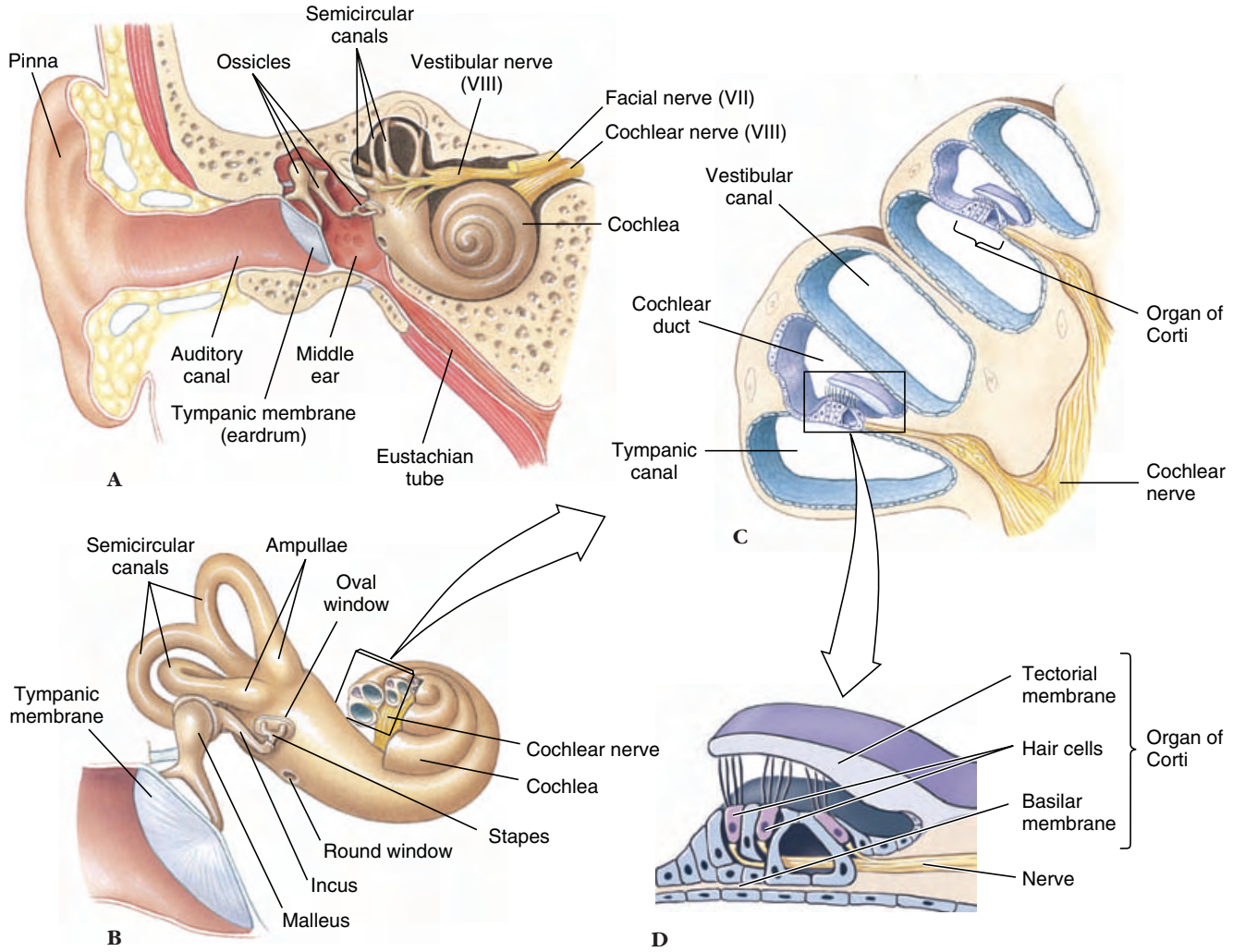


Figure 35-25

Human ear. **A,** Longitudinal section showing external, middle, and inner ear. **B,** Enlargement of middle ear and inner ear. The cochlea of the inner ear has been opened to show the arrangement of canals within. **C,** Enlarged cross section of cochlea showing the organ of Corti. **D,** Detail of ultrastructure of the organ of Corti.

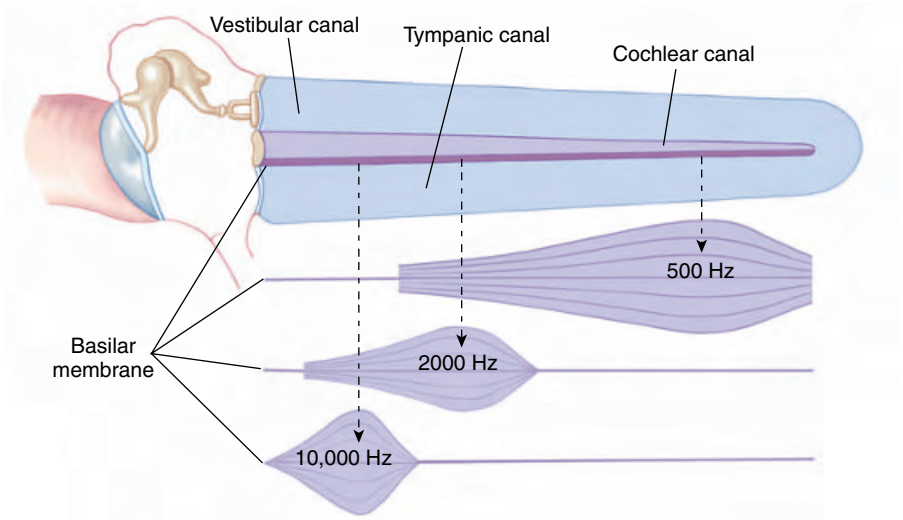


Figure 35-26

Frequency localization in the cochlea of the mammalian ear as it would appear with the cochlea stretched out. Sound waves transmitted to the oval window produce vibration waves that travel down the basilar membrane. High-frequency vibrations cause the membrane to resonate near the oval window. Low-frequency tones travel farther down the basilar membrane.

Although a function of such movements is not yet established, it has been suggested that this active response of these receptor cells in the organ of Corti might increase both the sensitivity and selectivity of hearing.

Equilibrium

In invertebrates, specialized sense organs for monitoring gravity and low-frequency vibrations often appear as **statocysts.** Each is a simple sac lined with hair cells and containing a heavy calcareous structure, the **statolith** (Figure 35-28). The delicate, hairlike filaments of sensory cells are activated by the shifting position of the statolith when the animal changes position. Statocysts are found in many invertebrate phyla from radiates to arthropods. All are built on similar principles.

The vertebrate organ of equilibrium is the **labyrinth.** It consists of two small chambers **(saccule** and **utricle)** and three **semicircular canals** (Figure 35-25B). The utricle and saccule are static balance organs that, like invertebrate statocysts, give information about the position of the head or body with respect to the force of gravity. As the head is tilted in one direction or another, stony accretions press on different groups of hair cells; these cells send nerve impulses to the brain, which interprets this information with reference to head position.

The semicircular canals of vertebrates are designed to respond to **rotational acceleration** and are relatively insensitive to linear acceleration. The three semicircular canals are at right angles to each other, one for each axis of rotation. They are filled with fluid (endolymph), and within each canal is a bulblike enlargement, the **ampulla,** which contains hair cells. The hair cells are embedded in a gelatinous membrane, the **cupula,** which projects into the fluid. The cupula is similar in structure to the cupula of the lateral line system of fishes (p. 516). When the head rotates, fluid in the canal at first tends not to move because of inertia. Since the cupula is attached, its free end is pulled in the direction opposite the direction of rotation (Figure 35-29). Bending of the cupula distorts and excites the hair cells embedded in it, and this stimulation increases the discharge rate over afferent nerve fibers leading from the ampulla to the brain. This increased discharge rate produces the sensation of rotation. Since the three canals of each ear are in different planes, acceleration in any direction stimulates at least one ampulla.

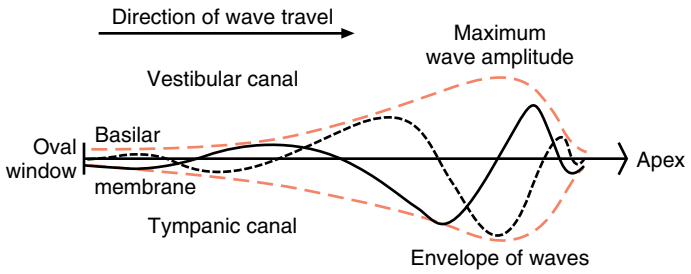


Figure 35-27

Traveling waves along the basilar membrane. The oval window is at left, and the cochlear apex at right. The two wave formations (*solid* and *dashed lines*) occur at separate instants of time. The curves in color represent the extreme displacements of the membrane by traveling waves.

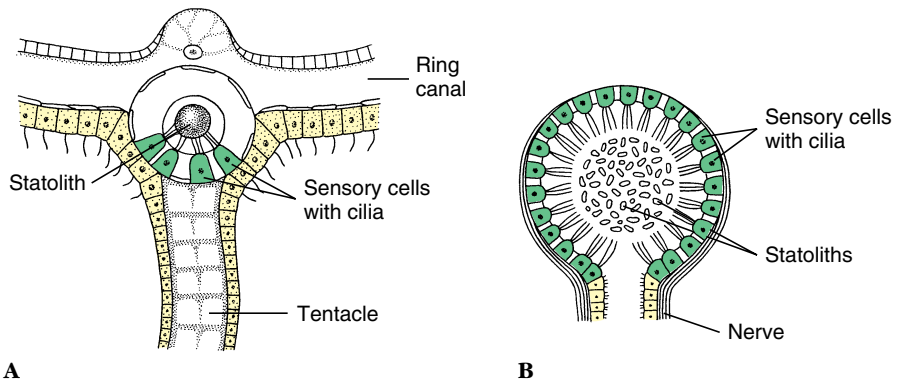


Figure 35-28

Types of statocysts, static balance organs of invertebrates. **A,** Statocyst of the medusa of the hydrozoan *Obelia.* **B,** Statocyst of the bivalve mollusc *Pecten.*

Photoreception: Vision

Light-sensitive receptors are called **photoreceptors.** These receptors range from simple light-sensitive cells scattered randomly on the body surface of many invertebrates (dermal light sense) to the exquisitely developed camera-type eye of vertebrates. Eyespots of astonishingly advanced organization appear even in some unicellular forms. That of the dinoflagellate *Nematodinium* bears a lens, a light-gathering chamber, and a photoreceptive pigment cup—all developed within a single-celled organism (Figure 35-30). The dermal light receptors of many invertebrates are of much simpler design. They are far less sensitive than optic receptors, but they are important in locomotory orientation, pigment distribution in chromatophores, photoperiodic adjustment of reproductive cycles, and other behavioral changes.

More highly organized eyes, many capable of excellent image formation, are based on one of two different principles: either a single-lens, camera-type

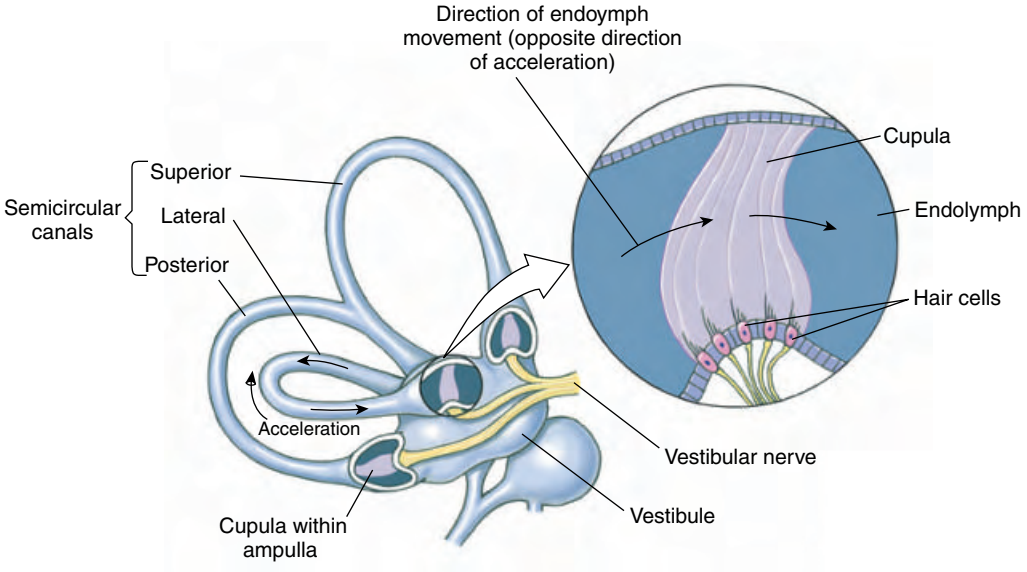


Figure 35-29

How the semicircular canals respond to angular acceleration. Because of inertia, endolymph in the semicircular canal corresponding to the plane of motion moves past the cupula in a direction opposite to that of angular acceleration. Movement of the cupula stimulates hair cells.

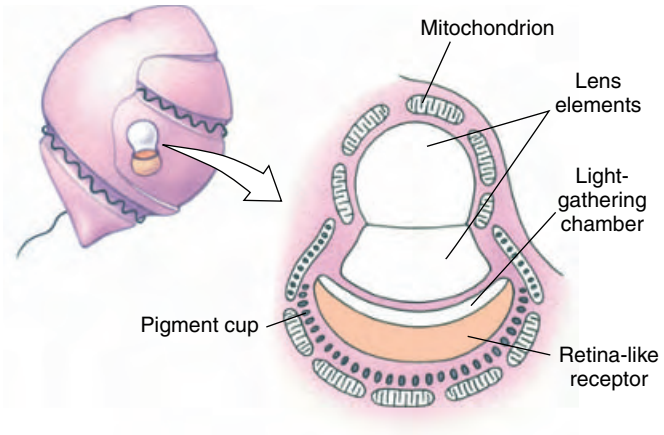


Figure 35-30

Eyespot of the dinoflagellate *Nematodinium.*

eye such as those of cephalopod molluscs and vertebrates; or a multifaceted (compound) eye as in arthropods. Arthropod **compound eyes** are composed of many independent visual units called **ommatidia** (Figure 35-31). The eye of a bee contains about 15,000 of these units, each of which views a separate narrow sector of the visual field. Such eyes form a mosaic of images of varying brightness from the separate units. Resolution (the ability to see objects sharply) is poor compared with that of a vertebrate eye. A fruit fly, for example, must be closer than 3 cm to see another fruit fly as anything but a single spot. However, a compound eye is especially well suited to detecting motion, as anyone who has tried to swat a fly knows.

Eyes of certain annelids, molluscs, and all vertebrates are built like a camera—or rather we should say that a camera is modeled somewhat after vertebrate eyes. A camera-type eye contains in the front a light-tight chamber and lens system, which focuses an image of the visual field on a light-sensitive surface (the retina) in the back (Figure 35-32).

The spherical eyeball is built of three layers: (1) a tough outer white **sclera** for support and protection, (2) middle **choroid coat,** containing blood vessels for nourishment, and (3) light-sensitive **retina** (Figure 35-32). The **cornea** is a transparent anterior modification of the sclera. A circular, pigmented curtain, the **iris,** regulates the size of the light opening, the **pupil.** Just behind the iris is the **lens,** a transparent, elastic oval disc that, with the aid of **ciliary muscles,** can alter the curvature of the lens and bend light rays to focus an image on the retina. In terrestrial vertebrates the cornea actually does most of the bending of light rays, whereas the lens adjusts focus for near and far objects. Between cornea and lens is an **outer chamber** filled with watery **aqueous**

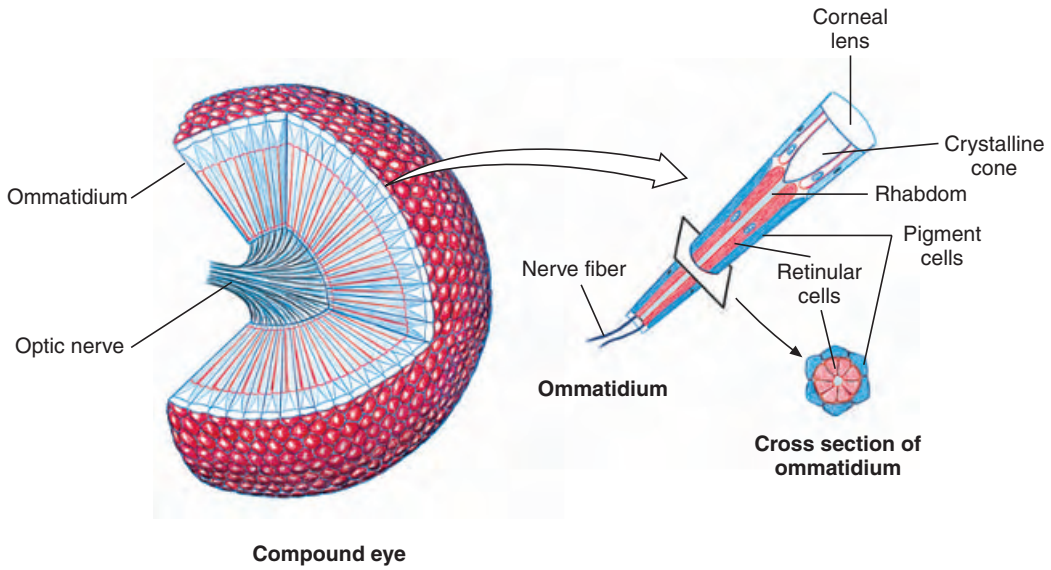


Figure 35-31
Compound eye of an insect. A single ommatidium is shown enlarged at right.

humor; between lens and retina is a much larger **inner chamber** filled with viscous **vitreous humor.**

The retina is composed of several cell layers (Figure 35-33). The outermost layer, closest to the sclera, consists of pigment cells. Adjacent to this layer are the photoreceptors, **rods** and **cones.** Approximately 125 million rods and 1 million cones are present in each human eye. Cones are primarily concerned with color vision in ample light; rods, with colorless vision in dim light. Next is a network of **intermediate neurons** (bipolar, horizontal, and amacrine cells) that process and relay visual information from the photoreceptors to the ganglion cells whose axons form the optic nerve. The network permits much convergence, especially for rods. Information from several hundred rods may converge on a single ganglion cell, an adaptation that greatly increases the effectiveness of rods in dim light. Cones show very little convergence. By coordinating activities between different ganglion cells, and adjusting the sensitivities of bipolar cells, horizontal and amacrine cells improve overall contrast and quality of the visual image.

The **fovea centralis** or **fovea,** the region of keenest vision, is located in the center of the retina (Figure 35-32), in direct line with the center of the lens and cornea. It contains only cones, a vertebrate specialization for diurnal (daytime) vision. The acuity of an animal's eyes depends on the density of cones in the fovea. The human fovea and that of a lion contain approximately 150,000 cones per square millimeter. But many water and field birds have up to 1 million cones per square millimeter. Their eyes are as good as our eyes would be if aided by eight-power binoculars.

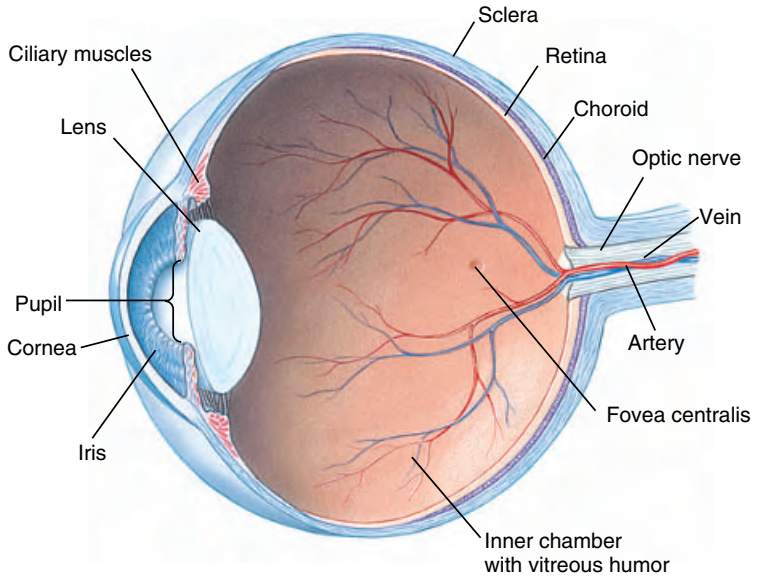


Figure 35-32
Structure of the human eye.

One of several marvels of the vertebrate eye is its capacity to compress the enormous range of light intensities presented to it into a narrow range that can be handled by optic nerve fibers. Light intensity between a sunny noon and starlit night differs by more than 10 billion to 1. Rods quickly saturate with high light intensity, but cones do not; they shift their operating range with changing ambient light intensity so that a high-contrast image is perceived over a broad range of light

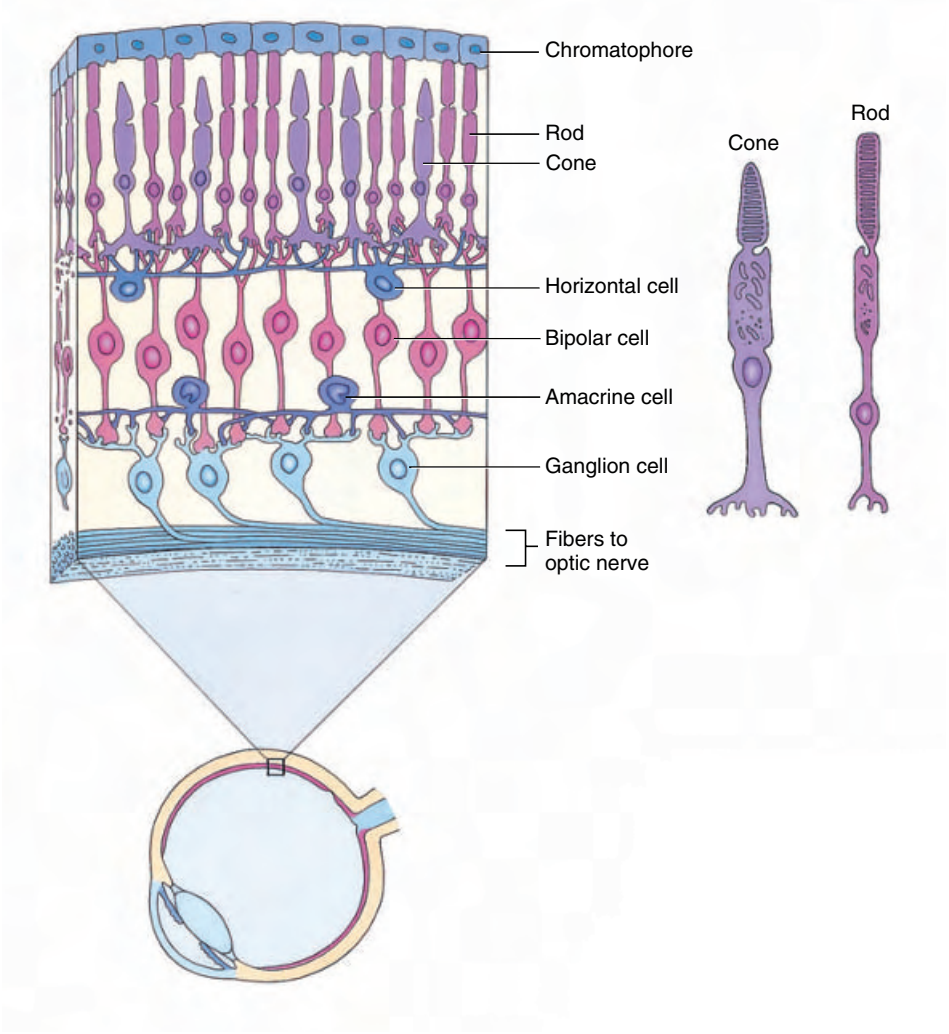


Figure 35-33
Structure of a primate retina, showing organization of intermediate neurons that connect photoreceptor cells to ganglion cells of the optic nerve.

conditions. This shift is made possible by complex interactions among the network of nerve cells that lie between the cones and the ganglion cells that generate the retinal output to the brain.

At the peripheral parts of the retina only rods are found. Rods are high-sensitivity receptors for dim light. At night, the cone-filled fovea is unresponsive to low levels of light and we become functionally color blind ("at night all cats are gray"). Under nocturnal conditions, the position of greatest visual acuity is not at the center of the fovea but at its edge. Thus it is easier to see a dim star at night by looking slightly to one side of it.

Chemistry of Vision

Both rods and cones contain light-sensitive pigments known as **rhodopsins.** Each rhodopsin molecule consists of a large protein, **opsin,** which behaves as an enzyme, and a small carotenoid molecule, **retinal,** a derivative of vitamin A. When a quantum of light strikes the photopigment and is absorbed by the rhodopsin molecule, retinal is isomerized, changing the shape of the molecule. This molecular change triggers the enzymatic activity of opsin, which sets in motion a biochemical sequence of several steps. This complex sequence behaves as an excitatory cascade that vastly amplifies the energy of a single photon to generate a nerve impulse in the rod or cone.

The amount of intact rhodopsin in the retina depends on the intensity of light reaching the eye. A dark-adapted eye contains much rhodopsin and is very sensitive to weak light. Conversely in a light-adapted eye, most of the rhodopsin is split into retinal and opsin. It takes approximately half an hour for a light-adapted eye to accommodate to darkness, while the rhodopsin level gradually increases.

Color vision

Cones function to perceive color and require 50 to 100 times more light for stimulation than do rods. Consequently, night vision is almost totally rod vision. Unlike humans, who have both day and night vision, some vertebrates specialize for one or the other. Strictly nocturnal animals, such as bats and owls, have pure rod retinas. Purely diurnal forms, such as the common gray squirrel and some birds, have only cones; they are virtually blind at night.

In 1802 the English physician and physicist Thomas Young speculated that we see color by relative excitation of three kinds of photoreceptors: one each for red, green, and blue. In the 1960s Young's prescient hypothesis was eventually supported through the combined work of several groups of researchers. Humans have three types of cones, each containing a visual pigment that responds to a particular wavelength of light (Figure 35-34). Blue cones absorb the most light at 430 nm, green cones at 540 nm, and red cones at 575 nm. Variation in the structure of opsin produces the different visual pigments found in rods and the three types of cones. Colors are perceived by comparing levels of excitation of the three different kinds of cones. For example, a light having a wavelength of 530 nm would excite green cones 95%, red cones about 70%, and blue cones not at all. This comparison is made both in nerve circuits in the

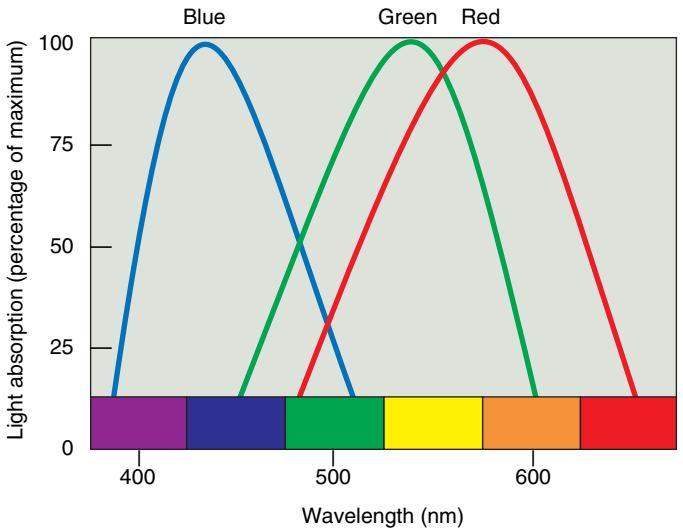


Figure 35-34
The absorption spectrum of human vision. Three types of visual pigments in cones absorb maximally at 430 nm (blue cones), 540 nm (green cones), and 575 nm (red cones).

retina and in the visual cortex of the brain, and the brain interprets this combination as green.

Color vision occurs in some members of all vertebrate groups with the possible exception of amphibians. Bony fishes and birds have particularly good color vision. Surprisingly, most mammals are color blind; exceptions are primates and a few other species such as squirrels.

Summary

The nervous system is a rapid communication system that interacts continuously with the endocrine system to control coordination of body function. The basic unit of nervous integration in all animals is the neuron, a highly specialized cell designed to conduct self-propagating impulses, called action potentials, to other cells. Action potentials are transmitted from one neuron to another across synapses which may be either electrical or chemical. The thin gap between neurons at chemical synapses is bridged by a chemical neurotransmitter molecule, which is released from the synaptic knob, and can be either stimulatory or inhibitory.

The simplest organization of neurons into a system is the nerve net of cnidarians, basically a plexus of nerve cells that, with additions, is the basis of nervous systems of several invertebrate phyla. With the appearance of ganglia (nerve centers) in bilateral flatworms, nervous systems differentiated into central and peripheral divisions. In vertebrates, the central nervous system consists of a brain and spinal cord. Fishes and amphibians have a three-part linear brain, whereas in mammals, the cerebral cortex has become a vastly enlarged multicomponent structure that has assumed the most important integrative activities of the nervous system. It completely overshadows the ancient brain, which is consigned to the role of relay center and to serving numerous unconscious but nonetheless vital functions such as breathing, blood pressure, and heart rate.

In humans the left cerebral hemisphere is usually specialized for language and mathematical skills while the right hemisphere is specialized for visual-spatial and musical skills.

The peripheral nervous system connects the central nervous system to receptors and effector organs. It is divided broadly into an afferent system, which conducts sensory signals to the central nervous system, and an efferent system, which conveys motor impulses to effector organs. This efferent system is subdivided into the somatic nervous system, which innervates skeletal muscle, and the autonomic nervous system, which innervates smooth and cardiac muscle and glands. The autonomic nervous system is subdivided into anatomically distinct sympathetic and parasympathetic systems, each of which sends fibers to most body organs. Generally the sympathetic system governs excitatory activities and the parasympathetic system governs maintenance and restoration of body resources.

Sensory organs are receptors designed especially to respond to internal or environmental change. The most primitive and ubiquitous sense is chemoreception. Chemoreceptors may be contact receptors such as the vertebrate sense of taste, or distance receptors such as smell, which detects airborne molecules. In both cases, a specific chemical interacts with a particular receptor and results in impulses that are transmitted to, and interpreted by, the brain. In spite of the similarity between these two senses, the sense of smell is far more sensitive and complex.

Receptors for touch, pain, equilibrium, and hearing are all mechanical force receptors. Touch and pain receptors are characteristically simply structures, but hearing and equilibrium are highly specialized senses based on special hair cells that respond to mechanical deformation. Sound waves received by the ear are mechanically amplified and transmitted to the inner ear where different areas of the cochlea respond to different sound frequencies. Equilibrium receptors, also located in the inner ear, consist of two saclike static balance organs and three semicircular canals that detect rotational acceleration.

Vision receptors (photoreceptors) are associated with special pigment molecules that photochemically decompose in the presence of light and, in doing so, trigger nerve impulses in optic fibers. The advanced compound eye of arthropods is especially well suited to detecting motion in the visual field. Vertebrates have a camera eye with focusing optics. The photoreceptor cells of the retina are of two kinds: rods, designed for high sensitivity with dim light, and cones, designed for color vision in daylight. Cones predominate in the fovea centralis of human eyes, the area of keenest vision. Rods are more abundant in peripheral areas of the retina.

Review Questions

1. Define the following terms: neuron, axon, dendrite, myelin sheath, afferent neuron, efferent neuron, association neuron.
2. Glial cells far outnumber neurons and contribute roughly half the weight of the mammalian nervous system. Offer examples of functions glial cells perform in the peripheral nervous system and in the central nervous system.
3. The concentration of potassium on the inside of a nerve cell membrane is higher than the concentration of sodium on the outside of the membrane. Yet the inside of the membrane (where the cation concentration is higher) is negative to the outside. Explain this observation in terms of the permeability properties of the membrane.
4. What ionic and electrical changes occur during the passage of an action potential along a nerve fiber?
5. Explain the different ways in which invertebrates and vertebrates have achieved high velocities for conduction of nerve impulses. Can you suggest why the invertebrate solution would not be suitable for the homeothermic birds and mammals?
6. Why is the sodium pump *indirectly* important to the action potential and to maintaining the resting membrane potential?
7. Describe the microstructure of a chemical synapse. Summarize what happens when an action potential arrives at a synapse.
8. Describe the cnidarian (radiate) nervous system. How is the tendency toward centralization of the nervous system manifested in flatworms, annelids, molluscs, and arthropods?
9. How does the vertebrate spinal cord differ morphologically from nerve cords of invertebrates?
10. The knee-jerk reflex is often called a stretch reflex because a sharp tap on the patellar ligament stretches the quadriceps femoris, the extensor muscle of the leg. Describe the components and sequence of events that lead to a "knee jerk." What is the difference between a reflex arc and a reflex act?
11. Name the major functions associated with the following brain structures: medulla, cerebellum, tectum, thalamus, hypothalamus, cerebrum, limbic system.
12. What functional activities are associated with the left and the right hemispheres of the cerebral cortex?
13. What is the autonomic nervous system and what activities does it perform that distinguish it from the central nervous system? Why can the autonomic nervous system be described as a "two-neuron" system?
14. Give the meaning of the statement, "The idea that all sense organs behave as biological transducers is a uniting concept in sensory physiology."
15. Chemoreception in vertebrates and insects is mediated through the clearly distinguishable senses of taste and smell. Contrast these two senses in humans in terms of anatomical location and nature of the receptors and sensitivity to chemical molecules.
16. Explain how the ultrasonic detectors of certain nocturnal moths are adapted to help them escape an approaching bat.
17. Outline the place theory of pitch discrimination as an explanation of the human ear's ability to distinguish between sounds of different frequencies.
18. Explain how the semicircular canals of the ear are designed to detect rotation of the head in any directional plane.
19. Explain what happens when light strikes a dark-adapted rod that leads to the generation of a nerve impulse. What is the difference between rods and cones in their sensitivity to light?
20. In 1802 Thomas Young hypothesized that we see color because the retina contains three kinds of receptors. What evidence substantiates Young's hypothesis? How can we perceive any color in the visible spectrum when our retinas contain only three classes of color cones?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

University of Arkansas for Medical Sciences. Links to gross anatomy, neuroscience, and microanatomy; much information organized in tables which should provide a good review and study tool for students.

Whole Brain Atlas Top 100 Brain Structures. Actually 106 structures, with photographs and MR images, CT scans, etc., of the structures, including pathology.

Shuffle Brain. Unique site features how the brain and mind work.

Neurological Disease Information. Human neurological diseases may be accessed via a clickable list.

Homeostasis: Animals. Introductory information on the nervous system, neurons, synapses, and reflex arcs, as well as the endocrine system.

Virtual Hospital: The Human Brain. Images, diagrams, and information on structures of the brain, cranial vessels, and the spinal cord.

Neurosciences on the Internet. An index of neuroscience resources: neurology, neurosurgery, psychiatry, psychology, and neurological diseases of humans.

Seeing, Hearing, and Smelling the World. A full text reprint of a Howard Hughes Medical Institute report on "making sense of our senses."

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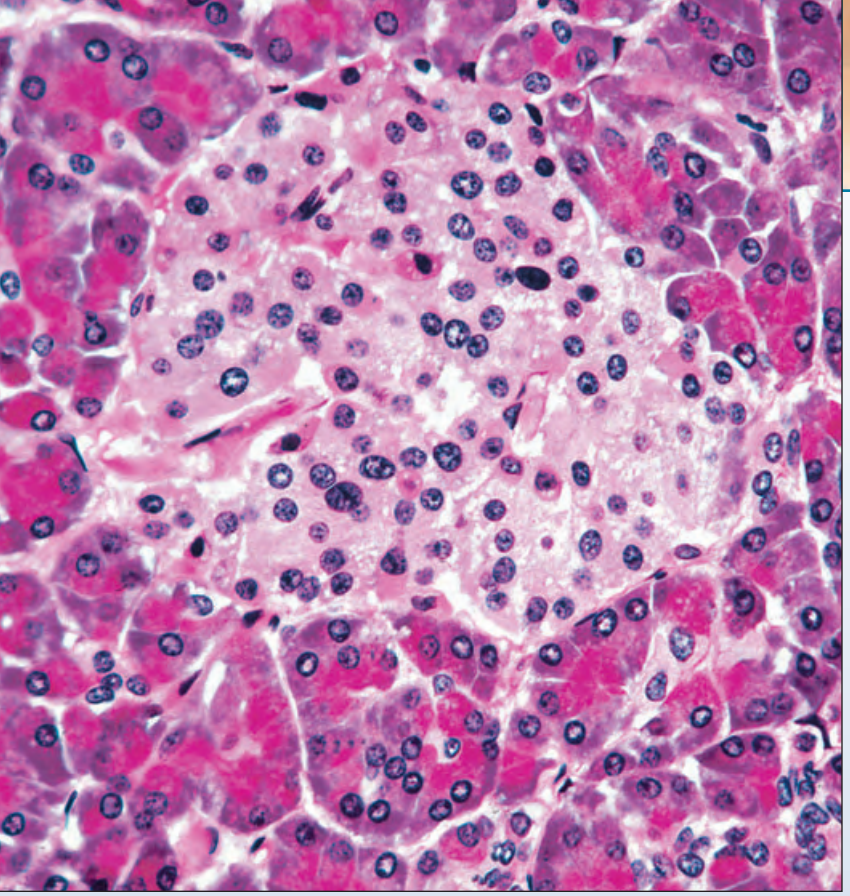


An endocrine islet of Langerhans, site of insulin synthesis, within the human pancreas.

CHAPTER

36

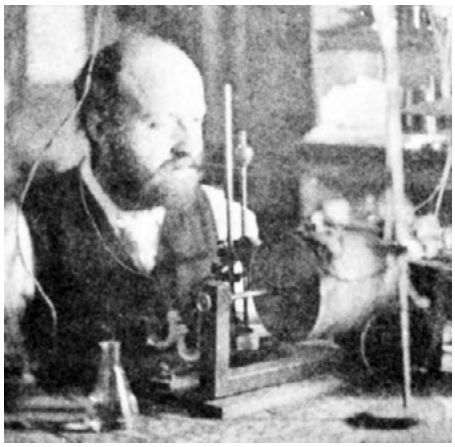
Chemical Coordination

Endocrine System

The Birth of Endocrinology

The birth date of endocrinology as a science is usually given as 1902, the year two English physiologists, W. H. Bayliss and E. H. Starling (Figure 36-1), demonstrated the action of a hormone in a classic experiment that is still considered a model of the scientific method. Bayliss and Starling were interested in determining how the pancreas secreted its digestive juice into the small intestine at the proper time of the digestive process. They wanted to test the hypothesis that acidic food entering the intestine triggered a nervous reflex that released pancreatic juice. To test this hypothesis, Bayliss and Starling cut away all nerves serving a tied-off loop of the small intestine of an anesthetized dog, leaving the isolated loop connected to the body only by its circulation. Injecting acid into the nerveless loop, they saw a pronounced flow of pancreatic juice. Thus, rather than a nervous reflex, some chemical messenger had circulated from the intestine to the pancreas, causing the pancreas to secrete. Yet acid itself could not be the factor because it had no effect when injected directly into the circulation.

Bayliss and Starling then designed the crucial experiment that was to usher in the new science of endocrinology. Suspecting that the chemical messenger originated in the mucosal lining of the intestine, they next prepared an extract of scrapings from the mucosa, injected it into the dog's circulation, and were rewarded with an abundant flow of pancreatic juice. They named the messenger present in the intestinal mucosa *secretin*. Later Starling coined the term **hormone** to describe all such chemical messengers, since he correctly surmised that secretin was only the first of many hormones awaiting discovery. ■



A

B

Figure 36-1
Founders of endocrinology. **A,** Sir William H. Bayliss (1860 to 1924). **B,** Ernest H. Starling (1866 to 1927).

The endocrine system, the second great integrative system controlling the body's activities, communicates by chemical messengers called **hormones** (Gr. *hormōn*, to excite). Hormones are chemical compounds released into the blood in small amounts and transported by the circulatory system throughout the body to distant **target cells** where they initiate physiological responses.

Many hormones are secreted by **endocrine glands,** small, well-vascularized ductless glands composed of groups of cells arranged in cords or plates. Since endocrine glands have no ducts, their only connection with the rest of the body is by the bloodstream; they must capture their raw materials from the extensive blood supply they receive and secrete their finished hormonal products into it. **Exocrine glands,** in contrast, are provided with ducts for discharging their secretions onto a free surface. Examples of exocrine glands are sweat glands and sebaceous glands of skin, salivary glands, and the various enzyme-secreting glands lining the walls of the stomach and intestine.

The classical definitions of hormones and endocrine glands given above, like so many other generalizations in biology, gradually are being altered as new information appears. Some hormones, such as certain neurosecretions, may never enter the general circulation. Furthermore, evidence suggests that many hormones, such as insulin, are synthesized in minute amounts in a variety of nonendocrine tissues (nerve cells, for example), and some, such as cytokines, are secreted by cells of the immune system (p. 774). Such hormones may function as **neurotransmitters** in the brain or as local tissue factors **(parahormones),** which stimulate cell growth or some biochemical process. Most hormones, however, are blood borne and therefore diffuse into every tissue space in the body.

The first formal experiment in endocrinology was performed in 1849 by a professor of physiology at the University of Gottingen, Professor Arnold Adolph Berthold. He conclusively demonstrated that a blood-borne signal was produced by the testes, and that this chemical was responsible for producing both physical and behavioral characteristics that distinguished an adult male rooster from immature chickens and adult male chickens that had been castrated (capons). Berthold castrated male chicks and divided them into three groups. He left one group of controls to grow normally without their testes, and he reimplanted the testes into the second group. The third group was implanted with testes from different chicks. As the chicks grew, he observed that the castrated group developed into capons, with no interest in hens, lacking rooster plumage and male aggressive behavior. The second and third groups of birds were indistinguishable from each other, with full male plumage, normal aggressive behavior and interest in hens. Berthold then killed the birds and dissected them. He found that the transplanted testes had developed their own blood supply and were functioning normally. From this classic experiment, Berthold concluded that testes must produce a blood-borne signal, since there was no nerve supply to the testes, which produced all characteristics of maleness.

Compared with the nervous system, the endocrine system is slow acting because of the time required for a hormone to reach the appropriate tissue, cross the capillary endothelium, and diffuse through tissue fluid to, and sometimes into, cells. The minimum response time is seconds and may be much longer. Hormonal responses in general are long lasting (minutes to days) whereas those under nervous control are short term (milliseconds to minutes). We expect to find endocrine control where a sustained effect is required, as in many metabolic, growth, and reproductive processes. Despite such differences, the nervous and endocrine systems function without sharp separation as a single, interdependent system. Endocrine glands often receive directions from the brain. Conversely, many hormones act on the nervous system and significantly affect a wide array of animal behaviors.

All hormones are low-level signals. Even when an endocrine gland is secreting maximally, the hormone is so greatly diluted by the large volume of blood it enters that its plasma concentration seldom exceeds 10^{-9} M (or one billionth of a 1 M concentration). Some target cells respond to plasma concentrations of hormone as low as 10^{-12} M. Since hormones have far-reaching and often powerful influences on cells, it is evident that their effects are vastly amplified at the cellular level.

Mechanisms of Hormone Action

Widespread distribution of hormones in the body permits certain hormones, such as the growth hormone of the pituitary gland, to affect most, if not all, cells during specific stages of cellular

differentiation. Other hormones produce highly specific responses only in certain target cells and at certain times. Such specificity is made possible by **receptor molecules** on or in target cells. A hormone will engage only those cells that display the receptor that, by virtue of its specific molecular shape, will bind with the hormone molecule. Other cells are insensitive to the hormone's presence because they lack the specific receptors. Hormones act through two kinds of receptors: **membrane-bound receptors** and **nuclear receptors.**

Membrane-Bound Receptors and the Second Messenger Concept

Many hormones, such as most amino acid derivatives, and the peptide hormones that are too large, or too polar, to pass through cell membranes, bind to receptor sites present on the surface of target cell membranes. The hormone and receptor form a complex that triggers a cascade of molecular events within a cell. The hormone thus behaves as a **first messenger** that causes the activation of a **second messenger** system in the cytoplasm. At least six different molecules have been identified as second messengers. Each works via a specific **kinase,** which causes activation or inactivation of rate-limiting enzymes which modify the direction and rate of cytoplasmic processes (Figure 36-2). Since many molecules of the second messenger are activated after a single hormone molecule has been bound, the message is amplified, perhaps many thousands of times.

Second messenger systems known to participate in hormone actions are **cyclic AMP** (cAMP), **cyclic GMP** (cGMP), **Ca^{++}/calmodulin, inositol-trisphosphate** (IP_3), and **diacylglycerol** (DAG). Cyclic AMP was the first to be investigated, and has been shown to mediate actions of many peptide hormones, including parathyroid hormone, glucagon, adrenocorticotropic hormone (ACTH), thyrotropic hormone (TSH), melanophore-stimulating hormone (MSH), and vasopressin. It also mediates action of epinephrine (also called adrenaline), an amino acid derivative.

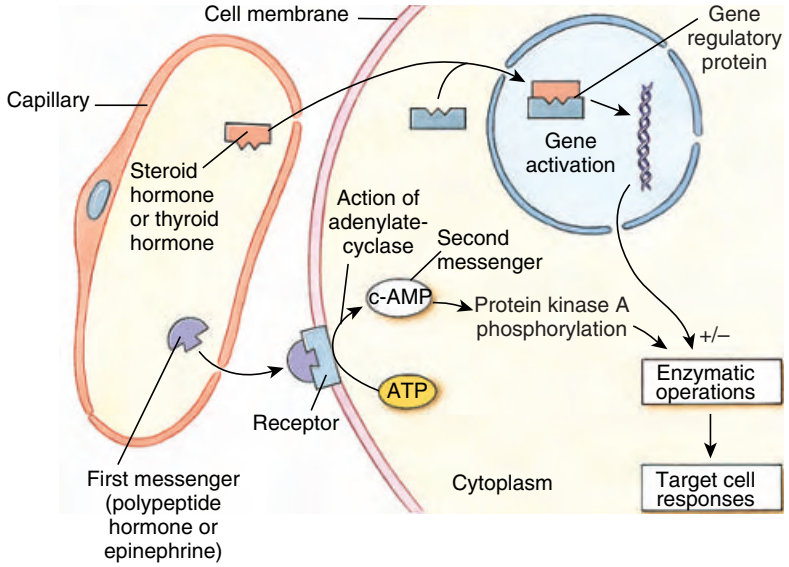


Figure 36-2

Mechanisms of hormone action. Peptide hormones and epinephrine act through second messenger systems, as for example, cyclic AMP, shown here. The combination of hormone with a membrane receptor stimulates the enzyme adenylate cyclase to catalyze formation of cyclic AMP (second messenger). Steroid hormones and thyroid hormones penetrate the cell membrane to combine with cytoplasmic or nuclear receptors that alter gene transcription.

Nuclear Receptors

Unlike peptide hormones and epinephrine, which are much too large to pass through cell membranes, **steroid hormones** (for example, estrogen, testosterone, and aldosterone), are lipid-soluble molecules that readily diffuse through cell membranes. Once inside the cytoplasm, steroid hormones bind selectively to receptor molecules of target cells. While these receptor molecules may be located in either cytoplasm or nucleus, their ultimate site of activity is the nucleus. The hormone-receptor complex, now known as a **gene regulatory protein,** then activates or inhibits specific genes. As a result, gene transcription is altered, since messenger RNA molecules are synthesized on specific sequences of DNA. Stimulation or inhibition of mRNA formation modifies production of key enzymes, thus setting in motion the hormone's observed effect (Figure 36-2). Thyroid hormones and the insect-molting hormone, ecdysone, also act through nuclear receptors.

Compared with peptide hormones that act *indirectly* through second messenger systems, steroids have a *direct* effect on protein synthesis because they bind a nuclear receptor that modifies specific gene activity.

Control of Secretion Rates of Hormones

Hormones influence cellular functions by altering rates of many different biochemical processes. Many affect enzymatic activity and thus alter cellular metabolism, some change membrane permeability, some regulate synthesis of cellular proteins, and some stimulate release of hormones from other endocrine glands. Because these are all dynamic processes that must adapt to changing metabolic demands, they must be regulated, not merely activated, by the appropriate hormones. This regulation is achieved by precisely controlled release of a hormone into the blood. However, the concentration of a hormone in the plasma depends on two factors: its rate of secretion and the rate at which it is inactivated and removed from the circulation. Consequently, if secretion is to be correctly controlled, an endocrine gland requires information

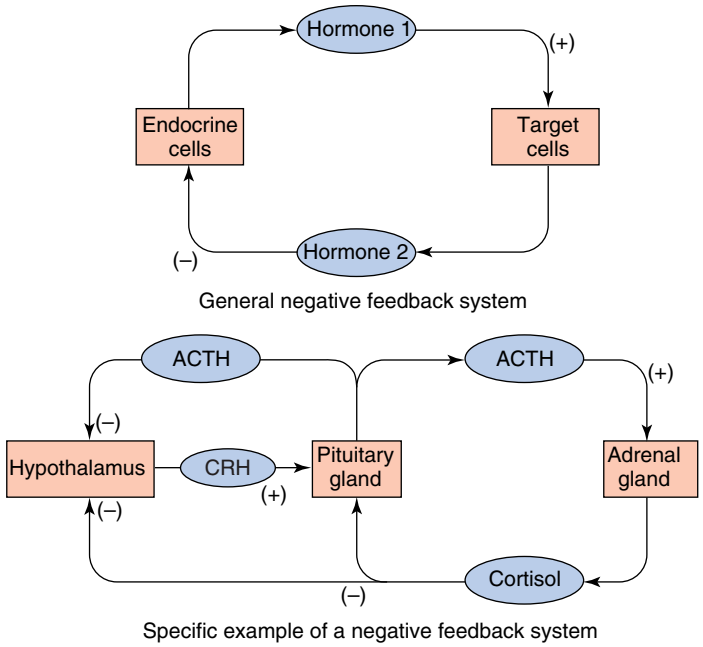


Figure 36-3
Negative feedback systems.

about the level of its own hormone(s) in the plasma.

Many hormones are controlled by negative feedback systems that operate between glands secreting the hormones and target cells (Figure 36-3). A feedback pattern is one in which output is constantly compared with a set point, like a thermostat. For example, CRH (corticotropin-releasing hormone), secreted by the hypothalamus, stimulates the pituitary (the target cells) to release ACTH. ACTH stimulates the adrenal gland (the target cells) to secrete cortisol. As the level of ACTH rises in the plasma, it acts on, or "feeds back" on, the hypothalamus to inhibit release of CRH. Similarly, as cortisol levels rise in the plasma, it "feeds back" on the hypothalamus and pituitary to inhibit release of both CRH and ACTH, respectively. Thus any deviation from the set point (a specific plasma level of each hormone) leads to corrective action in the opposite direction (Figure 36-3). Such a **negative feedback** system is highly effective in preventing extreme oscillations in hormonal output. However, hormonal feedback systems are more complex than a rigid "closed-loop" system such as the thermostat that controls the central heating system in a house, because hormonal feedback may be altered by input from the nervous system or by metabolites or other hormones.

Extreme oscillations in hormone output do sometimes occur under natural conditions. However, because they have the potential to disrupt finely tuned homeostatic mechanisms, such extreme oscillations, as a result of **positive feedback,** are highly regulated and possess an obvious shutoff mechanism. For example, hormones controlling parturition (childbirth) are shut off by birth of the young from the uterus; hormones controlling ovulation are shut off by release of an ovum from a follicle.

Invertebrate Hormones

In many metazoan phyla, the principal source of hormones is **neurosecretory cells,** specialized nerve cells capable of synthesizing and secreting hormones. Their products, called neurosecretions or neurosecretory hormones, are discharged directly into the circulation, and serve as a crucial link between the nervous and endocrine systems.

Neurosecretory hormones occur in all metazoan groups. An extensively studied neurosecretory process in invertebrates is control of development and metamorphosis of insects. In insects, as in other arthropods, growth is a series of steps in which the rigid, nonexpansible exoskeleton is periodically discarded and replaced with a new, larger one. Most insects undergo a process of metamorphosis (p. 424), in which a series of juvenile stages, each requiring formation of a new exoskeleton, end with a molt.

Insect physiologists have discovered that molting and metamorphosis are primarily controlled by interaction of two hormones, one favoring growth and differentiation of adult structures and another favoring retention of juvenile structures. These two hormones are **molting hormone** or **ecdysone,** produced by the prothoracic gland, and **juvenile hormone,** produced by the corpora allata (Figure 36-4). The structures of both hormones have been determined. Extraction from 1000 kg (about 1 ton) of silkworm pupae was required to show that ecdysone is a steroid.

Ecdysone is controlled by **prothoracicotropic hormone** or **PTTH.** This hormone is a polypeptide (molecular weight about 5000) produced by neurosecretory cells of the brain, and transported by axons to the corpora allata where it is stored. At intervals during juvenile growth, release of PTTH into the blood stimulates the prothoracic gland to secrete ecdysone. Ecdysone appears to act directly on the chromosomes to set in motion changes resulting in a molt, by favoring development of adult structures. It is held in check, however, by juvenile hormone, which favors development of juvenile characteristics. During juvenile life, juvenile hormone predominates and each molt yields another larger juvenile (Figure 36-4). Finally output of juvenile hormone decreases, allowing final metamorphosis to the adult stage.

The precise location of brain hormone in the brain of pupal tobacco hornworms was revealed by N. Agui by delicate

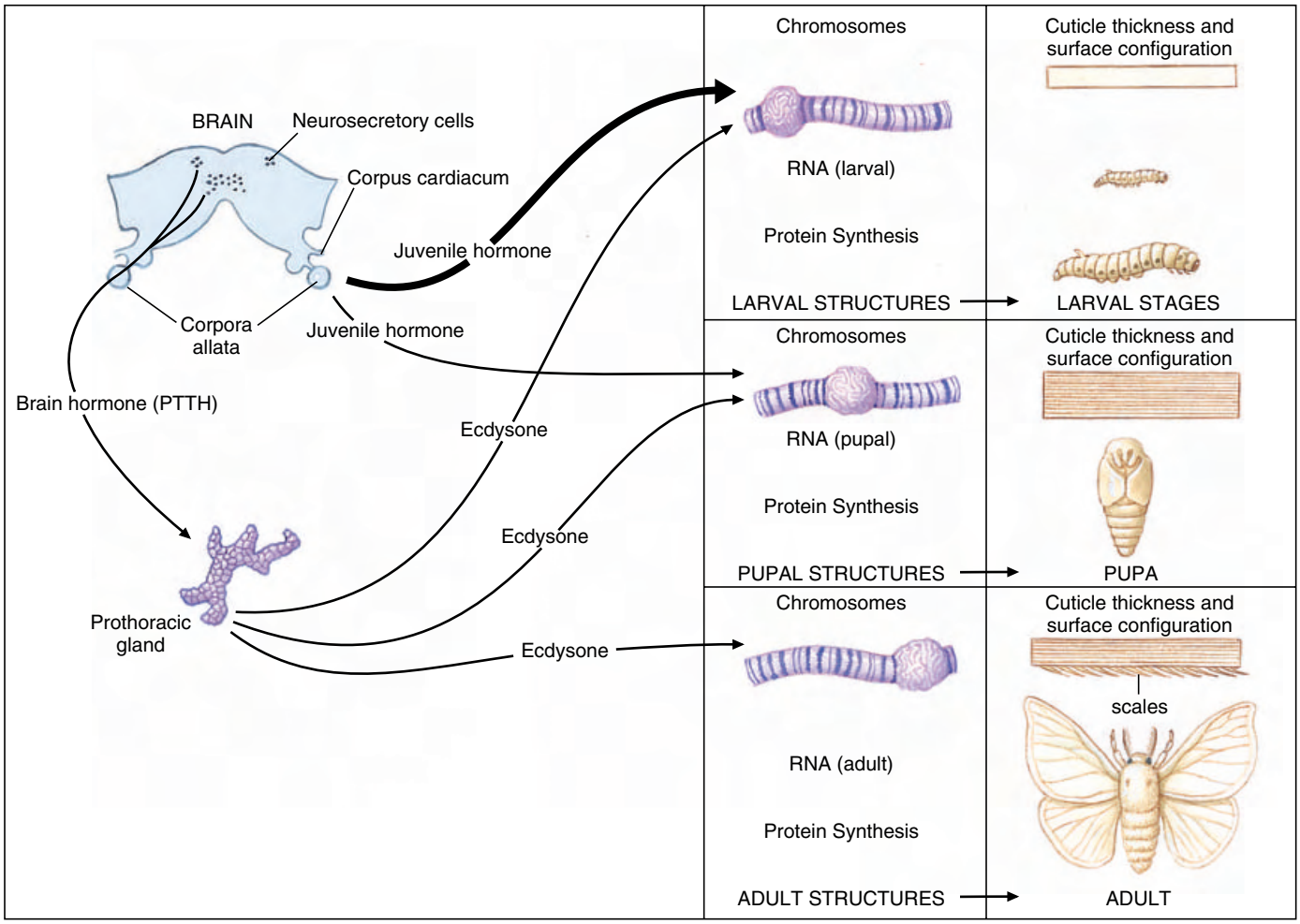


Figure 36-4

Endocrine control of molting in a moth, typical of insects having complete metamorphosis. Many moths mate in spring or summer, and eggs soon hatch into the first of several larval stages, called instars. After the final larval molt, the last and largest larva (caterpillar) spins a cocoon in which it pupates. The pupa overwinters, and an adult emerges in the spring to start a new generation. Juvenile hormone and ecdysone interact to control molting and pupation. Many genes are activated during metamorphosis, as seen by puffing of chromosomes (center column). Puffs form in sequence during successive molts. Changes in cuticle thickness and surface characteristics are shown at right.

microdissection. Using a human eyebrow hair, he was able to isolate the single cell in each brain hemisphere that contained brain hormone activity. Thus only two cells, each about 20 μm in diameter, produce this insect's total supply of PTTH. In an age when sophisticated instrumentation has removed much of the tedium (and some creativity) from research, it is refreshing to learn that certain biological mysteries succumb only to skillful use of the human hand.

Chemists have synthesized several potent analogs of juvenile hormone, which hold great promise as insecticides. Minute quantities of these synthetic analogs induce abnormal final molts or prolong or block development. Unlike chemical insecticides, they are highly specific and ecologically benign.

Vertebrate Endocrine Glands and Hormones

In the remainder of this chapter we describe some of the best understood and most important of vertebrate hormones. While the following discussion is limited principally to a brief overview of mammalian hormonal mechanisms (since laboratory mammals and humans have always been the objects of the most intensive research), we will point out some important differences in functional roles of hormones among different vertebrate groups.

Hormones of the Hypothalamus and Pituitary Gland

The pituitary gland, or **hypophysis,** is a small gland (0.5 g in humans) lying in a well-protected position between the roof of the mouth and floor of the brain (Figure 36-5). It is a two-part gland having a double embryological origin. The **anterior pituitary** (adenohypophysis) is derived embryologically from the roof

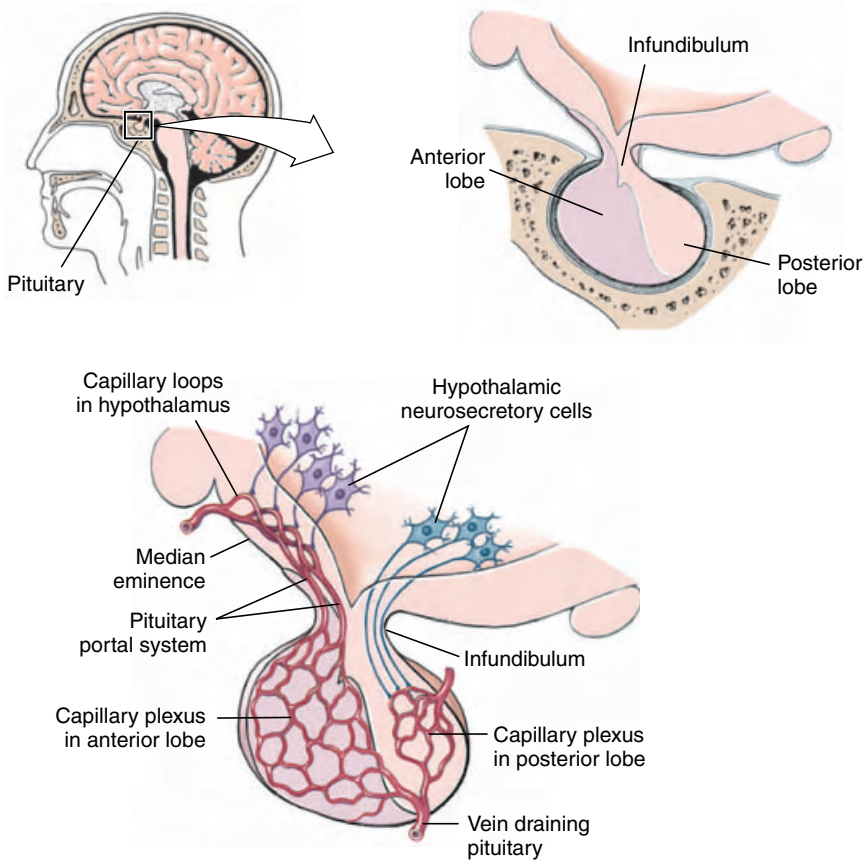


Figure 36-5
Human hypothalamus and pituitary gland. The posterior lobe is connected directly to the hypothalamus by neurosecretory fibers. The anterior lobe is indirectly connected to the hypothalamus by a portal circulation (shown in red) beginning in the base of the hypothalamus and ending in the anterior pituitary.

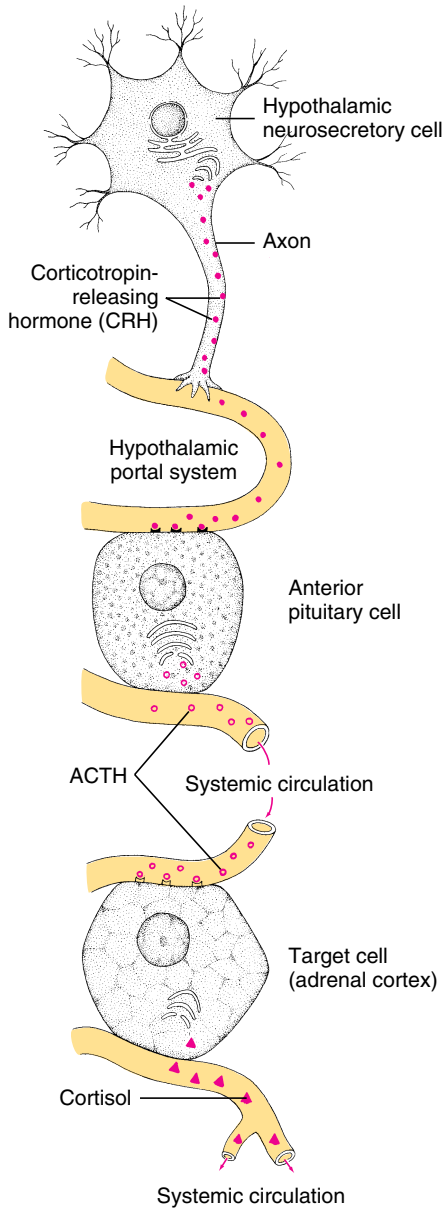


Figure 36-6
Relationship of hypothalamic, pituitary, and target-gland hormones. The hormone sequence controlling the release of cortisol from the adrenal cortex is used as an example.

of the mouth. The **posterior pituitary** (neurohypophysis) arises from a ventral portion of the brain, the **hypothalamus,** and is connected to it by a stalk, the **infundibulum.** Although the anterior pituitary lacks any anatomical connection to the brain, it is functionally connected to it by a special portal circulatory system. A portal circulation is one that delivers blood from one capillary bed to another (Figures 36-5 and 36-6). In this case, the portal circulation provides a link between neurosecretory cells of the hypothalamus and anterior pituitary gland.

Hypothalamus and Neurosecretion

Because of the strategic importance of the pituitary in influencing most hormonal activities in the body, the pituitary was once called the "master gland." This description is not appropriate, however, because the anterior pituitary hormones are regulated by a higher council, the neurosecretory centers of the hypothalamus. The hypothalamus is itself under ultimate control by the brain. The hypothalamus contains groups of neurosecretory cells, which are specialized nerve cells (Figure 36-5 and 36-6), that manufacture neurohormones, called **releasing hormones** or **release-inhibiting hormones** (or "factors"). These neurohormones travel down nerve fibers to their endings in the median eminence. Here they enter a capillary network to complete their journey to the anterior pituitary by way of the pituitary portal system. The hypothalamic hormones then stimulate or inhibit release of various anterior pituitary hormones. Several hypothalamic releasing and release-inhibiting hormones have been discovered, characterized chemically, and isolated in pure state (Table 36-1), although the identification and action of some of the hypothalamic hormones listed in Table 36-1 is still tentative.

Anterior Pituitary

The anterior pituitary consists of an **anterior lobe** (pars distalis) as shown in Figure 36-5, and an **intermediate**

TABLE 36.1

Hormones of the Vertebrate Pituitary

	Hormone	Chemical Nature	Principal Action	Hypothalamic Controls
Adenohypophysis				
Anterior lobe	Thyroid-stimulating hormone (TSH)	Glycoprotein	Stimulates thyroid hormone synthesis and secretion	TSH-releasing hormone (TRH)
	Follicle-stimulating hormone (FSH)	Glycoprotein	Female: follicle maturation and estrogen synthesis Male: stimulates sperm production	Gonadotropin-releasing hormone (GnRH)[1]
	Luteinizing hormone (LH)	Glycoprotein	Female: stimulates ovulation, corpus luteum formation, estrogen and progesterone synthesis Male: testosterone secretion	Gonadotropin-releasing hormone (GnRH)[1]
	Prolactin (PRL)	Protein	Mammary gland growth, milk synthesis, immune response and angiogenesis in mammals, parental behavior, electrolyte and water balance in lower vertebrates	Dopamine (prolactin release-inhibiting hormone or PIH) Prolactin releasing factor (PRF)?
	Growth hormone (GH) (somatotropin)	Protein	Stimulates growth, protein synthesis, mobilization of glycogen and fat stores	Growth hormone- releasing hormone (GHRH) Growth hormone release-inhibiting hormone (GHIH) or somatostatin
	Adrenocorticotropic hormone (ACTH)	Polypeptide	Stimulates glucocorticoid synthesis by adrenal cortex	Corticotropin-releasing hormone (CRH)
Intermediate lobe[2]	Melanocyte-stimulating hormone (MSH)	Polypeptide	Increased melanin synthesis by melanocytes in epidermis of ectotherms; function not clear in endotherms	Melanocyte-stimulating hormone-inhibiting hormone (MSHIH)
Neurohypophysis				
(Posterior lobe)	Oxytocin	Octapeptide	Milk ejection and uterine contractions, sexual behavior and pair bonding in monogamous species	
	Vasopressin[3] (antidiuretic hormone or ADH)	Octapeptide	Water reabsorption in mammalian kidneys	
	Vasotocin[4]	Octapeptide	Increases water reabsorption	

[1] One GnRH hormone regulates both FSH and LH, but some recent research experiments suggest a separate FSH-releasing hormone (FSH-RH).
[2] Birds and some mammals lack an intermediate lobe. In these forms, MSH is produced by the anterior lobe.
[3] In mammals.
[4] In all vertebrate classes except mammals.

lobe (pars intermedia), which is absent in some animals (including humans). The anterior pituitary produces seven hormones, and all but one are released by the anterior lobe.

Four hormones of the anterior pituitary are **tropic hormones** (from the Greek *tropē*, to turn toward) that regulate other endocrine glands (Table 36-1). **Thyroid-stimulating hormone (TSH)** or **thyrotropin** stimulates production of thyroid hormones by the thyroid gland. Two tropic hormones are commonly called **gonadotropins** because they act on the gonads (ovaries of females, testes of males). These are **follicle-stimulating hormone (FSH)** and **luteinizing hormone (LH).** FSH promotes egg production and secretion of estrogen in females, and supports sperm production in males. LH induces ovulation, corpus luteum production, and secretion of the female sex steroids, progesterone and estrogen. In males, LH promotes production of male sex steroids (primarily testosterone). It

once was called interstitial cell stimulating hormone (ICSH) in males, before it was discovered to be identical to LH in females. The fourth tropic hormone, **adrenocorticotropic hormone (ACTH),** increases production and secretion of steroid hormones from the adrenal cortex.

Prolactin and the structurally related **growth hormone (GH)** are proteins. Prolactin is essential for preparing mammary glands for lactation; after birth it is required for production of milk. Prolactin also has been implicated in parental behavior in a wide variety of vertebrates. Beyond its more traditional role in reproductive processes, prolactin regulates water and electrolyte balance in many species. More recently, prolactin has been shown to be a chemical mediator of the immune system and is important in formation of new blood vessels (angiogenesis). Unlike tropic hormones, prolactin acts directly on its target tissues rather than through other hormones.

GH (also called somatotropin) performs a vital role in governing body growth through its stimulatory effect on cellular mitosis, on synthesis of messenger RNA and protein, and on metabolism, especially in new tissue of young vertebrates. Growth hormone acts directly on growth and metabolism, as well as indirectly through a polypeptide hormone, **insulin-like growth factor (IGF)** or somatomedin, produced by the liver.

The only anterior pituitary hormone produced by the intermediate lobe is **melanocyte-stimulating hormone (MSH).** In cartilaginous and bony fishes, amphibians, and reptiles, MSH is a direct-acting hormone that promotes dispersion of the pigment melanin within melanocytes, causing darkening of the skin. In birds and mammals, MSH is produced by cells in the anterior pituitary rather than the intermediate lobe, but its physiological function remains unclear. MSH appears unrelated to pigmentation in endotherms, although it will cause darkening of the skin in humans if injected into the circulation. Until recently, many endocrinologists thought MSH was a vestigial hormone in mammals, but interest has been rekindled by studies showing that it enhances memory and growth of the fetus. In addition, MSH has been isolated from specific regions of the hypothalamus, where it has been linked to regulation of ingestive behaviors and metabolism in adult mammals. Future studies will determine if a similar role also exists for MSH during development. MSH and ACTH are derived from a precursor molecule that is transcribed and translated from a single gene.

Posterior Pituitary

The hypothalamus is the source of two hormones of the posterior lobe of the pituitary (Table 36-1). They are formed in neurosecretory cells in the hypothalamus, whose axons extend down the infundibular stalk and into the posterior lobe. The hormones are secreted from axon terminals ending in close proximity to blood capillaries, which the hormones enter when released (see Figure 36-5). In a sense the posterior lobe is not a true endocrine gland, but a storage and release center for hormones manufactured entirely in the hypothalamus. The two posterior lobe hormones of mammals, oxytocin and vasopressin, are chemically very much alike. Both are polypeptides consisting of eight amino acids and are called octapeptides (Figure 36-7). These hormones are among the fastest-acting hormones, since they are capable of producing a response within seconds of their release from the posterior lobe.

Oxytocin has two important specialized reproductive functions in adult female mammals. It stimulates contraction of uterine smooth muscles during parturition (birth of the young). In clinical practice, oxytocin is used to induce delivery during a difficult labor and to prevent uterine hemorrhage after birth. A second action of oxytocin is that of milk ejection by the mammary glands in response to suckling. Recent work also has established a role for oxytocin in pair-bonding behavior in both sexes in monogamous voles.

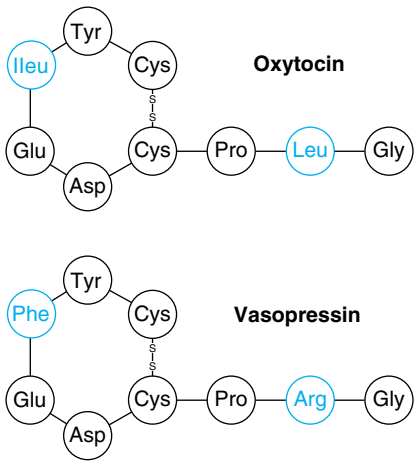


Figure 36-7
Posterior lobe hormones of mammals. Both oxytocin and vasopressin consist of eight amino acids (the two sulfur-linked cysteine molecules are considered a single amino acid, cystine). Oxytocin and vasopressin are identical except for amino acid substitutions in the blue positions. Abbreviations represent amino acids.

Vasopressin, the second posterior lobe hormone, acts on collecting ducts of the kidney to increase water reabsorption and thus restrict urine flow, as already described on p. 675. It is therefore often called **antidiuretic hormone.** Vasopressin also increases blood pressure through its generalized constrictor effect on smooth muscles of arterioles. Finally, vasopressin acts centrally to increase thirst, and therefore, drinking behavior.

All jawed vertebrates secrete two posterior lobe hormones that are quite similar to those of mammals. All are octapeptides, but their structures vary because of amino acid substitutions in three of eight amino acid positions in the molecule.

Of all posterior lobe hormones, **vasotocin** (Table 36-1) has the widest phylogenetic distribution and is believed to be the parent hormone from which other octapeptides evolved. It is found in all vertebrate classes except mammals. It is a water-balance hormone in amphibians, especially toads, in which it acts to conserve water by (1) increasing permeability of skin (to promote water absorption from the environment), (2) stimulating water reabsorption from the urinary bladder, and (3) decreasing urine flow. Action of vasotocin is best

understood in amphibians, but it appears to play some water-conserving role in birds and reptiles as well.

Pineal Gland

In all vertebrates the dorsal part of the brain, the diencephalon Figure 35-13, p. 734 gives rise to a sac-like evagination called the pineal complex, which lies just beneath the skull in a midline position. In ectothermic vertebrates the pineal complex contains glandular tissue and a photoreceptive sensory organ involved in pigmentation responses and in light-dark biological rhythms. In lampreys, many amphibians, lizards, and the tuatara (*Sphenodon*, p. 575), the median photoreceptive organ is so well developed, containing structures analogous to the lens and cornea of lateral eyes, that it is often called a third eye. In birds and mammals, the pineal complex is an entirely glandular structure called the pineal gland. The pineal gland produces the hormone **melatonin.** Melatonin secretion is strongly affected by exposure to light. Its production is lowest during daylight hours and highest at night. In nonmammalian vertebrates, the pineal gland is responsible for maintaining **circadian rhythms**—self-generated (endogenous) rhythms that are about 24 hours in length. A circadian rhythm serves as a biological clock for many physiological processes that follow a regular pattern.

In mammals, an area of the hypothalamus called the **suprachiasmatic nucleus** has become the primary circadian pacemaker, although the pineal gland still produces melatonin nightly and serves to reinforce the circadian rhythm of the suprachiasmatic nucleus. In birds and mammals in which seasonal rhythms in reproduction are regulated by **photoperiod,** melatonin plays a critical role in regulating gonadal activity. In long-day breeders, such as ferrets, hamsters, and deer mice, reduced light stimulation with shortening day length in autumn increases melatonin secretion, and in these species reproductive activity is suppressed during winter months. Lengthening days in the spring have the opposite effect and reproductive activities are resumed. Short-day breeders, such as white-tailed deer, silver fox, spotted skunk, and sheep, are stimulated by reduced day length in the fall; increasing melatonin levels in the fall are associated with increased reproductive activity. The role of melatonin is an indirect one in both cases since melatonin itself does not stimulate or inhibit the reproductive axis.

Only recently the pineal gland has been shown to produce subtle and incompletely understood effects on circadian and annual rhythms in nonphotoperiodic mammals (such as humans). For example, melatonin secretion has been linked to a sleeping and eating disorder in humans known as seasonal affective disorder (SAD). Some people living in northern latitudes, where day lengths are short in winter and when melatonin production is elevated, become depressed in winter, sleep long periods, and may go on eating binges. Often this wintertime disorder can be treated by exposure to sunlamps with full-spectrum light; such exposure depresses melatonin secretion by the pineal gland. Disturbed physiological rhythms associated with jet-lag and shift-work also have been linked to inappropriate melatonin rhythms.

Brain Neuropeptides

The blurred distinction between the endocrine and nervous systems is nowhere more evident than in the nervous system, where a growing list of hormonelike neuropeptides have been discovered in central and peripheral nervous systems of vertebrates and invertebrates. In mammals, approximately 40 neuropeptides (short chains of amino acids) have been located using immunological labeling with antibodies that can be visualized in histological sections under the microscope, and the list is still growing. Many are known to lead double lives—to be capable of behaving both as hormones, carrying signals from gland cells to their targets, and as neurotransmitters, relaying signals between nerve cells. For example, both oxytocin and vasopressin have been discovered at widespread sites in the brain by immunochemical methods. Related to this discovery is the fascinating observation that people and experimental animals injected with minute quantities of vasopressin experience enhanced learning and improved memory. This effect of vasopressin in brain tissue is unrelated to its well-known antidiuretic function in the kidney (p. 675). Several hormones, such as gastrin and cholecystokinin (p. 719) (which long had been supposed to function only in the gastrointestinal tract), have been discovered in the cerebral cortex, hippocampus, and hypothalamus. In addition to its gastrointestinal actions, cholecystokinin is known to function in control of feeding and satiety and may serve other functions as a brain neuroregulator.

The radioimmunoassay technique developed by Solomon Berson and Rosalyn Yalow about 1960 has revolutionized endocrinology and neurochemistry. First, antibodies to the hormone of interest (insulin, for example) are prepared by injecting a mammal, such as guinea pigs or rabbits, with the hormone. Then, a fixed amount of radioactively labeled insulin and unlabeled insulin antibodies is mixed with the sample of blood plasma to be measured. The native insulin in the blood plasma and the radioactive insulin compete for antibodies. The more insulin present in the sample, the less radioactive insulin will bind to the antibodies. Bound and unbound insulin are then separated, and their radioactivities are measured together with those of appropriate standards to determine the amount of insulin present in the blood sample. The method is so incredibly sensitive that it can measure the equivalent of a cube of sugar dissolved in one of the Great Lakes.

Among the dramatic developments in this field was the discovery in 1975 of endorphins and enkephalins, neuropeptides that bind with opiate receptors and influence perception of pleasure and pain (see note on p. 740). Endorphins and enkephalins are found

also in brain circuits that modulate several other functions unrelated to pleasure and pain, such as control of blood pressure, body temperature, body movement, feeding and reproduction. Even more intriguing, endorphins are derived from the same prohormone that gives rise to the anterior pituitary hormones ACTH and MSH.

Prostaglandins and Cytokines

Prostaglandins

Prostaglandins are derivatives of long-chain unsaturated fatty acids that were discovered in seminal fluid in the 1930s. At first they were thought to be produced only by the prostate gland (hence the name) but now have been found in virtually all mammalian tissues. Prostaglandins act as local hormones that have diverse actions on many different tissues, making generalizations about their effects difficult. Many of their effects, however, involve smooth muscle. In some tissues prostaglandins regulate vasodilation or vasoconstriction by their action on smooth muscle in walls of blood vessels. They are known to stimulate contraction of uterine smooth muscle during childbirth. There also is evidence that overproduction of uterine prostaglandins is responsible for painful symptoms of menstruation (dysmenorrhea) experienced by many women. Several inhibitors of prostaglandins that provide relief from these symptoms have now been approved as medicines. Among other actions of prostaglandins is their intensification of pain in damaged tissues, mediation of the inflammatory response, and involvement in fever.

Cytokines

For some years we have known that cells of the immune system communicate with each other and that this communication was crucial to the immune response. Now we understand that a large group of polypeptide hormones called **cytokines** (p. 774) mediate communication between cells participating in the immune response. Cytokines can affect the cells that secrete them, affect nearby cells, and like other hormones, they can affect cells in distant locations. Their target cells bear specific receptors for the cytokine bound to the surface membrane. Cytokines coordinate a complex network, with some target cells being activated, stimulated to divide and often to secrete their own cytokines. The same cytokine that activates some cells may suppress division of other target cells. Cytokines also are involved in formation of blood, and more recently, their role in regulation of energy balance by the central nervous systems is being explored.

Hormones of Metabolism

An important group of hormones adjusts the delicate balance of metabolic activities. Rates of chemical reactions within cells are often regulated by long sequences of enzymes. Although such sequences are complex, each step in a pathway is mostly self-regulating as long as the equilibrium between substrate, enzyme, and product remains stable. However, hormones may alter activity of crucial enzymes in a metabolic process, thus accelerating or inhibiting the entire process. It should be emphasized that hormones never initiate enzymatic processes; rather they alter their rate, speeding them up or slowing them down. The most important hormones of metabolism are those of the thyroid, parathyroid, adrenal glands, and pancreas, as well as the previously mentioned growth hormone of the anterior pituitary hormone. Finally, a new hormone, leptin, has been added to the list of metabolic hormones.

Thyroid Hormones

Two hormones, **triiodothyronine** and **thyroxine** (T_3 and T_4, respectively) are secreted by the thyroid gland. This large endocrine gland is located in the neck of all vertebrates. The thyroid is composed of thousands of tiny spherelike units, called follicles,

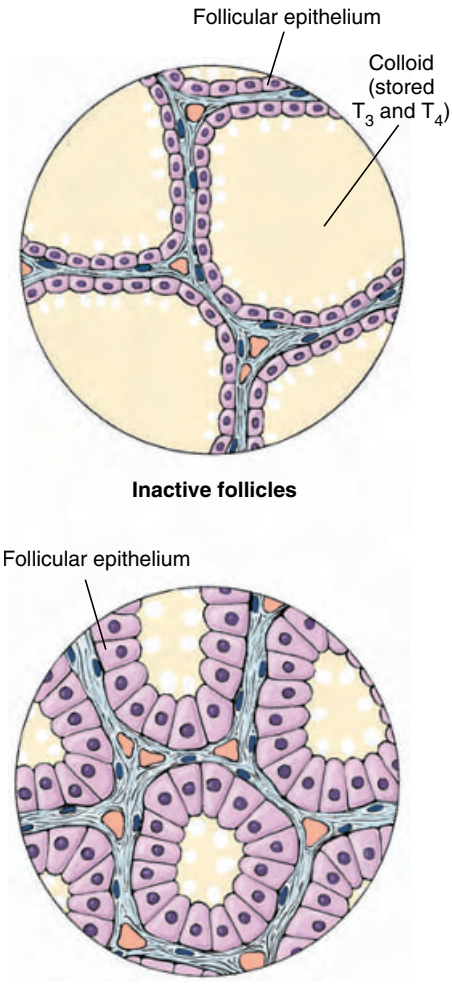


Figure 36-8
Appearance of thyroid gland follicles viewed through the microscope (approximately ×350). When inactive, follicles are distended with colloid, the storage form of thyroid hormones, and epithelial cells are flattened. When active, the colloid disappears as thyroid hormones are secreted into the circulation, and epithelial cells become greatly enlarged.

where thyroid hormones are synthesized, stored, and released into the bloodstream as needed. The size of the follicles, and amount of stored T_3 and T_4 they contain, depends on the activity of the gland (Figure 36-8).

A unique characteristic of the thyroid is its high concentration of **iodine;** in most animals this single gland contains well over half the body store of iodine. Epithelial cells of the thyroid follicles actively trap iodine from the blood and combine it with the amino acid tyrosine, creating the

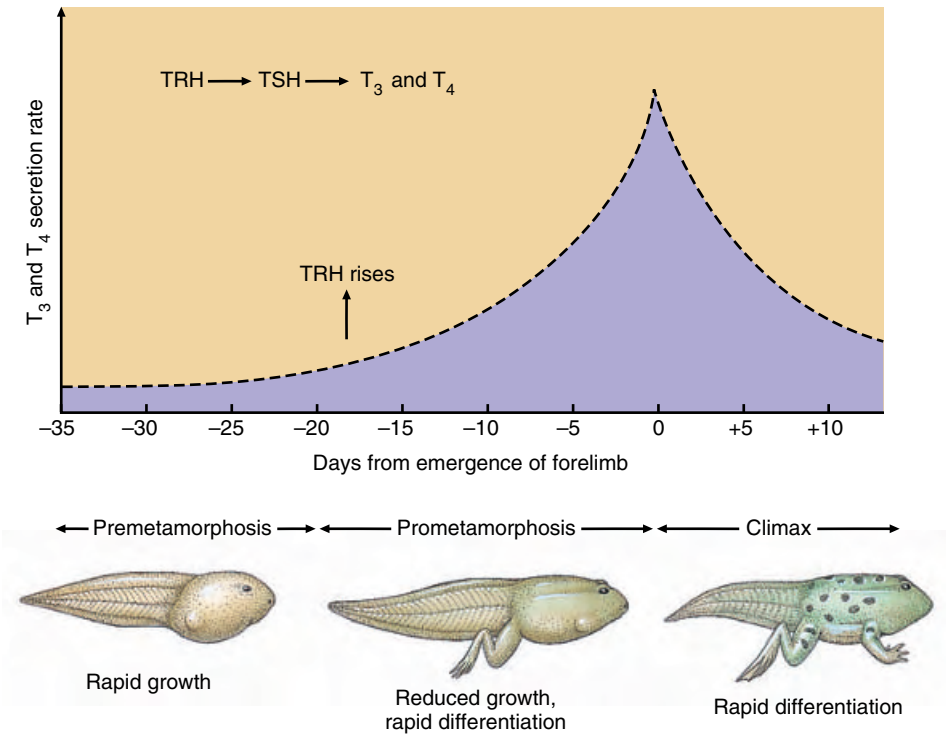


Figure 36-9

Effect of thyroid hormones (T_3 and T_4) on growth and metamorphosis of a frog. The release of TRH from the hypothalamus at the end of premetamorphosis sets in motion hormonal changes (increased TSH, T_3 and T_4) leading to metamorphosis. Thyroid hormone levels are maximal at the time forelimbs emerge.

two thyroid hormones. T_3 contains three iodine atoms, whereas T_4 contains four iodine atoms. T_4 is formed in much greater amounts than T_3, but in many animals T_3 is the more physiologically active hormone. T_4 is now considered a precursor to T_3. The most important actions of T_3 and T_4 are to (1) promote normal growth and development of the nervous system of growing animals, and (2) stimulate metabolic rate.

Undersecretion of thyroid hormones in fish, birds, and mammals dramatically impairs growth, especially of the nervous system. The human **cretin,** a mentally retarded dwarf, is the result of thyroid malfunction from a very early age. Conversely, oversecretion of thyroid hormones causes precocious development in all vertebrates, although its effect is particularly prominent in fish and amphibians. In frogs and toads, transformation from aquatic herbivorous tadpole without lungs or legs to semiterrestrial or terrestrial carnivorous adult with lungs and four legs, occurs when the thyroid gland becomes active at the end of larval development. Stimulated by a rise in thyroid hormone levels of the blood, metamorphosis and climax occur (Figure 36-9). Growth of frogs after metamorphosis is directed by the growth hormone.

In birds and mammals, control of oxygen consumption and heat production is the best known action of thyroid hormones. The thyroid maintains metabolic activity of homeotherms (birds and mammals) at a normal level. Oversecretion of thyroid hormones will speed up body processes by as much as 50%, resulting in irritability, nervousness, fast heart rate, intolerance of warm environments, and loss of body weight despite increased appetite. Undersecretion of thyroid hormones slows metabolic activities, leading to loss of mental alertness, slowing of heart rate, muscular weakness, increased sensitivity to cold, and weight gain. An important function of the thyroid gland is to promote adaptation to cold environments by increasing heat production. Thyroid hormones stimulate cells to produce more heat and store less chemical energy (ATP); in other words, thyroid hormones reduce efficiency of cellular oxidative phosphorylation (p. 66). Consequently many cold-adapted mammals have heartier appetites and eat more food in winter than in summer although their activity is about the same in both seasons. In winter, a larger portion of the food is being converted directly into body-warming heat.

Synthesis and release of thyroid hormones are governed by thyrotropic hormone (TSH) from the anterior pituitary gland (Table 36-1). TSH is regulated in turn by thyrotropin-releasing hormone (TRH) of the hypothalamus. As noted earlier, TRH is part of a higher regulatory council that controls the tropic hormones of the anterior pituitary. TRH and TSH control thyroid activity in an excellent example of negative feedback (p. 754). It can be overridden, however, by neural stimuli, such as exposure to cold, which directly stimulates increased release of TRH and thus TSH.

Some years ago, a condition called goiter was common among people living in the Great Lakes region of the United States and Canada, as well as some other parts of the world, such as the Swiss Alps. This type of goiter is an enlargement of the thyroid gland caused by deficiency of iodine in food and water. By striving to produce thyroid hormone with not enough iodine available, the gland hypertrophies, sometimes so much that the entire neck region becomes swollen (Figure 36-10). Goiter caused by iodine deficiency is seldom seen in North America because of the widespread use of iodized salt. However, it is estimated that even today 200 million people worldwide experience varying degrees of goiter, mostly in high mountains of South America, Europe, and Asia.

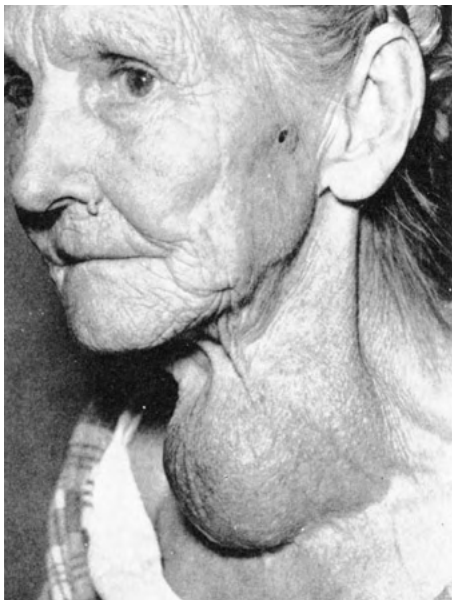


Figure 36-10
A large goiter caused by iodine deficiency. By enlarging enormously, the thyroid gland can extract enough iodine from the blood to synthesize the body's requirement for thyroid hormones.

Hormonal Regulation of Calcium Metabolism

Closely associated with the thyroid gland and in some animals buried within it are the **parathyroid glands.** These tiny glands occur as two pairs in humans but vary in number and position in other vertebrates. They were discovered at the end of the nineteenth century when the fatal effects of "thyroidectomy" were traced to unknowing removal of the parathyroid glands together with the thyroid gland. In birds and mammals, including humans, removal of the parathyroid glands causes the level of calcium in the blood to decrease rapidly. This decrease in calcium leads to a serious increase in nervous system excitability, severe muscular spasms and tetany, and finally death. Subsequently, it was discovered that the parathyroid glands secrete a hormone, **parathyroid hormone (PTH),** which is essential to maintenance of calcium homeostasis. Calcium ions are extremely important for formation of healthy bones. In addition, they are needed for neurotransmitter and hormone release, for muscle contraction, and for blood clotting.

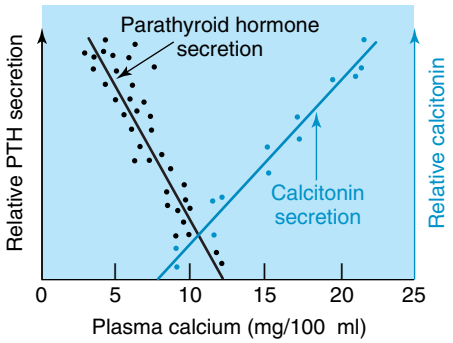


Figure 36-11
How rate of secretion of parathyroid hormone (PTH) and calcitonin respond to changes in blood calcium level in a mammal.

Before considering how hormones maintain calcium homeostasis, it is helpful to summarize mineral metabolism in bone, a densely packed storehouse of both calcium and phosphorus. Bone contains approximately 98% of the calcium and 80% of the phosphorus in humans. Although bone is second only to teeth as the most durable material in the body (as evidenced by survival of fossil bones for millions of years) it is in a state of constant turnover in living vertebrates. Bone-building cells **(osteoblasts)** synthesize organic fibers of bone matrix which later become mineralized with a form of calcium phosphate called hydroxyapatite. Bone-resorbing cells **(osteoclasts)** are giant cells that dissolve the bony matrix, releasing calcium and phosphate into the blood. These opposing activities allow bone constantly to remodel itself, especially in a growing animal, for structural improvements to counter new mechanical stresses on the body. They additionally provide a vast and accessible reservoir of minerals that can be withdrawn as needed for general cellular requirements.

The level of calcium in the blood is maintained by three hormones that coordinate the absorption, storage, and excretion of calcium ions. If blood calcium should decrease slightly, the parathyroid gland increases its secretion of **PTH.** This increase stimulates osteoclasts to dissolve bone adjacent to these cells, thus releasing calcium and phosphate into the bloodstream and returning blood calcium level to normal. PTH also decreases the rate of calcium excretion by the kidney and increases production of the hormone 1,25-dihydroxyvitamin D (see the following text). PTH levels vary inversely with blood calcium level, as shown in Figure 36-11.

A second hormone involved in calcium metabolism in all tetrapods is derived from vitamin D. Vitamin D, like all vitamins, is a dietary requirement. But unlike other vitamins, vitamin D may also be synthesized in the skin from a precursor by irradiation with ultraviolet light from the sun. Vitamin D is then converted in a two-step oxidation to a hormonal form, **1,25-dihydroxyvitamin D.** This steroid hormone is essential for active calcium absorption by the gut (Figure 36-12). Production of 1,25-dihydroxyvitamin D is stimulated by low plasma phosphate as well as by an increase in PTH secretion.

In humans, a deficiency of vitamin D causes rickets, a disease characterized by low blood calcium and weak, poorly calcified bones that tend to bend under postural and gravitational stresses. Rickets has been called a disease of northern winters, when sunlight is minimal. It once was common in the smoke-darkened cities of England and Europe.

A third calcium-regulating hormone, **calcitonin,** is secreted by specialized cells (C cells) in the thyroid gland of mammals and in the ultimobranchial gland of other vertebrates. Calcitonin is released in response to elevated levels of calcium in the blood. It rapidly suppresses calcium withdrawal from bone, decreases intestinal absorption of calcium, and increases excretion of calcium by the kidneys. Calcitonin therefore protects the body against an increase in level of calcium in the blood, just as parathyroid hormone protects it from a decrease in blood calcium (Figure 36-12). Calcitonin has been identified in all vertebrate groups, but its importance is uncertain because replacement of calcitonin is not required for maintenance of calcium homeostasis, at least in humans, if the thyroid

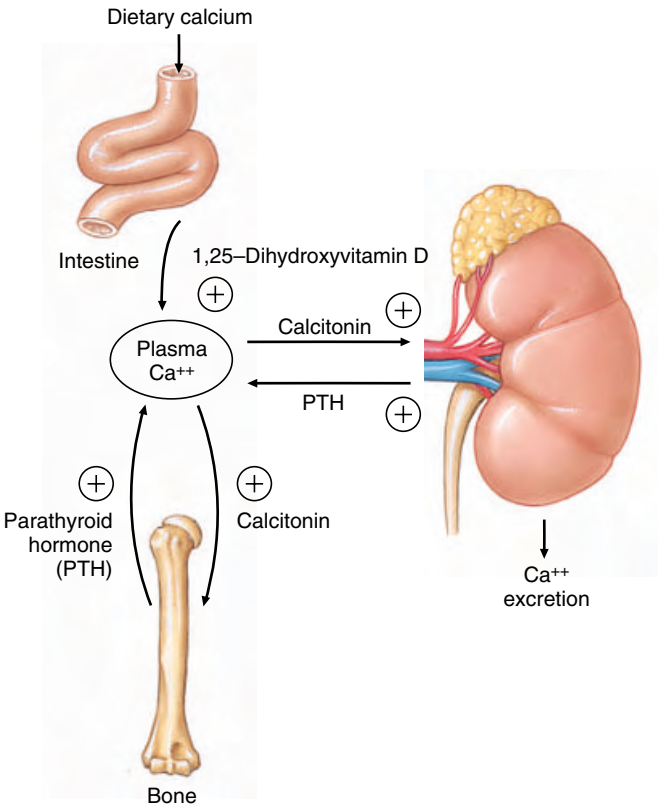


Figure 36-12
Regulation of blood calcium in birds and mammals.

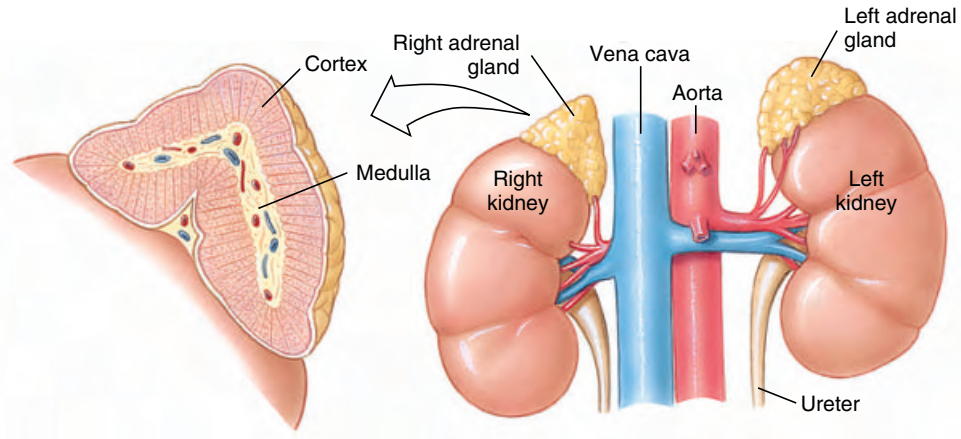


Figure 36-13
Paired adrenal glands of humans, showing gross structure and position on the upper poles of the kidneys. Steroid hormones are produced by the cortex. The sympathetic hormones epinephrine and norepinephrine are produced by the medulla.

gland is surgically removed (also removing the C cells).

Hormones of the Adrenal Cortex

The mammalian adrenal gland is a double gland composed of two unrelated types of glandular tissue: an outer region of adrenocortical cells, or **cortex,** and an inner region of specialized cells, the **medulla** (Figure 36-13). In nonmammalian vertebrates homologs of adrenocortical and medullary cells are organized quite differently; they may be intermixed or distinct, but never arranged in a cortex-medulla relationship as in mammals.

At least 30 different compounds have been isolated from adrenocortical tissue, all of them closely related lipoidal compounds known as steroids. Only a few of these compounds are true steroid hormones; most are various intermediates in the synthesis of steroid hormones from **cholesterol** (Figure 36-14). Corticosteroid hormones are commonly classified into two groups, according to their function: glucocorticoids and mineralocorticoids.

Glucocorticoids, such as **cortisol** (see Figure 36-14) and **corticosterone,** are concerned with food metabolism, inflammation, and stress. They promote synthesis of glucose from compounds other than carbohydrates, particularly amino acids and fats. The overall effect of this process, called **gluconeogenesis,** is to increase the level of glucose in the blood, thus providing a quick energy source for muscle and nervous tissue. Glucocorticoids are also important in diminishing the immune response to various inflammatory conditions. Because several diseases of humans are inflammatory diseases (for example, allergies, hypersensitivity, and rheumatoid arthritis), these corticosteroids have important medical applications.

The adrenal steroid hormones, especially the glucocorticoids, are remarkably effective in relieving symptoms of rheumatoid arthritis, allergies, and various disorders of connective tissue, skin, and blood. Following the report in 1948 by P. S. Hench and his colleagues at the Mayo Clinic that cortisone dramatically relieved the pain and crippling effects of advanced arthritis, the steroid hormones were hailed by the media as "wonder drugs." Optimism was soon dimmed, however, when it became apparent that severe side effects always attended long-term administration of anti-inflammatory steroids. Steroid therapy lulls the adrenal cortex into inactivity and may permanently impair the body's capacity to produce its own steroids. Today steroid therapy is applied with caution, because it is realized that the inflammatory response is a necessary part of the body's defenses.

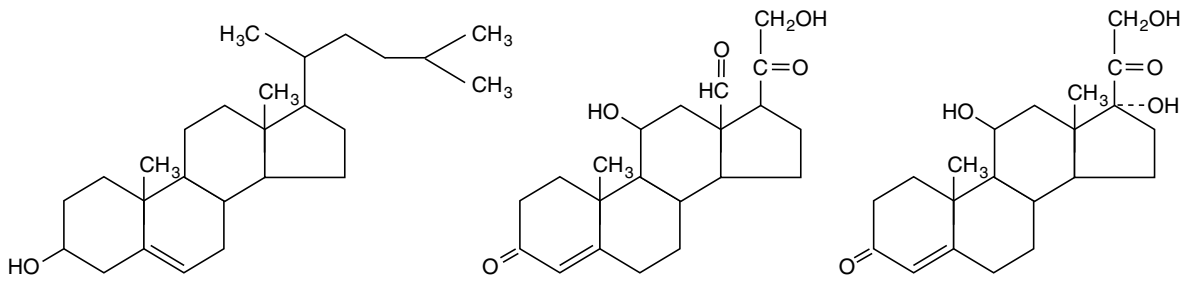


Figure 36-14

Hormones of the adrenal cortex. Cortisol (a glucocorticoid) and aldosterone (a mineralocorticoid) are two of several steroid hormones synthesized from cholesterol in the adrenal cortex.

Synthesis and secretion of glucocorticoids are controlled principally by ACTH of the anterior pituitary (see Figure 36-6), while ACTH is controlled by corticotropin-releasing hormone (CRH) of the hypothalamus (Table 36-1). As with pituitary control of the thyroid, a negative feedback relationship exists between CRH, ACTH, and the adrenal cortex (Figure 36-3). An increase in release of glucocorticoids suppresses output of CRH and ACTH; the resulting decline in blood level of CRH and ACTH then feeds back to the adrenal cortex to inhibit further release of glucocorticoids. An opposite sequence of events happens should the blood level of glucocorticoids drop: CRH and ACTH output increases which in turn stimulates secretion of glucocorticoids. CRH is known to mediate stressful stimuli through the adrenal axis.

Mineralocorticoids, the second group of corticosteroids, are those that regulate salt balance. **Aldosterone** (see Figure 36-14) is by far the most important steroid of this group. Aldosterone promotes tubular reabsorption of sodium and tubular secretion of potassium by the kidneys. Since sodium usually is in short supply in diets of many animals and potassium is in excess, the mineralocorticoids play vital roles in preserving the correct balance of blood electrolytes. The salt-regulating action of aldosterone is controlled by the renin-angiotensin system, described on p. 674 and by blood levels of potassium ions. High levels of potassium ions in the blood are a potent direct stimulator of aldosterone release from the adrenal cortex, thus promoting reabsorption of sodium into the blood and secretion of excess potassium ions into the urine.

The adrenocortical tissue also produces **androgens** (Gr. *andros*, man, + *genesis*, origin), which, as the name implies, are similar in effect to the male sex hormone, testosterone. Adrenal androgens promote some developmental changes that occur just before puberty in human males and females. Recent development of so-called **anabolic steroids,** synthetic hormones related to testosterone, has led to widespread abuse of steroids among athletes (see following note).

Use of anabolic steroids by athletes became major news following Ben Johnson's drug-fueled win of the 100-meter race at the 1988 Olympics. Despite almost universal condemnation by Olympic, medical, and college sports authorities, an unscientific and clandestine program of experimentation with anabolic steroids has become popular with many amateur and professional athletes in many countries. These synthetics (and testosterone and its precursors) cause hypertrophy of skeletal muscle and may improve performance that depends on strength. Unfortunately, they also have serious side effects, including testicular atrophy (and infertility), periods of irritability, abnormal liver function, and cardiovascular disease. In 1990, a National Institute of Drug Abuse survey reported that nearly 3% of high school seniors (5% of males and 0.5% of females) had used steroids at some time in their lives. More recent surveys suggest that steroid use among high school males has been stable since 1991, but use in high school females has shown a significant increase since then. Yesalis, C.E., C.K Barsukiewicz, A.N. Kopstein, and M.S. Bahrke. 1997. Trends in anabolic-androgenic steroid use among adolescents. Arch. Pediatr. Adolesc. Med. **151** (2):1197-1206). Use among adults and professional athletes is not well documented, although anecdotal evidence suggests that such drugs are popular among athletes in a variety of sports (the most famous recent athlete being Mark McGwire of the St. Louis Cardinals).

Hormones of the Adrenal Medulla

Adrenal medullary cells secrete two structurally similar hormones: **epinephrine (adrenaline)** and **norepinephrine (noradrenaline).** The adrenal medulla is derived embryologically from the same tissue that gives rise to the postganglionic sympathetic neurons of the autonomic nervous system (p. 736). Norepinephrine serves as a neurotransmitter at the endings of sympathetic nerve fibers. Thus functionally, as well as embryologically, the adrenal medulla can be considered a very large sympathetic ganglion.

It is not surprising then that adrenal medullary hormones and the sympathetic nervous system have the same general effects on the body. These effects center on responses to emergencies, such as fear and strong emotional states, flight from danger, fighting, lack of oxygen, blood loss, and exposure to pain. Walter B. Cannon, of homeostasis fame (p. 665), termed these "fight or flight" responses that are appropriate for survival. We

are familiar with the increased heart rate, tightening of the stomach, dry mouth, trembling muscles, general feeling of anxiety, and increased awareness that attends sudden fright or other strong emotional states. These effects are attributable to increased activity of the sympathetic nervous system and to rapid release into the blood of epinephrine from the adrenal medulla.

Epinephrine and norepinephrine have many other effects of which we are not as aware, including constriction of arterioles (which, together with increased heart rate, increases blood pressure), mobilization of liver glycogen and fat stores to release glucose and fatty acids for energy, increased oxygen consumption and heat production, hastening of blood coagulation, and inhibition of the gastrointestinal tract. These changes prepare the body for emergencies and are activated in stressful conditions.

Insulin and Glucagon from Islet Cells of the Pancreas

The pancreas is both an exocrine and an endocrine organ (Figure 36-15). The exocrine portion produces pancreatic juice, a mixture of digestive enzymes and bicarbonate ions conveyed by a duct to the digestive tract (see Chapter 34). Scattered within the extensive exocrine portion of the pancreas are numerous small islets of tissue, called **islets of Langerhans** (see Figure 36-15 and photograph on p. 751). This endocrine portion of the pancreas is only 1% to 2% of the total weight of the organ. The islets are without ducts and secrete their hormones directly into blood vessels that extend throughout the pancreas.

Two polypeptide hormones are secreted by different cell types within the islets: **insulin,** produced by **beta cells,** and **glucagon,** produced by **alpha cells.** Insulin and glucagon have antagonistic actions of great importance in metabolism of carbohydrates and fats. Insulin is essential for uptake of blood-borne glucose by cells, especially skeletal muscle cells.

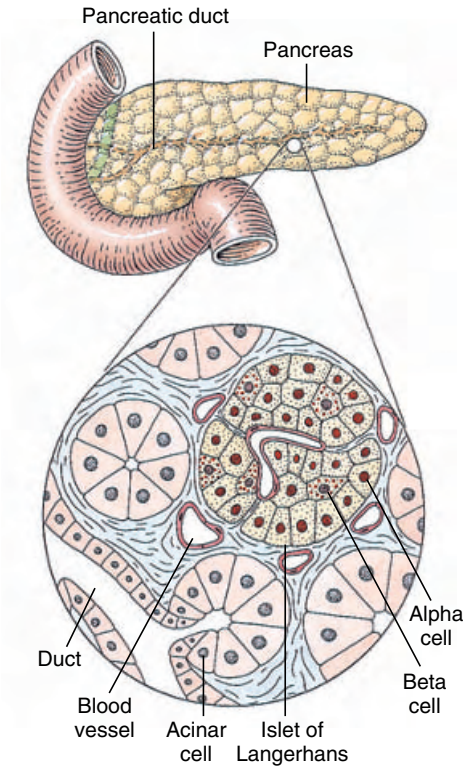


Figure 36-15

The pancreas is composed of two kinds of glandular tissue: exocrine acinar cells that secrete digestive juices that enter the intestine through the pancreatic duct, and endocrine islets of Langerhans. The islets of Langerhans secrete the hormones insulin and glucagon directly into the blood circulation.

Insulin promotes entry of glucose into body cells through its action on a glucose transporter molecule found in cell membranes. An important exception to this dependency on insulin for cellular glucose uptake are neurons, which do not require the presence of insulin for glucose uptake. This independence from insulin is very important because unlike other cells of the body, neurons almost exclusively use glucose as an energy source. Cells of the rest of the body, however, require insulin to use glucose; without insulin the level of glucose in the blood rises to abnormally high levels, a condition called hyperglycemia. When this level exceeds the transport maximum of the kidney (see note on p. 673) sugar (glucose) appears in the urine. Insulin deficiency also inhibits uptake of amino acids by skeletal muscle, and fats and muscle are broken down to provide energy. Body cells starve while the urine abounds in the very substance the body craves. The disease, called **diabetes mellitus,** afflicts nearly 5% of the human population in varying degrees of severity. If left untreated, it can lead to severe damage to kidneys, eyes, and blood vessels, and it can greatly shorten life expectancy.

In 1982, insulin became the first hormone produced by genetic engineering (recombinant DNA technology, p. 97) to be marketed for human use. Recombinant insulin has the exact structure of human insulin and therefore will not stimulate an immune response, which has often been a problem for diabetics receiving insulin purified from pig or cow pancreas.

The first extraction of insulin in 1921 by two Canadians, Frederick Banting and Charles Best, was one of the most dramatic and important events in the history of medicine. Many years earlier two German scientists, J. Von Mering and O. Minkowski, discovered that surgical removal of the pancreas of dogs invariably caused severe symptoms of diabetes, resulting in the animal's death within a few weeks. Many attempts were made to isolate the diabetes preventive factor, but all failed because powerful protein-splitting digestive enzymes in the exocrine portion of the pancreas destroyed the hormone during extraction procedures. Following a hunch, Banting, in collaboration with Best and his physiology professor J. J. R. Macleod, tied off the pancreatic ducts of several dogs. This caused the exocrine portion of the gland with its hormone-destroying enzyme to degenerate, but left the islets' tissues healthy long enough for Banting and Best to extract insulin successfully from these glands. Injected into another dog, the insulin immediately lowered the level of sugar in the blood (Figure 36-16). Their experiment paved the way for commercial extraction of insulin from slaughterhouse animals. It meant that millions of people with diabetes, previously doomed to invalidism or death, could look forward to more normal lives.

Glucagon, the second hormone of the pancreas, has several effects on carbohydrate and fat metabolism that are opposite to the effects of insulin. For example, glucagon raises the blood glucose level (by converting liver glycogen to glucose), whereas insulin lowers blood glucose. Glucagon and insulin do not have the same effects in all vertebrates, and in some, glucagon is lacking altogether. Glucagon is an example of a hormone that operates through the cyclic AMP second-messenger system.

Growth Hormone and Metabolism

Growth hormone (GH) is a particularly important metabolic hormone in young animals during growth and development. It acts directly on long bones to promote cartilaginous growth and bone formation by cell division and protein synthesis, thus producing an increase in length and density of bone. GH increases the release of fat from adipose tissue stores and glycogen from liver stores for energy metabolism. Thus, GH is considered a **diabetogenic hormone,** since oversecretion leads to an increase in blood glucose and can result in insulin insensitivity or diabetes. If produced in excess, GH causes giantism. A deficiency of this hormone in a human child leads to dwarfism. GH also acts indirectly on growth via stimulation of **insulin-like growth factor (IGF)** or somatomedin release from the liver. This polypeptide hormone promotes mobilization of glycogen and fat stores necessary for growth processes.

Figure 36-16
Charles H. Best and Sir Frederick Banting in 1921 with the first dog to be kept alive by insulin.

The Newest Hormone—Leptin

Following discovery of the *ob* gene in 1994, which codes for this newest hormone, J. Friedman and coworkers soon coined the term, **leptin** (Gr. *leptos*, thin), for the circulating hormone, produced by white fat cells (adipose tissue). Subsequently, receptors for leptin have been found in many tissues, but the primary site of action of leptin appears to be the brain, particularly the hypothalamus. Leptin is an important hormone that regulates eating behavior and energy balance as part of a feedback system that informs the brain as to the energy status of the periphery. Leptin has become immensely significant in the study of sateity signals and energy expenditure, since these studies relate to the overall problem of human obesity (p. 718). It is of interest that blood plasma levels of leptin mirror those of insulin, which also provides an important feedback signal to the brain.

Summary

Hormones are chemical messengers synthesized by special endocrine and other cells and transported by the blood to target cells where they affect cell function by altering specific biochemical processes. Specificity of response is ensured by the presence on or in target cells of protein receptors that bind only selected hormones. Hormone effects are vastly amplified in target cells by acting through one of two basic mechanisms. Many hormones, including epinephrine, glucagon, vasopressin, and some hormones of the anterior pituitary, cause production of a "second messenger," such as cyclic AMP, that relays the hormone's message from a surface receptor to a cell's biochemical machinery. Steroid hormones and thyroid hormones operate through nuclear receptors. A hormone-receptor complex is formed that alters protein synthesis by stimulating or inhibiting gene transcription.

Most invertebrate hormones are products of neurosecretory cells. The best understood invertebrate endocrine system is that controlling molting and metamorphosis in insects. A juvenile insect grows by passing through a series of molts under control of two hormones, one (ecdysone) favoring molting to an adult and the other (juvenile hormone) favoring retention of juvenile characteristics. Ecdysone is under the control of a neurosecretory hormone (PTTH) from the brain.

The vertebrate endocrine system is orchestrated by the hypothalamus. Release of all anterior pituitary hormones is primarily regulated by hypothalamic neurosecretory products called releasing hormones (or release-inhibiting hormones). The hypothalamus also produces two neurosecretory hormones, which are stored in and released from the posterior lobe of the pituitary. In mammals these two hormones are oxytocin, which stimulates milk production and uterine contractions during parturition; and vasopressin (antidiuretic hormone), which acts on the kidney to restrict urine production, causes vasoconstriction of blood vessels, and increases thirst. In amphibians, reptiles, and birds, vasotocin replaces vasopressin as the water-balance hormone.

The anterior lobe of the pituitary produces seven well-characterized hormones. Four of these are tropic hormones that regulate subservient endocrine glands: thyrotropic hormone (TSH), which controls secretion of thyroid hormones; adrenocorticotropic hormone (ACTH), which stimulates release of steroid hormones by the adrenal cortex; and follicle-stimulating hormone (FSH) and luteinizing hormone (LH), which act on ovaries and testes. Three direct-acting hormones are (1) prolactin, which plays several diverse roles, including

stimulation of milk production; (2) growth hormone, which governs body growth and metabolism; and (3) melanocyte-stimulating hormone (MSH), which controls melanocyte dispersion in ectothermic vertebrates.

The pineal gland, a derivative of the pineal complex of the diencephalon of the brain, produces the hormone melatonin. In many vertebrates, melatonin, which is released in response to darkness, maintains circadian rhythms. In birds and mammals that are seasonal breeders, melatonin provides information regarding daylength, and thereby indirectly regulates seasonal reproductive activity.

Recent application of ultrasensitive radioimmunochemical techniques has revealed many neuropeptides in the brain, several of which behave as neurotransmitters in the brain but as hormones elsewhere in the body. The classical definition of a hormone has been modified to include other chemical messengers, such as prostaglandins and cytokines, which originate in sources other than clearly defined endocrine glands.

Several hormones play important roles in regulating cellular metabolic activities. Two thyroid hormones, triiodothyronine (T_3) and thyroxine (T_4), control growth, development of the nervous system, and cellular metabolism. Calcium metabolism is regulated principally by three hormones: parathyroid hormone from the parathyroid glands, a hormonal derivative of vitamin D, 1,25-dihydroxyvitamin D, and calcitonin from the thyroid gland. Parathyroid hormone and 1,25-dihydroxyvitamin D increase plasma calcium levels; calcitonin decreases plasma calcium levels.

The principal steroid hormones of the adrenal cortex are glucocorticoids, which stimulate formation of glucose from non-glucose sources (gluconeogenesis), and mineralocorticoids, which regulate blood electrolyte balance. The adrenal medulla is the source of epinephrine and norepinephrine, which have many effects, including assisting the sympathetic nervous system in emergency responses. They also increase energy substrates in the blood for use in emergency situations.

Glucose metabolism is regulated by the antagonistic action of two pancreatic hormones. Insulin is needed for cellular use of blood glucose and uptake of amino acids in muscle. Glucagon opposes the action of insulin.

The most recently discovered hormone, leptin, is secreted by adipose tissue and feeds back to the hypothalamus to modulate food intake and energy balance.

Review Questions

1. Outline the famous experiment of Berthold that marks the first endocrine experiment. What might the hypothesis have been?
2. Provide definitions for the following: hormone, endocrine gland, exocrine gland, hormone receptor molecule.
3. Hormone receptor molecules are the key to understanding specificity of hormone action on target cells. Describe and distinguish between receptors located on the cell surface and those located in the nucleus of target cells. Name two hormones whose action is mediated through each type of receptor.
4. What is the importance of feedback systems in the control of hormonal output? Offer an example of a hormonal feedback pattern.
5. Explain how the three hormones involved in insect growth—ecdysone, juvenile hormone, and PTTH—interact in molting and metamorphosis.
6. Name seven hormones produced by the anterior pituitary gland. Why are four of these seven hormones called "tropic hormones"? Explain how secretion of the anterior pituitary hormones is controlled by neurosecretory cells in the hypothalamus.
7. Describe the chemical nature and function of two posterior lobe hormones, oxytocin and vasopressin. What is distinctive about the way these neurosecretory hormones are secreted compared with the neurosecretory release hormones that control the anterior pituitary hormones?
8. What is the evolutionary origin of the pineal gland of birds and mammals? Explain the role of the pineal hormone, melatonin, in regulating seasonal reproductive rhythms in birds and mammals. Does melatonin have any function in humans?
9. What are endorphins and enkephalins? What are prostaglandins?
10. What are some functions of the recently described hormones called cytokines?
11. What are the two most important functions of the thyroid hormones?
12. Explain how you would interpret the graph in Figure 36-10 to show that PTH and calcitonin act in a complementary way to control blood calcium level.
13. Describe the principal functions of the two major groups of adrenal cortical steroids, the glucocorticoids and the mineralocorticoids. To what extent do these names provide clues to their function?
14. Where are the hormones epinephrine and norepinephrine produced and what is their relationship to the sympathetic nervous system and its response to emergencies?
15. Explain the actions of hormones of the islets of Langerhans on the level of glucose in the blood. What is the consequence of insulin insufficiency as in the disease diabetes mellitus?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Endocrines and Reproduction. Valuable information on the endocrine system and hormones vital in reproduction.

Diabetes. CDC fact sheet on diabetes.

Anabolic Steroids and Impact on the Human Body Explained in Drug-Free Resource Net. How steroids increase body muscle yet lead to dangerous—even fatal—side effects is the focus of this site.

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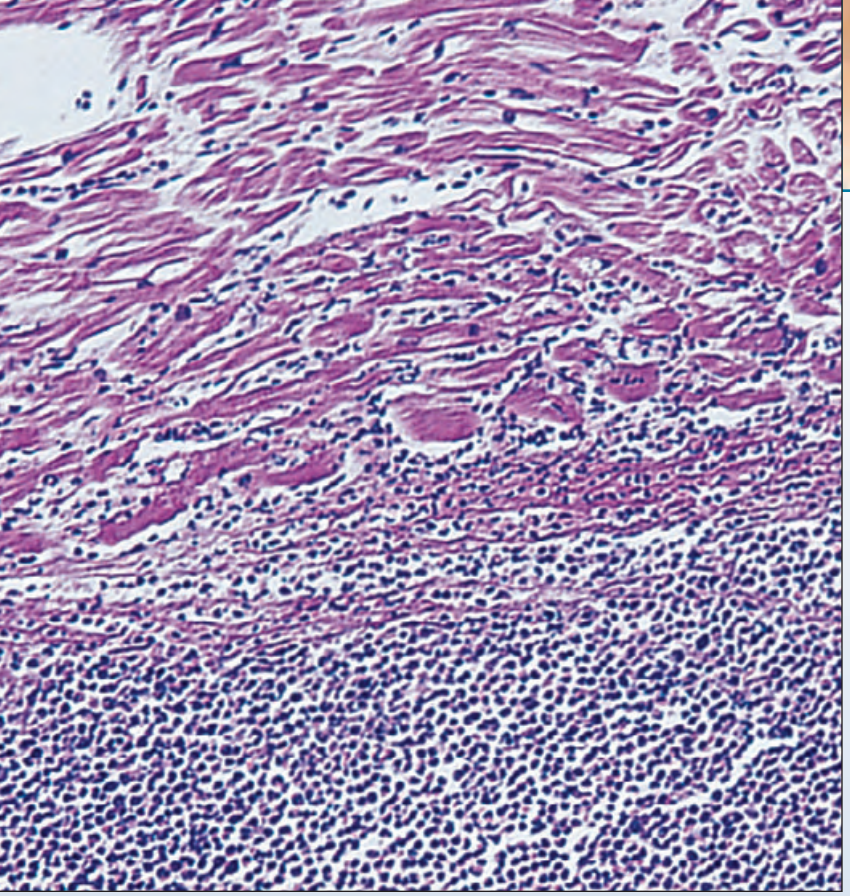

Section of abcess in heart muscle.

CHAPTER

37

Immunity

The Language of Cells in Immunity

For almost 100 years scientists have known that certain cells in an animal could secrete substances that affected various processes in other, target cells, for example, metabolism, physiology, or differentiation; however, the means of this communication between cells remained a mystery. Much of the shroud was lifted by more recent discoveries. Specific signal molecules, often proteins or peptides, are secreted by certain cells. Target cells have receptors protruding through their outer membranes that specifically bind the signal molecules and only those molecules. Binding of a signal causes changes in the part of the receptor molecule (or in an associated membrane protein) that extends into the cytoplasm, and this initiates a cascade of activations involving protein kinases and phosphorylases (enzymes that transfer phosphate groups). Transcription factors are mobilized. In the nucleus the transcription factors initiate transcription of formerly inactive genes, leading to synthesis of the products they encode.

We now know that hormones affect target cells by this mechanism (Chapter 36), and it is also the scheme by which cells of the immune system communicate with each other and with other cells. Signal molecules of the immune system are called *cytokines*. Cytokines and their receptors are the language of communication in the immune system. They perform an intricate and elaborate ballet of activation and regulation, causing some cells to proliferate, suppressing proliferation of others, and stimulating secretion of additional cytokines or defense molecules. Precise signalling among cells and exact performance of their duties are essential to maintainence of human health and defense against invading viruses, bacteria, and parasites and for prevention of unrestrained cell division, as in cancer. Successful establishment of invaders in our bodies depends on evasion or subversion of our immune system, and inappropriate response of immune cells may itself produce disease. We have learned to manipulate the immune response so that we can transplant organs between individuals, but complete failure in its cell communication results in profound disease, such as AIDS. ■

The immune system is located throughout the body of an animal, and it is as crucial to survival as the respiratory, circulatory, nervous, skeletal, or any other system. Every animal's environment is filled with an incredible number of parasites and potential parasites: flatworms, nematodes, arthropods, single-celled eukaryotes, bacteria, and viruses. Whether any parasite can survive in that animal (the **host**), and severity of the disease the parasite may cause, depends largely on the response of the host defense system.

Susceptibility and Resistance

A host is **susceptible** to a parasite if the host cannot eliminate the parasite before the parasite can become established. The host is **resistant** if its physiological status prevents establishment and survival of the parasite. Corresponding terms from the viewpoint of a parasite would be **infective** and **noninfective.**

These terms deal only with the success or failure of infection, not with mechanisms producing the result. Mechanisms that increase resistance (and correspondingly reduce susceptibility and infectivity) may involve either attributes of a host not related to active defense mechanisms or specific defense mechanisms mounted by a host in response to a foreign invader. It is important to remember that these terms are relative, not absolute; for example, one individual organism may be more or less resistant than another, and a single individual may be more or less resistant at different times of its life, depending on age, health, and environmental exposure.

The term **immunity** is often used as synonymous with resistance, but it is also associated with the sensitive and specific immune response exhibited by vertebrates. However, because many invertebrates can be immune to infection by various agents, a more concise statement is that *an animal demonstrates immunity if it possesses tissues capable of recognizing and protecting the animal against nonself invaders*. Most animals show some degree of **innate (nonspecfic) immunity,** a mechanism of defense that does not depend on prior exposure to the invader. In addition to having innate immunity, vertebrates—and invertebrates to a lesser extent—develop **acquired (specific) immunity,** which is specific to a particular nonself material, requires time for its development, and occurs more quickly and vigorously on secondary response. Many innate mechanisms discussed in the next section *are dramatically influenced and strengthened in vertebrates as a consequence of acquired immune responses.*

Frequently resistance conferred by immune mechanisms is not complete. In some instances a host may recover clinically and be resistant to a specific challenge, but some parasites may remain and reproduce slowly, as in toxoplasmosis (p. 230), Chagas' disease (p. 226), and malaria (p. 231). This condition is called **premunition.**

Innate Defense Mechanisms

Physical and Chemical Barriers

The unbroken surface of most animals provides a barrier to invading organisms. It may be tough and cornified, as in many terrestrial vertebrates, or sclerotized, as in arthropods. Soft outer surfaces are usually protected by a layer of mucus, which lubricates the surface and helps dislodge particles from it.

A variety of antimicrobial substances are present in body secretions of vertebrates. Chemical defenses present in many vertebrates include a low pH in the stomach and vagina and hydrolytic enzymes in secretions of the alimentary tract. Mucus is produced by mucous membranes lining the digestive and respiratory tract of vertebrates and contains parasiticidal substances such as **IgA** and **Lysozyme.** IgA is a class of antibody (p. 772) that can cross cellular barriers easily and is an important protective agent in the mucus of the intestinal epithelium. IgA is present also in saliva and sweat. Lysozyme is an enzyme that attacks the cell wall of many bacteria.

Various cells, including those involved in the acquired immune response, liberate protective compounds. A family of low-molecular-weight glycoproteins, the **interferons,** are released by a variety of eukaryotic cells in response to invasion by intracellular parasites (including viruses) and other stimuli. **Tumor necrosis factor (TNF)** is produced mainly by cells called **macrophages** (see following text). TNF is a major mediator of inflammation (p. 777) and in sufficient concentration causes **fever.** Fever in mammals is one of the most common symptoms of infection. The protective role of fever, if any, remains unclear, but high body temperature may destabilize certain viruses and bacteria.

The intestine of most animals harbors a population of bacteria that seem not to be harmed by host defenses, nor do they elicit any protective defense response. In fact, the normal intestinal microflora in vertebrates tends to inhibit establishment of pathogenic microbes.

Substances in normal human milk can kill intestinal protozoa such as *Giardia lamblia* and *Entamoeba histolytica* (Chapter 11), and these substances may be important in protection of infants against these and other infections. Antimicrobial elements in human breast milk include lysozyme, IgA, interferons, and leukocytes (white blood cells, see Chapter 33).

Some species of mammals are susceptible to infection with parasites such as *Schistosoma mansoni* (Chapter 14), and others are partially or completely resistant. Without mediation by antibody, macrophages of more resistant species (rats, guinea pigs, rabbits) kill schistosome juveniles, but macrophages of susceptible species do not.

Complement is a series of enzymes that are activated in sequence as a host response to invading organisms. Activation of complement by the

classical pathway (so called only because it was discovered first) depends on fixed antibody and so is an effector mechanism in the acquired immune response following text. Complement activated by the **alternative pathway,** is an important innate defense against invasion by bacteria and some fungi. Classical and alternative pathways share some, but not all, components. In the alternative pathway, the first component is activated spontaneously in the blood and binds to cell surfaces. This event initiates a cascade of activations, ultimately resulting in cell lysis. The host's own cells are not lysed by the alternative pathway because regulatory proteins rapidly inactivate the first active component of complement when it binds to host cells but not to foreign cells.

Cellular Defenses: Phagocytosis

For defense against an invader an animal's cells must recognize when a substance does not belong; they must recognize *nonself*. **Phagocytosis** illustrates nonself recognition, and it also serves as a process for removing senescent cells and cellular debris from the host. Phagocytosis occurs in almost all metazoa and is a feeding mechanism in many single-celled organisms (p. 220). A cell that has this ability is a **phagocyte.** Phagocytes engulf a particle within an invagination of the phagocyte's cell membrane. The invagination becomes pinched off, and the particle becomes enclosed within an intracellular vacuole. Other cytoplasmic vacuoles called **lysosomes** join with the particle-containing vacuole and pour in digestive enzymes to destroy the particle. Lysosomes of many phagocytes also contain enzymes that catalyze production of cytotoxic **reactive oxygen intermediates (ROIs)** and **reactive nitrogen intermediates (RNIs).** Examples of ROIs are superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and hydroxyl radical (OH•). RNIs include nitric oxide (NO) and its oxidized forms, nitrite (NO_2^-) and nitrate (NO_3^-). All such intermediates are potentially toxic to invasive microorganisms or parasites.

Phagocytes and Other Defense Cells

Many invertebrates have specialized cells that function as itinerant troubleshooters within the body, acting to engulf or encapsulate foreign material (see Table 37-3) and repair wounds. Such cells are variously known as amebocytes, hemocytes, or coelomocytes in different animals. If a foreign particle is small, it is engulfed by phagocytosis; but if it is larger than about 10 μm, it is usually encapsulated. Arthropods can encapsulate a foreign object by deposition of melanin around it, either from the cells of the capsule or by precipitation from the hemolymph (blood).

In vertebrates several categories of cells are capable of phagocytosis. **Monocytes** arise from stem cells in the bone marrow (Figure 37-1) and give rise to the **mononuclear phagocyte system (reticuloendothelial [RE] system),** which are phagocytic cells stationed around the body. The RE system includes **macrophages** in lymph nodes, spleen, and lung, **Kupffer cells** in sinusoids of the liver; and **microglial cells** in the central nervous system. Macrophages also have important roles in the specific immune response of vertebrates (see following text).

Some **polymorphonuclear leukocytes (PMNs),** a name that refers to the highly variable shape of their nucleus, are circulating phagocytes in blood. Another name for these leukocytes is **granulocytes,** which alludes to the many small granules that can be seen in their cytoplasm after treatment with appropriate stains. According to the staining properties of their granules, granulocytes are further subdivided into **neutrophils, eosinophils,** and **basophils.** Neutrophils are the most abundant, and they provide the first line of phagocytic defense in an infection. Eosinophils in normal blood account for about 2% to 5% of the total leukocytes, and basophils are the least numerous at about 0.5%. A high **eosinophilia** (eosinophil count in the blood) is often associated with allergic diseases and parasitic infections.

Several other kinds of cells, including basophils, are not important as phagocytes but are important cellular components of the defense system. **Mast cells** are basophil-like cells found in the dermis and other tissues. When they are stimulated to do so (in inflammation, p. 777), basophils and mast cells release a number of pharmacologically active substances that affect surrounding cells. **Lymphocytes,** including **T lymphocytes (T cells)** and **B lymphocytes (B cells),** are crucial in the acquired immune response of vertebrates. **Natural killer (NK) cells** are lymphocytelike cells that can kill virus-infected and tumor cells in absence of antibody. They release substances onto the target-cell surface to lyse it.

Acquired Immune Response in Vertebrates

The specialized system of nonself recognition possessed by vertebrates results in increased resistance to *specific* foreign substances or invaders on repeated exposures. Investigations on the mechanisms involved are currently intense, and our knowledge of them is increasing rapidly.

The immune response is stimulated by a specific foreign substance called an **antigen,** and, circularly, an antigen is any substance that will stimulate an immune response. Antigens may be any of a variety of substances with a molecular weight of over 3000. They are most commonly proteins and are usually (but not always) foreign to the host. The immune response has two arms, known as **humoral** and **cellular.** Humoral immunity is based on **antibodies,** which are both on cell surfaces and dissolved in blood and lymph, whereas cellular immunity is entirely associated with cell surfaces. There is

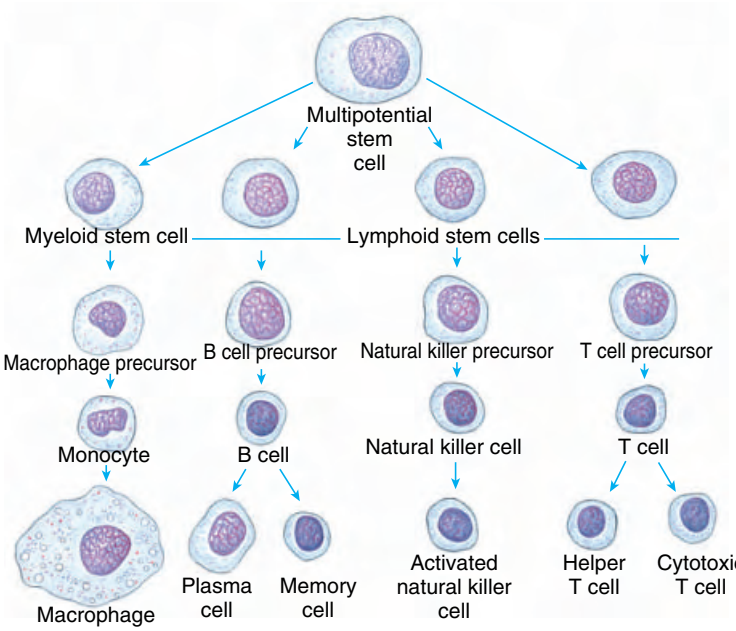

Figure 37-1

Lineage of some cells active in immune response. These cells, as well as red blood cells and other white blood cells are derived from multipotential stem cells in the bone marrow. B cells mature in bone marrow and are released into blood or lymph. Precursors of T cells go through a period in the thymus gland. Precursors of macrophages circulate in blood as monocytes.

extensive communication and interaction among cells of the two arms.

Basis of Self and Nonself Recognition

Major Histocompatibility Complex

We have known for many years that nonself recognition is very specific. If tissue from one individual is transplanted into another individual of the same species, the graft will grow for a time and then die as immunity against it rises. In the absence of drugs that modify the immune system, tissue grafts will grow successfully only if they are between identical twins or between individuals of highly inbred strains of animals. The molecular basis for this nonself recognition involves certain proteins embedded in the cell surface. These proteins are coded by certain genes, now known as the **major histocompatibility complex (MHC).** MHC proteins are among the most variable known, and unrelated individuals almost always have different genes. There are two types of MHC proteins: class I and class II. Class I proteins are found on the surface of virtually all cells, whereas class II MHC proteins are found only on certain cells participating in immune responses, such as lymphocytes and macrophages.

The capability of an immune response develops over a period of time in the early development of the organism. All substances present at the time the capacity develops are recognized as self in later life. Unfortunately, the system of self and nonself recognition sometimes breaks down, and an animal may begin to produce antibodies against some part of its own body. This condition leads to one of several known *autoimmune diseases*, such as rheumatoid arthritis, multiple sclerosis, lupus, and insulin-dependent diabetes mellitus.

Recognition Molecules

We discuss the role of MHC proteins in nonself recognition in the following text, but MHC proteins are not themselves the molecules that recognize foreign substances. This task falls to two basic types of molecules, the genes for which probably evolved from a common ancestor: **antibodies** and **T-cell receptors.** Each vertebrate individual has an enormous variety of antibodies, *each of which binds specifically* to one particular antigen (or part of the antigen), even though that antigen may have never been present in the body previously. There are probably an equal number of different T-cell receptors, each also specific for a particular antigen.

A major problem of immunology is understanding how the mammalian genome could contain the information needed to produce at least a million different antibodies. The answer seems to be that antibody genes occur in pieces, rather than as continuous stretches of DNA, and that the antigen-recognizing sites (variable regions) of the heavy and light chains of the antibody molecules are pieced together from information supplied by separate DNA sequences, which can be shuffled to increase the diversity of the gene products. The immense repertoire of antibodies is achieved in part by complex gene rearrangements and in part by frequent somatic mutations that produce additional variation in protein structure of the variable regions of the heavy and light antibody chains. Analogous processes occur in the production of genes for T-cell receptors.

Antibodies

Antibodies are proteins called **immunoglobulins.** They are borne in the surface of B lymphocytes or secreted by cells **(plasma cells)** derived from B cells. The basic antibody molecule consists of four polypeptide strands: two identical light chains and two identical heavy chains held together in a Y-shape by disulfide bonds and hydrogen bonds (Figure 37-2). The amino acid sequence toward the ends of the Y varies in both the heavy and light chains, according to the specific antibody molecule (the **variable region**), and this variation determines with which antigen the antibody can bind. Each of the ends of the Y forms a cleft that acts as the antigen-binding site (Figure 37-2), and specificity of the molecule depends on the shape of the cleft and properties of the chemical groups that line its walls. The remainder of the antibody is

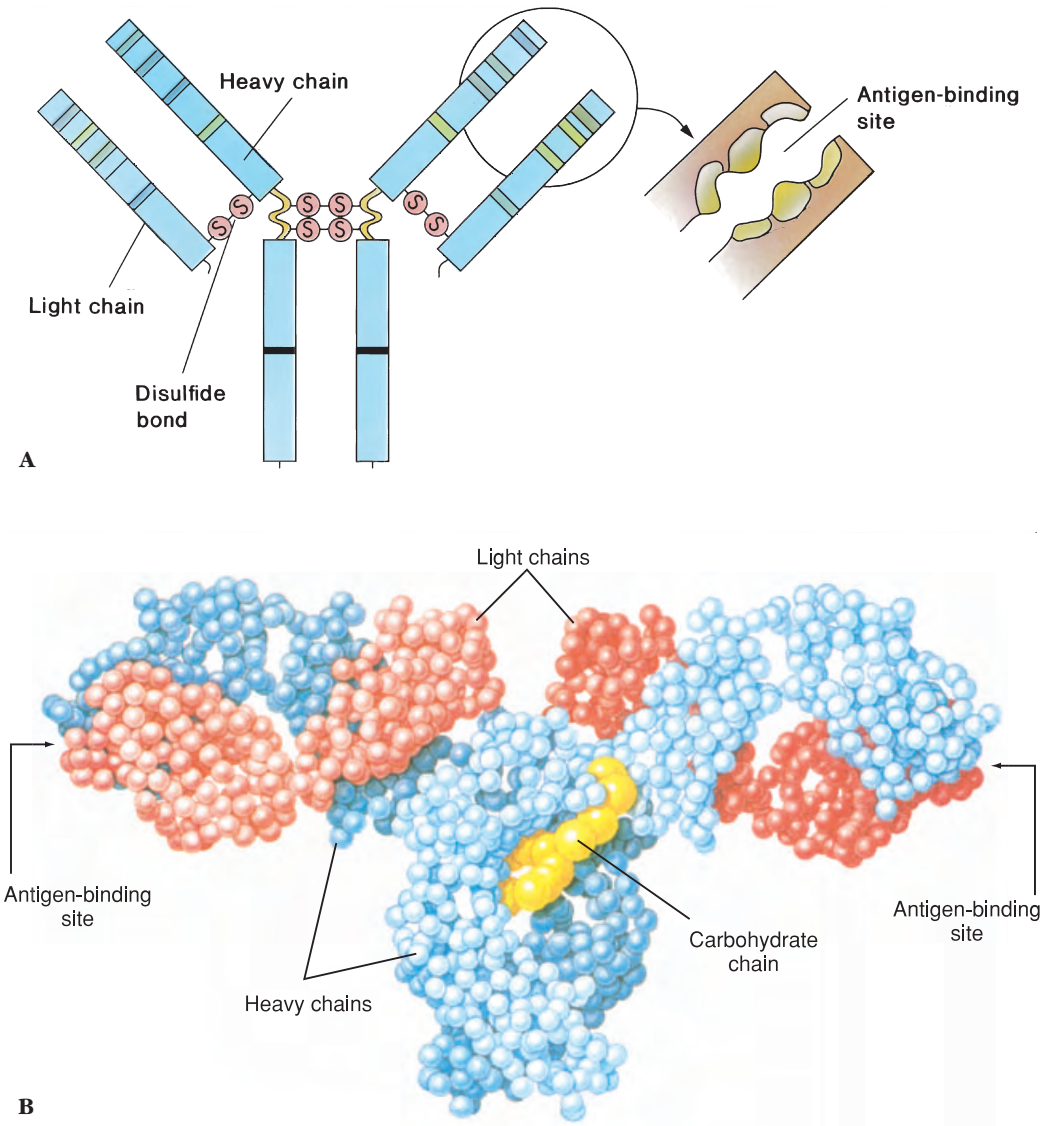

Figure 37-2

A, Antibody molecule is composed of two shorter polypeptide chains (light chains) and two longer chains (heavy chains) held together by covalent disulfide bonds. These are further subdivided into variable and constant regions that have independent folding units, or domains, of about 110 amino acids. The folding pattern is more complex than that shown here. Interchain disulfide bonds at the hinge region give the molecule flexibility at that point. The variable domains of both the light and heavy chains have hypervariable ends, which serve as the antigen-binding sites. **B,** Molecular model of antibody molecule.

known as the **constant region.** The variable end of the antibody molecule is often called **Fab,** for **a**ntigen-**b**inding **f**ragment, and the constant end is known as **Fc,** for **c**rystallizable **f**ragment (Figure 37-2). The so-called constant region is not really constant: the light chains can be either of two types, and the heavy chains may be any of five types. The type of heavy chain determines the **class** of the antibodies, known as **IgM, IgG** (now familiar to many people as *gamma globulin*), **IgA, IgD,** and **IgE.** The class of the antibody determines the specific role of the antibody in the immune response (for example, whether the antibody is secreted or held on a cell surface) but not the antigen it recognizes.

Functions of Antibody in Host Defense Antibodies can mediate destruction of an invader (antigen) in a number of ways. A foreign particle, for example, becomes coated with antibody molecules as their Fab regions become bound to it. Macrophages recognize the projecting Fc regions and are stimulated to engulf the particle. This is the process of **opsonization.** Antibodies also may be able to neutralize toxins that are secreted by an invader.

Another important process, particularly in destruction of bacterial cells, is interaction with complement activated by the classical pathway. As noted previously, the first component in the classical pathway is activated by bound antibody. The end result in both pathways can be the same, that is, lysis of a foreign cell. Both pathways may also lead to opsonization or enhancement of inflammation. Binding of complement to antigen-antibody complexes

can facilitate clearance of these potentially harmful masses by phagocytic cells.

Antibody bound to the surface of an invader may trigger contact killing of the invader by host cells in what is known as **antibody-dependent, cell-mediated cytotoxicity (ADCC).** Receptors for Fc of bound antibody on a microorganism or tumor cell cause natural killer cells to adhere to them and pour forth the cytotoxic contents of their vacuoles.

T-Cell Receptors

T-cell receptors are transmembrane proteins on the surfaces of T cells. Like antibodies, T-cell receptors have a constant region and a variable region. The constant region extends slightly into the cytoplasm and the variable region, which binds with specific antigens, extends outward. Most T-cells also bear other transmembrane proteins closely linked to the T-cell receptors, which serve as **accessory** or **coreceptor** molecules. These are of one of two types: **CD4** or **CD8.**

Subsets of T Cells

Lymphocytes are **activated** when they are stimulated to move from their recognition phase, in which they simply bind with particular antigens, to a phase in which they proliferate and differentiate into cells that function to eliminate the antigens. We also speak of activation of effector cells, such as macrophages, when they are stimulated to carry out their protective function.

Communication between cells in the immune response, regulation of the response, and certain effector functions are performed by different kinds of T cells. Although morphologically similar, subsets of T cells can be distinguished by characteristic proteins in their surface membranes. For example, cells with the coreceptor protein CD4 (for **c**luster of **d**ifferentiation) are $CD4^+$ and those with CD8 are described as $CD8^+$. Until recently immunologists believed that certain

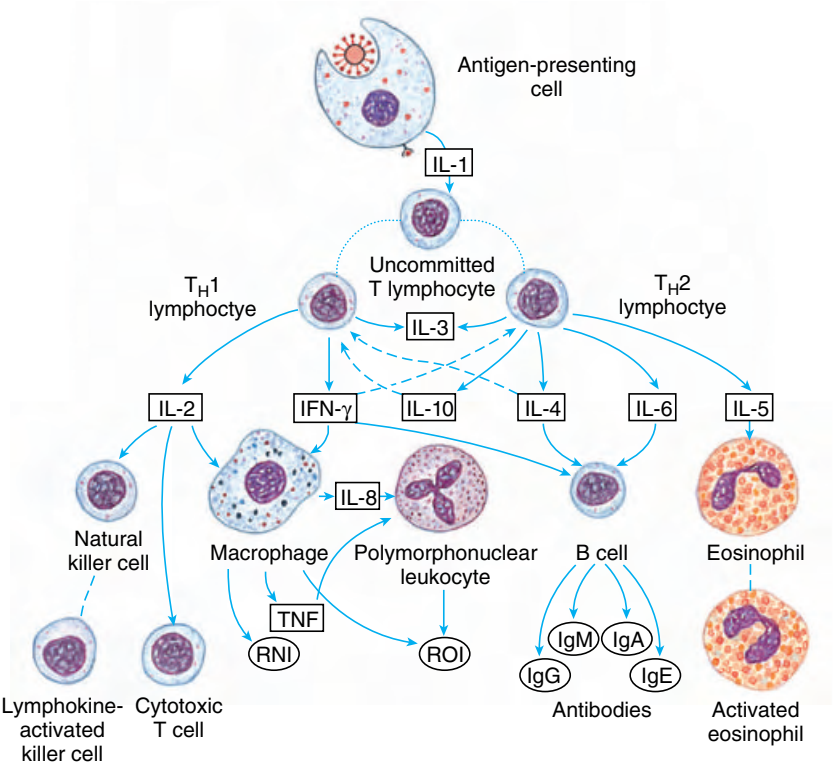

Figure 37-3

Major pathways involved in cell-mediated (T_H1) and humoral (T_H2) immune responses as mediated by cytokines. Solid arrows indicate positive signals and broken arrows indicate inhibitory signals. Broken lines without arrows indicate path of cellular activation. *IFN-γ*, interferon-γ, *Ig*, immunoglobulin; *IL* interleukin; *T_H*, T helper cells; *TNF*, tumor necrosis factor; *RNI* and *ROI*, toxic substances released onto invader.

$CD4^+$ cells (T helper or T_H) activated immune responses, and certain $CD8^+$ cells (T suppressors) downregulated such responses. Present evidence now suggests a more complicated web of interactions (Figure 37-3). Some T_H cells (designated T_H1) activate cell-mediated immunity while suppressing the humoral response, and others (called T_H2) activate humoral and suppress cell-mediated immunity.

Cytotoxic T lymphocytes (CTLs) are $CD8^+$ cells that kill target cells expressing certain antigens. A CTL binds tightly to the target cell and secretes a protein that causes pores to form in the cell membrane, resulting in lysis.

Cytokines

The 1980s saw rapid advances in our knowledge of how cells of immunity communicate with each other. They do this by means of protein hormones called **cytokines** (Table 37-1). Cytokines can produce their effects on the same cells that produce them, on cells nearby, or on cells distant in the body from those that produced the cytokine.

Interleukins were originally so called because they are synthesized by leukocytes and have their effect on leukocytes. We now know that some other kinds of cells can produce interleukins, and interleukins produced by leukocytes can affect other kinds of cells.

Generation of a Humoral Response: T_H2 Arm

When an antigen is introduced into a body, it binds to a specific antibody on the surface of an appropriate B cell, but this binding is usually not sufficient to activate the B cell to multiply. Some of the antigen is taken up by **antigen-presenting cells (APCs),** such as macrophages, that partially digest the antigen. The APCs then incorporate portions of the antigen into their own cell surface, bound in the cleft of MHC

TABLE 37.1

Some Important Cytokines

Cytokine	Principal Source	Function
Interleukin-1 (IL-1)	Activated macrophages	Mediates inflammation, activates T and B cells
Interleukin-2 (IL-2)	$CD4^+$ cells, some from $CD8^+$ cells	Major growth factor for T and B cells, enhances cytolytic activity of natural killer cells, causing them to become **lymphocyte-activated (LAK) cells**
Interleukin-3 (IL-3)	$CD4^+$ cells	Multilineage colony-stimulating factor; promotes growth and differentiation of all cell types in bone marrow
Interleukin-4 (IL-4)	Mostly by T_H2 $CD4^+$ cells	Growth factor for B cells, some $CD4^+$ T cells, and mast cells; suppresses T_H1 differentiation
Interleukin-5 (IL-5)	Certain $CD4^+$ cells	Activates eosinophils; acts with IL-2 and IL-4 to stimulate growth and differentiation of B cells
Interleukin-6 (IL-6)	Macrophages, endothelial cells, fibroblasts, and T_H2 cells	Important growth factor for B cells late in their differentiation
Interleukin-8 (IL-8)	Antigen-activated T cells, macrophages, endothelial cells, fibroblasts, and platelets	Activating and chemotactic factor for neutrophils, and to a lesser extent, other PMNs
Interleukin-10 (IL-10)	T_H2 $CD4^+$ cells	Inhibits T_H1, $CD8^+$, NK, and macrophage cytokine synthesis
Interleukin-12 (IL-12)	Monocytes, macrophages, neutrophils, dendritic cells, and B cells	Activates NK cells and T cells; potently induces production of IFN-γ, shifts immune response to T_H1
Transforming growth factor-β (TGF-β)	Macrophages, lymphocytes, and other cells	Inhibits lymphocyte proliferation, CTL and LAK cell generation, and macrophage cytokine production
Interferon-γ (IFN-γ)	Some $CD4^+$ and almost all $CD8^+$ cells	Strong macrophage-activating factor; causes a variety of cells to express class II MHC molecules; promotes T and B cell differentiation; activates neutrophils and NK cells; activates endothelial cells to allow lymphocytes to pass through walls of vessels
Tumor necrosis factor (TNF)	Activated macrophages	Major mediator of inflammation; low concentrations activate endothelial cells, activate PMNs, stimulate macrophages and cytokine production (including IL-1, IL-6, and TNF itself); higher concentrations cause increased synthesis of prostaglandins, resulting in fever

II protein (Figures 37-4 and 37-5). That portion of the antigen presented on the surface of the macrophage or other APC is called the **epitope** (or **determinant**). The macrophages also secrete IL-1, which stimulates T_H2 cells. The specific T-cell receptor for that particular epitope recognizes the epitope bound to the MHC II protein. Binding of the T-cell receptor to the epitope-MHC II complex is enhanced by the coreceptor CD4, which itself binds to the constant portion of the MHC II protein (Figure 37-5). Bound CD4 molecule also transmits a stimulation signal to the interior of the T cell. Activation of the T-cell further requires interaction of additional costimulatory and adhesion signals from other proteins on the surface of the macrophage and T cell. CD8 coreceptors function in a similar way on $CD8^+$ cells; they enhance binding of the T-cell receptor and transmit a stimulatory signal into the T cell.

Many aspects of immunology have been greatly assisted by the discovery of a method for producing stable clones of cells that will produce only one kind of antibody. Such monoclonal antibodies will bind only to *one kind* of antigenic determinant (most proteins bear many different antigenic determinants and thus stimulate the body to produce complex mixtures of antibodies). *Monoclonal* antibodies are made by fusing normal antibody-producing plasma cells with a continuously growing plasma cell line, producing a hybrid of the normal cell with one that can divide indefinitely in culture. This cell line is called a *hybridoma*. Clones are selected from among the hybrids and are grown to become "factories" that

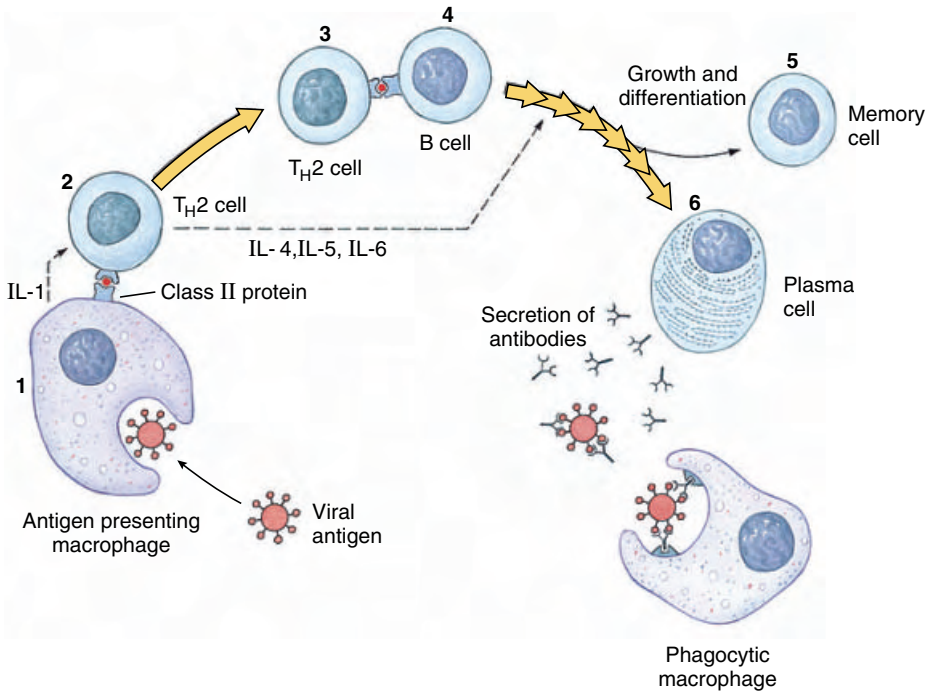

Figure 37-4
Humoral immune response. (1) Macrophage consumes antigen, partially digests it, and displays portions on its surface, along with class II MHC protein, and secretes interleukin-1 (IL-1). (2) T_H2 cell, stimulated by IL-1, recognizes antigen and class II protein on macrophage, is activated, and secretes interleukins 4, 5, and 6 (IL-4, IL-5, IL-6). (3) T_H2 then activates B cell which carries antigen and class II protein on its surface. IL-4, IL-5, and IL-6 stimulate proliferation of B cell line. (4) Activated B cells finally produced many plasma cells that secrete antibody. (5) Some B-cell progeny become memory cells. (6) Antibody produced by plasma cells binds to antigen and stimulates macrophages to consume antigen (opsonization).

produce almost unlimited quantities of one specific antibody. Hybridoma techniques discovered in 1975 have become one of the most important research tools for the immunologist.

Activated T_H2 cells secrete IL-4, IL-5 and IL-6, which activate the B cell that has the same epitope and class II MHC protein on its surface. The B cell multiples rapidly and produces many plasma cells, which secrete large quantities of antibody for a period of time, then die. Thus if we measure the concentration of antibody **(titer)** soon after the antigen is injected, we can detect little or none. Titer then rises rapidly as plasma cells secrete the antibody, and it may decrease somewhat as they die and antibody is degraded (Figure 37-6). However, if we give another dose of antigen **(challenge),** there is little or no lag, and antibody titer rises quicker to a higher level than after the first dose. This is the **secondary** or **anamnestic response,** and it occurs because some of the activated B cells gave rise to long-lived **memory cells.** There are many more memory cells present in the body than the original B lymphocyte with the appropriate antibody on its surface, and they rapidly multiply to produce additional plasma cells. Existence of the anamnestic response has great practical value because it is the basis for protective vaccines.

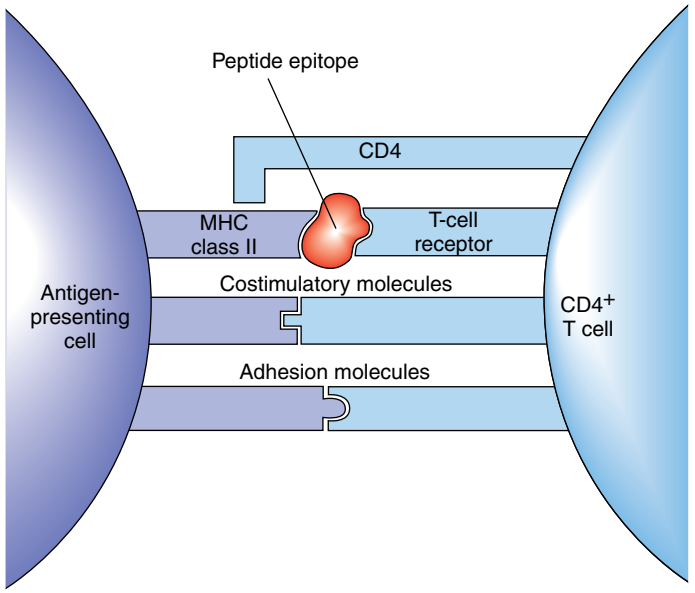

Figure 37-5
Interacting molecules during activation of a T helper cell.

Cell-Mediated Response: T_H1 Arm

Many immune responses involve little, if any, antibody and depend on the action of cells only. In cell-mediated immunity (CMI) the epitope of an antigen is also presented by ACPs, but the T_H1 arm of the immune response is activated and the T_H2 arm suppressed. Effector cells are macrophages, PMNs, cytotoxic T cells, and activated natural killer cells. The specific interaction of lymphocyte and antigen that generates a CMI greatly influences subsequent events in the nonspecific response we call **inflammation.**

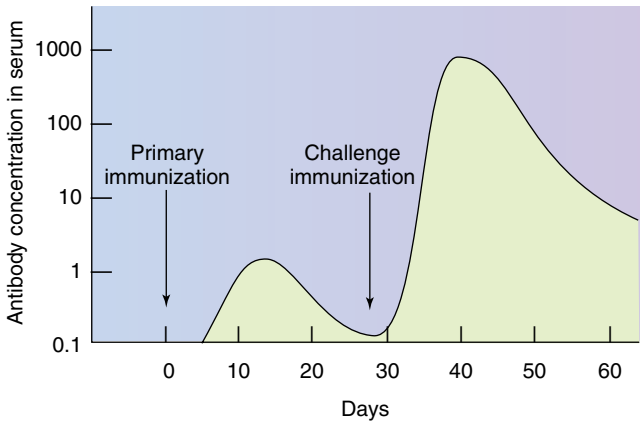

Figure 37-6

Typical immunoglobulin response after primary and challenge immunizations. The secondary response is a result of the large numbers of memory cells produced after the primary B-cell activation.

Only a few years ago transplantation of organs from one person to another seemed impossible. Then physicians began to transplant kidneys and depress the immune response to the recipient. It was very difficult to immunosuppress the recipient enough that the new organ would not be rejected and at the same time not leave the patient defenseless against infection. Since discovery of a fungus-derived drug called cyclosporine, not only kidneys, but also hearts, lungs, and livers can be transplanted. Cyclosporine inhibits IL-2 and affects CTLs more than T_Hs. It has no effect on other white cells or on healing mechanisms, so that a patient can still mount an immune response but not reject the transplant. However, the patient must continue to take cyclosporine because if the drug is stopped, the body will recognize the transplanted organ as foreign and reject it.

Like humoral immunity, CMI shows a secondary response due to large numbers of memory T cells produced from the original activation. For example, a second tissue graft (challenge) between the same donor and host will be rejected much more quickly than the first.

Inflammation

Inflammation is a vital process in mobilization of body defenses against an invading organism or other tissue damage and in repair of damage thereafter. The course of events in the inflammatory process is greatly influenced by the prior immunizing experience of the body with the invader and by the duration of the invader's presence or its persistence in the body. The processes by which an invader is actually destroyed, however, are themselves nonspecific. Manifestations of inflammation are **delayed type hypersensitivity (DTH)** and **immediate hypersensitivity,** depending on whether the response is cell mediated or antibody mediated.

The DTH reaction is a type of CMI in which the ultimate effectors are activated macrophages. The term *delayed type hypersensitivity* is derived from the fact that a period of 24 hours or more elapses from the time of antigen introduction until a reponse is observed in an immunized subject. This is because T_H1 cells with specific receptors in their surface for that particular antigen require some time to arrive at the antigen site, recognize the epitopes displayed by the antigen-presenting cells (APCs), and become activated and secrete IL-2, tumor necrosis factor (TNF, and interferon-γ (IFN-γ). TNF causes endothelial cells of the blood vessels to express on their surface certain molecules to which leukocytes adhere: first neutrophils and then lymphocytes and monocytes. TNF also causes endothelium to secrete inflammatory cytokines such as IL-8, which increase the mobility of leukocytes and facilitate their passage through the endothelium. TNF and IFN-γ also cause endothelial cells to change shape, favoring leakage of macromolecules and passage of cells. Escape of fibrinogen from blood vessels leads to conversion of fibrinogen to fibrin, and the area becomes swollen and firm.

As monocytes pass out of blood vessels, they become activated macrophages, which are the main effector cells of a DTH. They phagocytize particulate antigen, secrete mediators that promote local inflammation, and secrete cytokines and growth factors that promote healing. If the antigen is not destroyed and removed, its chronic presence leads to deposition of fibrous connective tissue, or **fibrosis.** Nodules of inflammatory tissue called **granulomas** may accumulate around persistent antigen and are found in numerous parasitic infections (Figure 37-7).

Immediate hypersensitivity is quite important in some parasitic infections. This reaction involves degranulation of mast cells in the area. Their surfaces bear receptors for Fc portions of antibody, especially IgE. Occupation of these sites by antigen-specific antibodies enhances degranulation of mast cells when the Fab portions bind the particular antigen. There is a rapid release of several mediators, such as histamine, that cause dilation of local blood vessels and increased vascular permeability. Escape of blood plasma into the surrounding tissue causes swelling **(wheal),** and engorgement of vessels with blood produces redness, the characteristic **flare** (Figure 37-8). Systemic immediate hypersensitivity is **anaphylaxis,** which may be fatal if not treated rapidly. The swelling and change in permeability of capillaries allow antibodies and leukocytes to move from capillaries and easily reach the invader. The first phagocytic line of defense is neutrophils, which may last a few days, then macrophages (either fixed or differentiated from monocytes) become predominant.

Some degree of cell death **(necrosis)** always occurs in inflammation, but necrosis may not be prominent if the inflammation is minor. When the necrotic debris is confined within a localized area, the pus (spent leukocytes

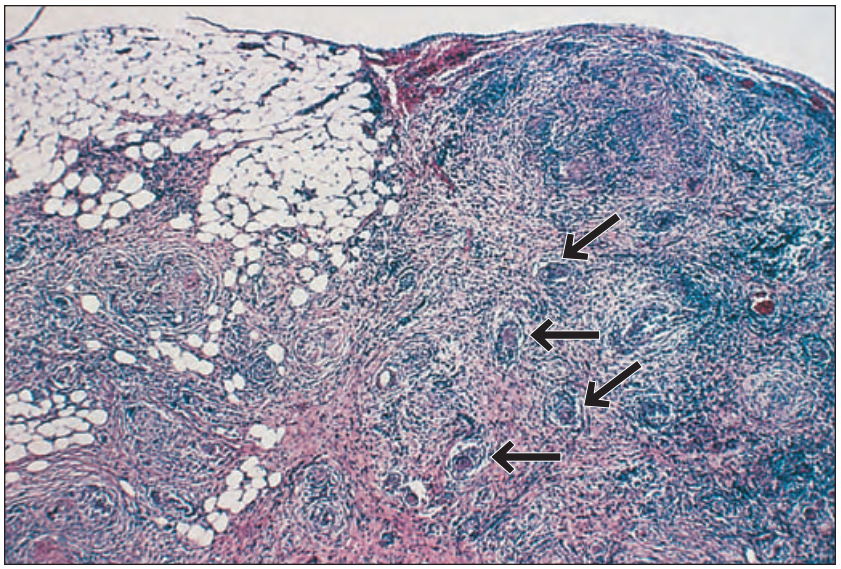

Figure 37-7
Granulomatous reaction around eggs *(arrows)* of *Schistosoma mansoni* in mesenteries.

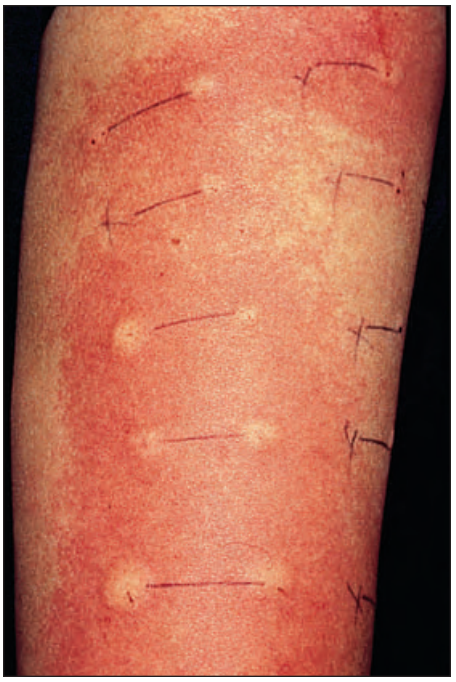

Figure 37.8
Wheal and flare reactions around sites of antigen injection for allergy testing.

and tissue fluid) may increase in hydrostatic pressure, forming an **abscess.** An area of inflammation that opens out to a skin or mucous surface is an **ulcer.**

Immediate hypersensitivity in humans is the basis for allergies and asthma, which are quite undesirable conditions, leading one to wonder why they evolved. Some scientists believe that the allergic response originally evolved to help the body ward off parasites because only allergens and parasite antigens stimulate production of large quantities of IgE. Avoidance of or reduction in effects of parasites would have conferred a selective advantage in human evolution. The hypothesis is that in absence of heavy parasitic challenge, the immune system is free to react against other substances, such as ragweed pollen. People now living where parasites remain abundant are less troubled with allergies than are those living in relatively parasite-free areas.

Acquired Immune Deficiency Syndrome (AIDS)

AIDS is an extremely serious disease in which the ability to mount an immune response is disabled severely. It is caused by **human immunodeficiency virus (HIV).** The first case of AIDS was recognized in 1981, and by 1998, over 30 million people worldwide were infected with HIV/AIDS, of whom 90% were in developing countries of Asia and sub-Saharan Africa. HIV infection virtually always progresses to AIDS after a latent period of some years. To the best of our current knowledge, AIDS is a terminal disease. AIDS patients are continuously plagued by infections with microbes and parasites that cause insignificant problems in persons with normal immune responses. HIV preferentially invades and destroys $CD4^+$ lymphocytes. CD4 protein is the major surface receptor for the virus. Normally, $CD4^+$ cells make up 60% to 80% of the T-cell population; in AIDS they can become too rare to be detected. T_H1 cells are relatively more depleted than T_H2 cells, which upsets the balance of immunoregulation and results in persistent, nonspecific B cell activation.

Blood Group Antigens

ABO Blood Types

Blood cells differ chemically from person to person, and when two different (incompatible) blood types are mixed, **agglutination** (clumping together) of erythrocytes results. The basis of these chemical differences is naturally occurring antigens on the membranes of red blood cells. The best known of these inherited immune systems is the ABO blood group (p. 124). Antigens A and B are inherited as codominant alleles of a single gene. Homozygotes for a recessive allele at the same gene have type O blood, which lacks A and B antigens. Thus, as shown in Table 37-2, an individual with, for example, genes I^A/I^A or I^A/i develops A antigen (blood type A). The presence of an I^B gene produces B antigens (blood type B), and for the genotype I^A/I^B both A and B antigens develop on the erythrocytes (blood type AB). Epitopes of A and B also are present on the surfaces of many epithelial and most endothelial cells.

There is an odd feature about the ABO system. Normally we would expect that a type A individual would develop antibodies against type B cells only if cells bearing B epitopes were first introduced into the body. In fact, type A persons acquire anti-B antibodies soon after birth, even without exposure to type B cells. Similarly, type B individuals come to carry anti-A

TABLE 37.2

Major Blood Groups

Blood Type	Genotype	Antigens on Red Blood Cells	Antibodies in Serum	Can Give Blood To	Can Receive Blood From	Frequency in United States (%) Whites	Blacks	Asians
O	*i/i*	None	Anti-A and anti-B	All	O	45	48	31
A	I^A/I^A, I^A/i	A	Anti-B	A, AB	O, A	41	27	25
B	I^B/I^B, I^B/i	B	Anti-A	B, AB	O, B	10	21	34
AB	I^A/I^B	AB	None	AB	All	4	4	10

antibodies at a very early age. Type AB blood has neither anti-A nor anti-B antibodies (since if it did, it would destroy its own blood cells), and type O blood has both anti-A and anti-B antibodies. There is evidence that the antibodies develop as a response to A and B epitopes on intestinal microorganisms when the intestine becomes colonized with bacteria after birth. Presumably, small and unnoticed infections with the bacteria occur. The antibodies thus produced cross-react with the A and B epitopes on erythrocytes.

We see then that the blood-group names identify their *antigen* content. Persons with type O blood are called universal donors because, lacking antigens, their blood can be infused into a person with any blood type. Even though it contains anti-A and anti-B antibodies, these are so diluted during transfusion that they do not react with A or B antigens in a recipient's blood. Persons with AB blood are universal recipients because they lack antibodies to A and B antigens. In practice, however, clinicians insist on matching blood types to prevent any possibility of incompatibility.

Rh Factor

Karl Landsteiner, an Austrian—later American—physician discovered ABO blood groups in 1900. In 1940, 10 years after receiving the Nobel Prize, he made still another famous discovery. This was a blood group called the Rh factor, named after rhesus monkeys, in which it was first found. Approximately 85% of white individuals in the United States have the factor (positive) and the other 15% do not (negative). The Rh factor is encoded by a dominant allele at a single gene. Rh-positive and Rh-negative bloods are incompatible; shock and even death may follow their mixing when Rh-positive blood is introduced into an Rh-negative person who has been sensitized by an earlier transfusion of Rh-positive blood. Rh incompatibility accounts for a peculiar and often fatal **hemolytic disease of the newborn (erythroblastosis fetalis).** If an Rh-negative mother has an Rh-positive baby (father is Rh-positive) she can become immunized by fetal blood during the birth process. Anti-Rh antibodies are predominately IgG and can cross the placenta during a subsequent pregnancy and agglutinate fetal blood. Erythroblastosis fetalis normally is not a problem in cases of ABO incompatibility between mother and fetus because antibodies to ABO antigens are primarily IgM and cannot cross the placenta.

The genetics of the Rh factor are very much more complicated than it was believed when the factor was first discovered. Some authorities think that three genes located close together on the same chromosome are involved, whereas others adhere to a system of one gene with many alleles. In 1968 a revision of the single gene concept listed 37 alleles necessary to account for the phenotypes then known. Furthermore, the frequency of the various alleles varies greatly between whites, Asians, and blacks.

Erythroblastosis fetalis can now be prevented by giving an Rh-negative mother anti-Rh antibodies just after the birth of her first child. These antibodies remain long enough to neutralize any Rh-positive fetal blood cells that may have entered her circulation, thus preventing her own antibody machinery from being stimulated to produce the Rh-positive antibodies. Active, permanent immunity is blocked. The mother must be treated after every subsequent pregnancy (assuming the father is Rh^+). If the mother has already developed an immunity, however, the baby may be saved by an immediate, massive transfusion of blood free of antibodies.

Immunity in Invertebrates

One of the principal tests of the ability of invertebrate tissues to recognize nonself is by grafting of a piece of tissue from another individual of the same species **(allograft)** or a different species **(xenograft)** onto the host. If the graft grows in place with no host response, the host tissue is treating it as self, but if cell response and rejection of the graft occur, the host exhibits immune recognition. Most invertebrates tested in this way reject xenografts; and almost all can reject allografts to some degree (Table 37-3). Interestingly, nemertines and molluscs apparently do not reject allografts. It is curious that some animals with quite simple body organization, such as Porifera and Cnidaria, can reject allografts; this response may be an adaptation to avoid loss of integrity of the individual sponge or colony under conditions of crowding, with attendant danger of overgrowth or fusion with

TABLE 37.3

Some Invertebrate Leukocytes and Their Functions

Group	Cell Types and Functions	Phagocytosis	Encapsulation	Allograft Rejection	Xenograft Rejection
Sponges	Archaeocytes (wandering cells that differentiate into other cell types and can act as phagocytes)	+	+	+*	+*
Cnidarians	Amebocytes: "lymphocytes"	+		+	+
Nemertines	Agranular leukocytes; granular macrophagelike cells	+		−	±
Annelids	Basophilic amebocytes (accumulate as "brown bodies"), acidophilic granulocytes	+	+	+	+
Sipunculids	Several types	+	+	±	+
Insects	Several types, depending on family; e.g., plasmatocytes, granulocytes, spherule cells, coagulocytes (blood clotting)	+	+	−	±
Crustaceans	Granular phagocytes; refractile cells that lyse and release contents	+	+	−	+
Molluscs	Amebocytes	+	+	−	+
Echinoderms	Amebocytes, spherule cells, pigment cells, vibratile cells (blood clotting)	+	+	+	+
Tunicates	Many types, including phagocytes; "lymphocytes"	+	+	+	+

Data from Lackie, A. M. 1980. Parasitology **80**:393–412. (See Lackie's article for references.)
*Transplantation reactions occur, but the extent to which the leukocytes are involved is unknown.

other individuals. American cockroaches (*Periplaneta americana*) reject allografts from the same source more quickly upon second exposure; thus they show at least short-term immunological memory.

Hemocytes of molluscs release degradative enzymes during phagocytosis and encapsulation, and bactericidal substances occur in body fluids of a variety of invertebrates. Substances functioning as opsonins have been reported in annelids, insects, crustaceans, echinoderms, and molluscs.

Bacterial infection in some insects stimulates production of antibacterial proteins, but these proteins show broad-spectrum activity and are not specific for a single infective agent. Specific, induced responses that demonstrate memory upon challenge, resembling acquired immunity of vertebrates, have been found in American cockroaches.

Contact with infectious organisms can bring the defense systems of snails into enhanced levels of readiness that last for up to two months or more. Susceptibility of snail hosts of the trematode *Schistosoma mansoni* depends heavily on genotype of the snail. Excretory/secretory products of the trematode stimulate motility of hemocytes from resistant snails but inhibit motility of hemocytes from susceptible hosts. Hemocytes from resistant snails encapsulate the trematode larva and apparently kill it with superoxide and H_2O_2 and then destroy it by phagocytosis (Figure 37-9). It appears that the cytokine interleukin-1 is present in resistant snails and is responsible for activating the hemocytes.

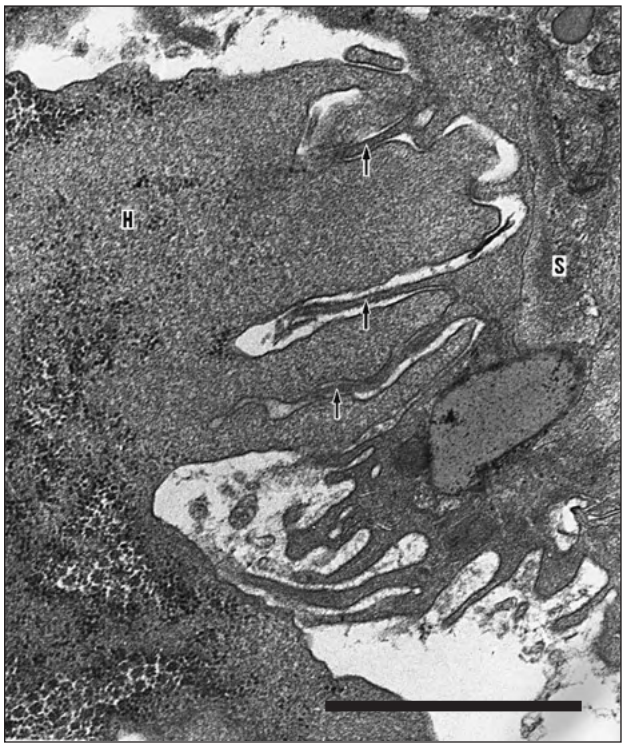

Figure 37-9
Electron micrograph of a hemocyte **(H)** from a schistosome-resistant strain of a snail attacking a a *Schistosoma mansoni* larva **(S)** under in vitro conditions. Note the hemocyte processes apparently engaged in phagocytosis of portions of the larval tegument (*arrows*). (Scale bar = 1 μm.)

Summary

A plethora of viral, prokaryotic, and eukaryotic parasites exists in every animal's environment, and a defense (immune) system is crucial to survival. Immunity can be defined concisely as possession of tissues capable of recognizing and protecting the animal against nonself invaders. Most animals have some amount of innate (nonspecific) immunity, and vertebrates develop acquired (specific) immunity. The surface of most animals provides a physical barrier to invasion, and vertebrates have a variety of antimicrobial substances in their body secretions.

Phagocytes engulf particles and usually digest or kill them with enzymes and cytotoxic secretions. Many invertebrates have specialized cells that can perform defensive phagocytosis. Several kinds of vertebrate cells, especially macrophages and neutrophils, are important phagocytes, and cells of the mononuclear phagocyte system (RE system) reside in various sites in the body. Eosinophils are important in allergies and many parasitic infections. Basophils, mast cells, T and B lymphocytes, and natural killer cells are not phagocytic but play vital roles in defense.

An immune response is elicited by an antigen. Vertebrates demonstrate increased resistance to *specific* foreign substances (antigens) on repeated exposure, and the resistance is based on a vast number of specific recognition molecules: antibodies and T-cell receptors. Nonself recognition depends on markers in cell surfaces known as major histocompatibility (MHC) proteins. Antibodies are borne on the surfaces of B lymphocytes (B cells) and in solution in the blood after secretion by the progeny of B cells, the plasma cells. T-cell receptors occur only on the surfaces of T lymphocytes (T cells).

The cells of immunity communicate with each other and with other cells in the body by means of protein hormones called cytokines such as interleukins, tumor necrosis factor, and interferon-γ. The two arms of the vertebrate immune response are the humoral response (T_H2), involving antibodies, and the cell-mediated response (T_H1), involving cell surfaces only. When one arm is activated or stimulated, its cells produce cytokines that tend to suppress activity in the other arm. Activation of either arm requires that the antigen be consumed by an APC (antigen-presenting cell, usually a macrophage), which partially digests the antigen and presents its determinant (epitope) on the surface of the APC along with an MHC class II protein. Extensive communication by cytokines and activation (and suppression) of various cells in the response leads to production of specific antibody or proliferation of T cells with the specific receptors that recognize the antigenic epitope. After the initial response, memory cells remain in the body and are responsible for enhanced response on next exposure to the antigen.

Damage to the immune response done by HIV (human immunodeficiency virus) in production of AIDS (acquired immune deficiency syndrome) is due primarily to destruction of a crucial set of T cells: those bearing the CD4 coreceptor on their surface.

Inflammation is an important part of the body's defense; it is greatly influenced by prior immunizing experience with an antigen.

People have genetically determined antigens in the surfaces of their red blood cells (ABO blood groups and others); blood types must be compatible in transfusions, or the transfused blood will be agglutinated by antibodies in the recipient.

Many invertebrates show nonself recognition by rejection of xenografts or allografts or both. In some cases they may show enhanced response on repeated exposure.

Review Questions

1. Distinguish susceptibility from resistance, and innate (nonspecific) from acquired (specific) immunity.
2. What are some examples of innate defense mechanisms that are chemical in nature? What is complement?
3. After a phagocyte has engulfed a particle, what usually happens to the particle?
4. What are some important phagocytes in vertebrates?
5. What is the molecular basis of self and nonself recognition in vertebrates?
6. What is the difference between T cells and B cells?
7. What is a cytokine? What are some functions of cytokines?
8. Outline the sequence of events in a humoral immune response from the introduction of antigen to the production of antibody.
9. Define the following: plasma cell, secondary response, memory cell, complement, opsonization, titer, challenge, cytokine, natural killer cell, interleukin-2.
10. What are the functions of CD4 and CD8 proteins on the surface of T cells?
11. In general, what are consequences of activation of the T_H1 arm of the immune response? Activation of the T_H2 arm?
12. Distinguish between class I and class II MHC proteins.
13. Describe a typical inflammatory response.
14. What is a major mechanism by which HIV damages the immune system in AIDS?
15. Give the genotypes of each of the following blood types: A, B, O, AB. What happens when a person with type A gives blood to a person with type B? With type AB? With type O?
16. What causes hemolytic disease of the newborn (erythroblastosis fetalis)? Why does the condition not arise in cases of ABO incompatibility?
17. Give some evidence that cells of many invertebrates bear molecules on their surface that are specific to the species and even to a particular individual animal.
18. Give an example of immunological memory in invertebrates.

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Howard Hughes Medical Institute Biomedical Research:Immunity. Recent developments in this field. Links to more information.

Monoclonal Antibody Technology. MIT hypertextbook description of the technology associated with production of monoclonal antibodies.

Immune Explorer. Interactive site explores the biology of the immune system.

Specific Immunity. This page and links describe both humoral and cell-mediated immunity, with a link to information on the chemistry and physiology of inflammation.

Nonspecific Immunity. Describes the skin and various epithelia and their role in defense.

HIV InSite. Gateway to AIDS knowledge. Links to a variety of peer-reviewed articles on HIV infection, many statistics from the University of California at San Francisco.

OLC Student Center Website

Killer whale in performance at the Vancouver Public Aquarium.

CHAPTER

38

Animal Behavior

The Lengthening Shadow of One Man

People always have been fascinated by the behavior of animals. For as long as people have walked the earth, their lives have been touched by, indeed interwoven with, the lives of other animals. People hunted animals, fished them, domesticated them, ate them and were eaten by them, made pets of them, revered them, hated and feared them, immortalized them in art, song, and verse, fought them, and loved them. The very survival of ancient people depended on knowledge of wild animals' habits and behaviors. As the hunting societies of primitive people gave way to agricultural civilizations, an awareness was retained of the interrelationship with other animals, and the need to understand their behaviors increased. Even today zoos attract more visitors than ever before; wildlife television shows are increasingly popular; game-watching safaris to Africa constitute a thriving enterprise; and millions of pet animals share the cities with us—more than a half million pet dogs live in New York City alone.

Despite our long-standing interest in the behavior of animals, the science of animal behavior is a newcomer to biology. Charles Darwin, with the uncanny insight of genius, prepared for the reception of animal behavior by showing how natural selection would favor specialized behavioral patterns for survival. Darwin's pioneering book, *The Expression of the Emotions of Man and Animals,* published in 1872, mapped a strategy for behavioral research still in use today. However science in 1872 was unprepared for Darwin's central insight that behavioral patterns, no less than bodily structures, are selected and have evolutionary histories. Another 60 years would pass before such concepts would begin to flourish within behavioral science.

It was Ralph Waldo Emerson who said that an institution is the lengthening shadow of one man. For Charles Darwin the shadow is long indeed, for he brought into being entire fields of knowledge, such as evolution, ecology, and finally, after a long gestation, animal behavior. Above all, he altered the way we think about ourselves, the earth we inhabit, and the animals that share it with us. ■

In 1973, the Nobel Prize in Physiology or Medicine was awarded to three pioneering zoologists, Karl von Frisch, Konrad Lorenz, and Niko Tinbergen (Figure 38-1). The citation stated that these three were the principal architects of the new science of **ethology,** the scientific study of animal behavior, particularly under natural conditions. It was the first time any contributor to the behavioral sciences was so honored, and it meant that the discipline of animal behavior, which really has its roots in the work of Charles Darwin, had arrived.

A

B

C

Figure 38-1
Pioneers of the science of ethology. **A,** Konrad Lorenz (1903 to 1989). **B,** Karl von Frisch (1886 to 1982). **C,** Niko Tinbergen (1907 to 1988).

The Science of Animal Behavior

Behavioral biologists have traditionally asked two kinds of questions about behavior: *how* animals behave and *why* they behave as they do. "How" questions are concerned with immediate or **proximate causation.** For example, a biologist might wish to explain the singing of a male white-throated sparrow in the spring in terms of hormonal or neural mechanisms. Such physiological or mechanistic causes of behavior are proximate factors. Alternatively, a biologist might ask what function singing serves the sparrow, and then seek to understand those events in the ancestry of birds that led to springtime singing. These are "why" questions that focus on **ultimate causation,** the evolutionary origin and purpose of a behavior. These are really independent approaches to behavior, because understanding *how* the sparrow sings does not depend on what function singing serves, and vice versa. Students of animal behavior consider this distinction significant. Studies of proximate and ultimate causation are both important, but each may be of limited value in understanding the other.

The study of animal behavior has arisen from several different historical roots, and there is no universally accepted term for the whole subject. **Comparative psychology** emerged from efforts to find general laws of behavior that would apply to many species, including humans. Early research that depended heavily on inference was later replaced by replicable experimental approaches that concentrated on a few species, particularly white rats, pigeons, dogs, and occasionally primates. Following criticisms that the discipline lacked an evolutionary perspective and focused too narrowly on the white rat as a model for other organisms, many comparative psychologists developed more truly comparative investigations, some of these conducted in the field.

The aim of a second approach, **ethology,** has been to describe the behavior of an animal in its *natural habitat*. Most ethologists have been zoologists. Their laboratory has been the out-of-doors, and early ethologists gathered their data by field observation. They also conducted experiments, often with nature providing the variables, but increasingly ethologists have manipulated the variables for their own purposes by using animal models, playing recordings of animal vocalizations and altering the habitat. Modern ethologists also conduct many experiments in the laboratory where they can test their predictions under closely controlled conditions. However, ethologists usually take pains to compare laboratory observations with observations of free-ranging animals in undisturbed natural environments.

Ethology emphasizes the importance of ultimate factors affecting behavior. One of the great contributions of von Frisch, Lorenz, and Tinbergen was to demonstrate that behavioral traits are measurable entities like anatomical or physiological traits. This was to become the central theme of ethology: behavioral traits can be isolated and measured and they have evolutionary histories.

Sociobiology, the ethological study of social behavior, originated with the 1975 publication of E. O. Wilson's *Sociobiology: The New Synthesis*. Wilson describes social behavior as reciprocal communication of a cooperative nature (transcending mere sexual activity) that permits a group of organisms of the same species to become organized in a cooperative manner. In a complex system of social interactions, individuals are highly dependent on others for their daily living. While

social behavior appears in many groups of animals, Wilson identified four "pinnacles" of complex social behavior. These are (1) colonial invertebrates, such as the Portuguese man-of-war (p. 262), which is a tightly-knit composite of individual organisms; (2) social insects, such as ants, bees, and termites, which have developed sophisticated systems of communication; (3) nonhuman mammals, such as dolphins, elephants, and some primates, which have highly developed social systems; and (4) humans.

The inclusion by Wilson of human behavior in sociobiology, and his references to the genetic foundation of many human social behaviors, has been strongly criticized. Complex systems of human social interactions, including religion, economic systems, and such objectionable characteristics as racism, sexism, and war, are emergent properties (p. 6) of human culture and its history. Is it meaningful to search for a specific genetic basis or justification for such phenomena? Many would answer "no," and look instead to the field of sociology, rather than sociobiology, to help us understand the complex, emergent properties of human societies.

Much of the work by comparative psychologists, ethologists, and those studying sociobiology can be found under the discipline of behavioral ecology. Behavioral ecologists often focus on how individuals are expected to behave to maximize their reproductive success. They then concentrate on a particular aspect of behavior, such as mate choice, foraging or parental investment.

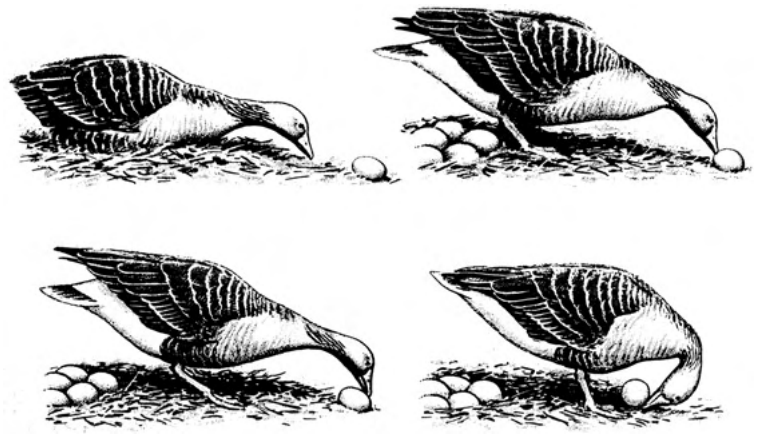

Figure 38-2
Egg-rolling behavior of the greylag goose *(Anser anser).*

Describing Behavior: Principles of Classical Ethology

Early behaviorists, through step-by-step analysis of the behavior of animals in nature, focused on the relatively invariant components of behavior. From such studies emerged several concepts that were first popularized in Tinbergen's influential book. *The Study of Instinct* (1951).

Some basic concepts of animal behavior can be illustrated by considering the egg-retrieval response of the greylag goose (Figure 38-2), described by Lorenz and Tinbergen in a famous paper published in 1938. If Lorenz and Tinbergen presented a female greylag goose with an egg a short distance from her nest, she would rise, extend her neck until the bill was just over the egg and then bend her neck, pulling the egg carefully into the nest.

Although this behavior appeared to be intelligent, Tinbergen and Lorenz noticed that if they removed the egg once the goose had begun her retrieval, or if the egg being retrieved slipped away and rolled down the outer slope of the nest, the goose would continue the retrieval movement without the egg until she was again settled comfortably on her nest. Then, seeing that the egg had not been retrieved, she would begin the egg-rolling pattern all over again.

Thus the bird performed egg-rolling behavior as if it were a program that, once initiated, had to run to completion. Lorenz and Tinbergen viewed egg-retrieval as a "fixed" pattern of behavior: a motor pattern that is mostly invariable in its performance. A behavior of this type, carried out in an orderly, predictable sequence is often called **stereotypical behavior.** Of course, stereotyped behavior may not be performed identically on all occasions. But it should be recognizable, even when performed inappropriately. Further experiments by Tinbergen disclosed that the greylag goose was not particularly discriminating about what she retrieved. Almost any smooth and rounded object placed outside the nest would trigger the egg-rolling behavior; even a small toy dog and a large yellow balloon were dutifully retrieved. But once the goose settled down on such objects, they obviously did not feel right and she discarded them.

Lorenz and Tinbergen realized that presence of an egg outside the nest must act as a stimulus, or trigger, that released egg-retrieval behavior. Lorenz termed the triggering stimulus a **releaser;** a simple feature in the environment that would trigger a certain innate behavior. Or, because the animal usually responded to some specific aspect of the releaser (sound, shape, or color, for example) the effective stimulus was called a **sign stimulus.** Behaviorists have described hundreds of examples of sign stimuli. In every case the response is highly predictable. For example, the alarm call of adult herring gulls always releases a crouching freeze-response in their chicks. Or, to cite an example given in an earlier chapter (p. 741), certain nocturnal moths take evasive maneuvers or drop to the ground when they hear the ultrasonic cries of bats that feed on them; most other sounds do not release this response.

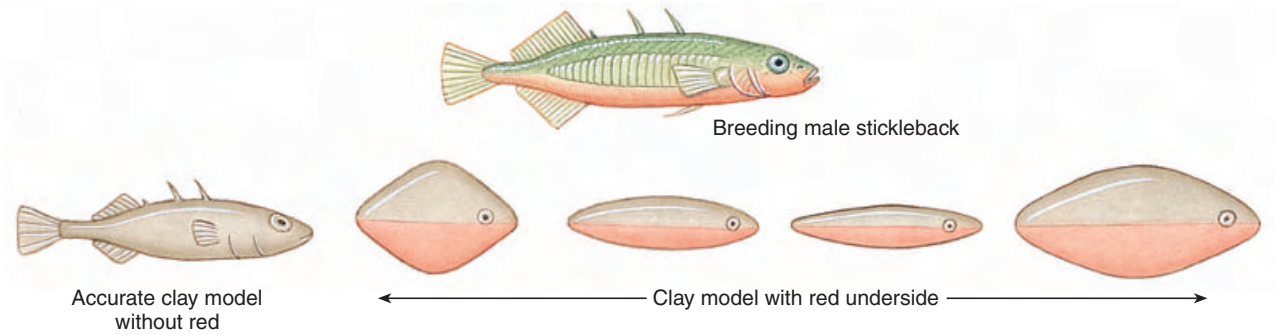

Figure 38-3
Stickleback models used to study territorial behavior. The carefully made model of a stickleback (*left*), without a red belly, is attacked much less frequently by a territorial male stickleback than the four simple red-bellied models.

Figure 38-4
Two models of an English robin. The bundle of red feathers is attacked by male robins, whereas the stuffed juvenile bird (*right*) without a red breast is ignored.

These examples illustrate the predictable and programmed nature of much animal behavior. This is even more evident when stereotyped behavior is released inappropriately. In the spring the male three-spined stickleback, a small fish, selects a territory that it defends vigorously against other males. The underside of the male becomes bright red, and the approach of another red-bellied male will release a threat posture or even an aggressive attack. Tinbergen's suspicion that the red belly of the male served as a releaser for aggression was reinforced when a passing red postal truck evoked attack behavior from the males in his aquarium. Tinbergen then carried out experiments using a series of models, which he presented to the males. He found that they vigorously attacked any model bearing a red stripe, even a plump lump of wax with a red underside. Yet a carefully made model that closely resembled a male stickleback but lacked the red belly was ignored (Figure 38-3). Tinbergen discovered other examples of stereotyped behavior released by simple sign stimuli. Male English robins furiously attacked a bundle of red feathers placed in their territory but ignored a stuffed juvenile robin without the red feathers (Figure 38-4).

We have seen in the examples above that there are costs to programmed behavior because it may lead to improper responses. Fortunately for red-bellied sticklebacks and red-breasted English robins, their aggressive response toward red works appropriately most of the time because red objects are uncommon in the worlds of these animals. But why don't these and other animals simply use reasoning to choose the correct response rather than relying mostly on automatic responses? Under conditions that are relatively consistent and predictable, automatic preprogrammed responses may be most efficient. Even if they can or could, thinking about or learning the correct response may take too much time. Releasers have the advantage of focusing the animal's attention on the relevant signal, and the release of a preprogrammed stereotyped behavior will enable an animal to respond rapidly when speed may be essential for survival.

Control of Behavior

From the beginning, the mostly invariable and predictable nature of stereotyped behavior suggested to behaviorists that they were dealing with inherited, or **innate,** behavior. Many kinds of preprogrammed behavior appear suddenly in animals and are indistinguishable from similar behavior performed by older, experienced individuals. Orb-weaving spiders build their webs without practice, and male crickets court females without lessons from more experienced crickets or by learning from trial and error. To such behaviors the term innate, or instinctive, has been applied. Such words suggest that these behavioral patterns

are absolutely committed and will develop in the same way regardless of environment. This idea, called instinct theory, has fallen out of fashion with behavioral scientists because it cannot be shown that a behavior develops independently of experience. Critics of instinct theory argue that all forms of behavior depend on an interaction of the organism and environment, beginning with the fertilized egg. Genes code for proteins and not directly for behavior. Even with web-building spiders and courting crickets, the environment is bound to have some influence. Given a different environment in which to develop, the resulting behavior may be different.

Nevertheless, it seems incontestable that many complex sequences of behavior in invertebrate animals are largely invariate in their execution, are not learned, and appear to be programmed by rules. It is easy to understand why programmed behavior is important for survival, especially for animals that never know their parents. They must be equipped to respond to the world immediately and correctly as soon as they emerge into it. It is also evident that more complex animals with longer lives and with parental care or other opportunities for social interactions may improve or change their behavior by learning.

The Genetics of Behavior

The hereditary transmission of most innate behavior is complex, with many interacting genes regulating each behavioral trait. However, there are a few examples of behavioral differences within species that show simple Mendelian transmission from parents to offspring. Perhaps the most convincing example is the inheritance of hygienic behavior in bees. Honey bees are susceptible to a bacterial disease, American foulbrood (*Bacillus larvae*). A bee larva that catches foulbrood dies. If the bees remove dead larvae from the hive they reduce the chance of the infection spreading.

Some strains of bees, called "hygienic," uncap hive cells containing rotting larvae and carry them out of the hive. W. C. Rothenbuhler found that there are two components to this behavior: first removal of cell caps, and second removal of larvae. Hygienic bees have homozygous recessive genotypes for two different genes. Uncapping behavior is performed by individuals homozygous for a recessive allele, *u,* at one gene, and removal behavior is performed by individuals homozygous for a recessive allele, *r,* at a second gene. When Rothenbuhler crossed hygienic bees (*u/u r/r*) with a nonhygienic strain (*U/U R/R*), he found that all the hybrids (*U/u R/r*) were nonhygienic. Thus only workers having both genes in the homozygous recessive condition show the complete behavior. Next, Rothenbuhler performed a "backcross" between the hybrids and the hygienic parental strain. As we should expect if hygienic behavior is transmitted by allelic variation of two genes, four different kinds of bees resulted (Figure 38-5). Approximately one-quarter of the bees were homozygous recessive for both *u* and *r* and showed the complete behavior: they both uncapped the cells and removed the bees. Another quarter of the offspring (*u/u R/r* or *u/u R/R*) uncapped but did not remove dead bees. Another quarter (*U/u r/r* or *U/U r/r*) did not uncap, but would remove the larvae if another worker uncapped the cells. Workers that were homozygous or heterozygous for the dominant allele at both genes (*U/u R/r*) would not perform either part of the cleaning behavior (Figure 38-5). The results showed clearly that each component of the cleaning behavior

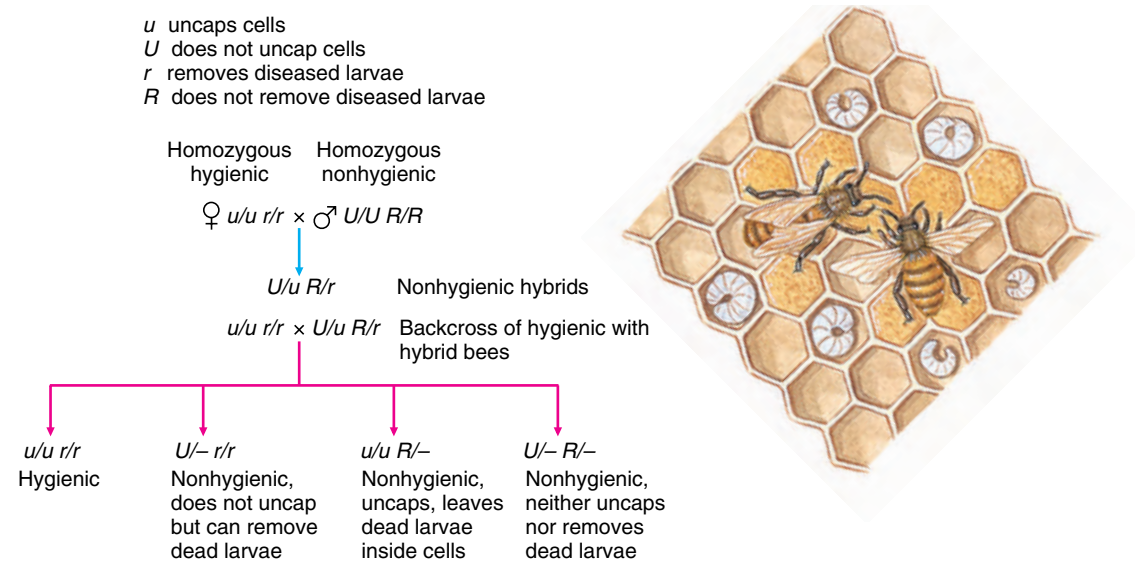

Figure 38-5

The genetics of hygienic behavior in honey bees, as demonstrated by W. C. Rothenbuhler. The results are explained by assuming that there are two independently assorting genes, one associated with uncapping cells containing diseased larvae, and the other associated with removing the larvae from the cells. See text for further explanation.

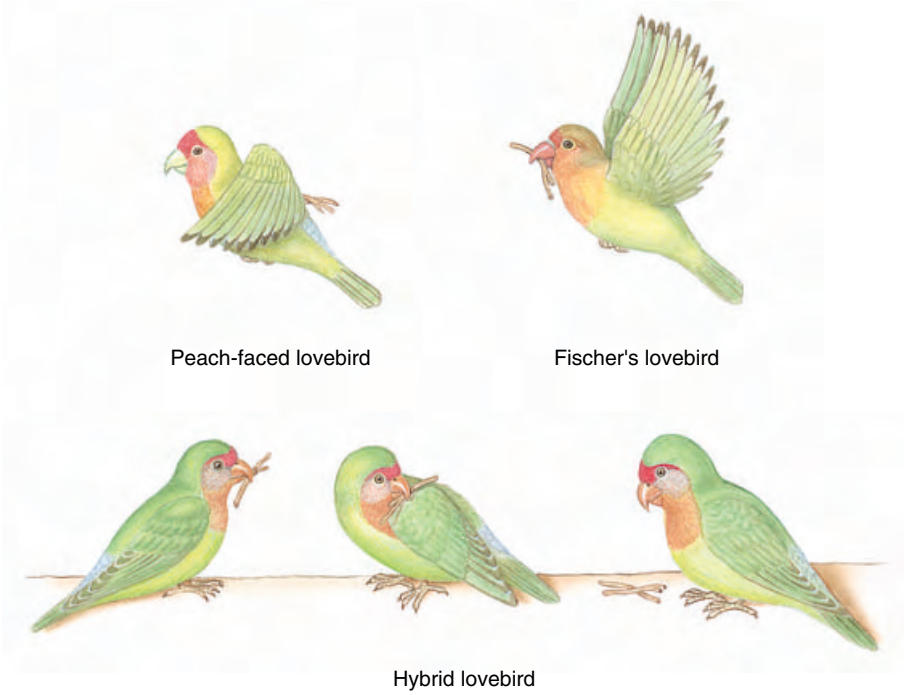

Figure 38-6
Confused behavior in hybrid lovebirds (*Agapornis* sp.). The peach-faced lovebird carries nest-building material tucked into its feathers; Fischer's lovebird carries nest-building material in its beak. The hybrids attempted both carrying methods, neither method accomplished successfully.

was associated with one, independently segregating gene.

Most inherited behaviors do not show simple segregation and independence; instead, hybrids of subspecies or species commonly show intermediate or confused behavior. A classic study of the effect of cross-breeding on behavior was carried out by W. C. Dilger on nest-building behavior in different species of lovebirds. Lovebirds are small parrots of the genus *Agapornis* (Figure 38-6). Each species has its own method of courtship and technique for carrying nesting material. Fischer's lovebirds (*A. personata fischeri*) cut long strips of nesting material from vegetation, then carry this to the nest, one strip at a time. Peach-faced lovebirds (*A. roseicollis*) carry several strips of torn nesting material at one time by tucking them into feathers of the lower back and rump. Dilger, who was able to cross the two species successfully, found that hybrids displayed a confused conflict between a tendency to carry material in the feathers (inherited from the peach-faced lovebirds) and a tendency to carry material in the bill (inherited from Fischer's lovebird) (see Figure 38-6). The hybrids attempted both feather-tucking and bill-carrying but performed neither behavior correctly. The hybrids had inherited a behavior that was intermediate between that of the parents. With experience hybrids improved their carrying ability by tending to carry the material in their bills, like Fischer's lovebird.

Learning and the Diversity of Behavior

Another aspect of behavior is learning, which we define as the modification of behavior through experience. An excellent model system for studying learning processes has been the marine opisthobranch snail *Aplysia* (Figure 38-7), a subject of intense experimentation by E. R. Kandel and his associates. The gills of *Aplysia* are partly covered by the mantle cavity and open to the outside by a siphon (Figure 38-8). If one prods the siphon, *Aplysia* withdraws its siphon and gills and folds them in the mantle cavity.

Figure 38-7
The sea hare *Aplysia* sp., an opisthobranch gastropod used in many neurophysiological and behavioral studies.

This simple protective response, called gill withdrawal reflex, will be repeated when *Aplysia* extends its siphon again. But if the siphon is touched repeatedly, *Aplysia* decreases the gill-withdrawal response and finally comes to ignore the stimulus altogether. This behavior modification illustrates a widespread form of learning called **habituation.** If now *Aplysia* is given a noxious stimulus (for example, an electric shock) to the head at the same time the siphon is touched, it becomes **sensitized** to the stimulus and withdraws its gills as completely as it did before habituation occurred. Sensitization, then, can reverse any previous habituation.

The mechanisms of habituation and sensitization in *Aplysia* are known because these behaviors constitute a rare instance in which the nervous pathways involved have been completely revealed. Receptors in the siphon are connected through sensory neurons (black pathways in Figure 38-8) to motor neurons (blue pathway in Figure 38-8) that control the gill-withdrawal muscles and muscles of the mantle cavity. Kandel found that repeated stimulation of the siphon diminished the release of synaptic transmitter from the sensory neurons. Sensory neurons continue to fire when the siphon is probed but, with less

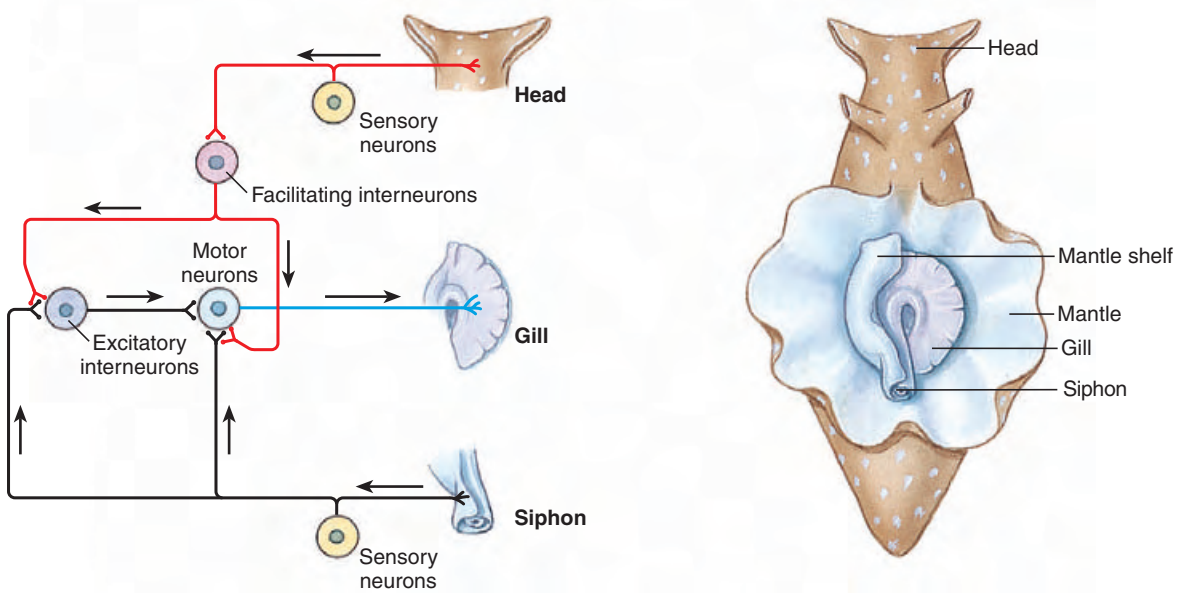

Figure 38-8
Neural circuitry concerned with habituation and sensitization of the gill-withdrawal reflex in the marine snail *Aplysia*. See text for explanation.

neurotransmitter being released into the synapse, the system becomes less responsive.

Sensitization requires the action of a different kind of neuron called a facilitating interneuron. These interneurons make connections between sensory neurons in the animal's head and motor neurons that control muscles of the gill and mantle (see Figure 38-8). When sensory neurons in the head are stimulated by an electric shock, they fire the facilitating interneurons, which end on the synaptic terminals of the sensory neurons (red pathways in Figure 38-8). These endings in turn cause an *increase* in the amount of transmitter released by the siphon sensory neurons. This release increases the state of excitation in the excitatory interneurons and motor neurons leading to the gill and mantle muscles. The motor neurons now fire more readily than before. The system is now sensitized because any stimulus to the siphon will produce a strong gill-withdrawal response.

Kandel's studies indicate that strengthening or weakening of the gill-withdrawal reflex involves changes in levels of transmitter in existing synapses. However, we know that more complex kinds of learning may involve formation of new neural pathways and connections, as well as changes in existing circuits.

Imprinting

Another kind of learned behavior is **imprinting,** the imposition of a stable behavior in a young animal by exposure to particular stimuli during a critical period in the animal's development. As soon as a newly hatched gosling or duckling is strong enough to walk, it follows its mother away from the nest. After it has followed the mother for some time it follows no other animal. But, if the eggs are hatched in an incubator or if the mother is separated from the eggs as they hatch, the goslings follow the first large object they see. As they grow, the young geese prefer the artificial "mother" to anything else, including their true mother. The goslings are said to be imprinted on the artificial mother.

Imprinting was observed at least as early as the first century A.D. when the Roman naturalist Pliny the Elder wrote of "a goose which followed Lacydes as faithfully as a dog." Konrad Lorenz was the first to study imprinting objectively and systematically. When Lorenz hand-reared goslings, they formed an immediate and permanent attachment to him and waddled or swam after him wherever he went (see Figure 38-9). They could no longer be induced to follow their own mother or another human being. Lorenz found that the imprinting period is confined to a brief sensitive period in the individual's early life and that once established the imprinted bond usually is retained for life.

What imprinting shows is that the brain of the goose (or the brain of numerous other birds and mammals that show imprinting-like behavior) accommodates the imprinting experience. Natural selection favors evolution of a brain that imprints in this way, in which following the mother and obeying her commands are important for survival. The fact that a gosling can be made to imprint to a mechanical toy duck or a person under artificial conditions is a cost to the system that can be tolerated because goslings seldom encounter these stimuli in their natural environment. The disadvantages of the system's simplicity are outweighed by the advantages of its reliability.

We will cite one final example to complete our consideration of learning. The males of many species of birds have characteristic territorial songs that identify the singers to the other birds and announce territorial rights to other males of that species.

Figure 38-9
Ducklings imprinted on Konrad Lorenz follow him as faithfully as they would a natural mother.

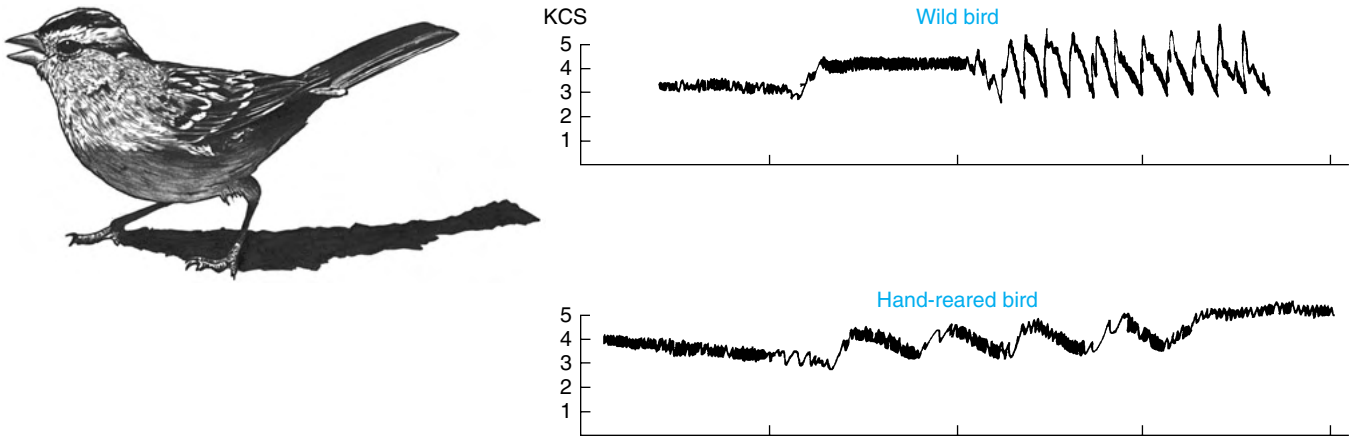

Figure 38-10
Sound spectrograms of songs of white-crowned sparrows, *Zonotrichia leucophrys. Top,* natural songs of wild bird; *bottom,* abnormal song of isolated bird.

Like many other songbirds, the male white-crowned sparrow must learn the song of its species by hearing the song of its father. If the sparrow is hand-reared in acoustic isolation in the laboratory, it develops an abnormal song (Figure 38-10). But if the isolated bird is allowed to hear recordings of normal white-crowned sparrow songs during a critical period of 10 to 50 days after hatching, it learns to sing normally. It even imitates the local dialect it hears.

It might appear from this result that characteristics of the song are determined by learning alone. However, if during the critical learning period, the isolated male white-crowned sparrow is played a recording of another species of sparrow, even a closely related one, it does not learn the song. It learns only the song appropriate to its own species. Thus although the song must be learned, the brain is constrained to recognize and to learn vocalizations produced by males of its species alone. Learning the wrong song would result in behavioral chaos, and natural selection favors a system that eliminates such errors.

Social Behavior

When we think of "social" animals we are apt to think of highly structured honey bee colonies, herds of antelope grazing on the African plains (Figure 38-11), schools of herring, or flocks of starlings. But social behavior of animals *of the same species* living together is by no means limited to such obvious examples in which individuals influence one another.

In the broad sense, any interaction resulting from the response of one animal to another of the same species represents social behavior. Even a pair of rival males fighting over possession of a female display a social interaction, despite our perceptual bias as people that might encourage us to label it antisocial. Social aggregations are only one kind of social behavior, and indeed not all aggregations of animals are social.

Clouds of moths attracted to a light at night, barnacles attracted to a common float, or trout gathering in the coolest pool of a stream are groupings of animals responding to environmental signals. Social aggregations, on the

Figure 38-11
Mixed herd of topi and common zebra grazing on the savanna of tropical Africa.

other hand, depend on signals from the animals themselves. They remain together and do things together by influencing one another.

Not all animals showing sociality are social to the same degree. While all sexually reproducing species must at least cooperate enough to achieve fertilization, among some animals breeding is about the only adult sociality to occur. Alternatively, swans, geese, albatrosses, and beavers, to name just a few, form strong monogamous bonds that last a lifetime. The most persistent social bonds usually form between mothers and their young and, for birds and mammals, these bonds usually terminate at fledging or weaning.

Advantages of Sociality

Living together may be beneficial in many ways. One obvious benefit for social aggregations is defense, both passive and active, from predators. Musk-oxen that form a passive defensive circle when threatened by a wolf pack are much less vulnerable than an individual facing the wolves alone.

As an example of active defense, a breeding colony of gulls, alerted by the alarm calls of a few, attack predators *en masse;* this collective attack is certain to discourage a predator more effectively than individual attacks. Members of a town of prairie dogs, although divided into social units called coteries, cooperate by warning each other with a special bark when danger threatens. Thus every individual in a social organization benefits from the eyes, ears, and noses of all other members of the group. Experimental tests using a wide variety of predators and prey support the notion that the more animals there are in a group, the less likely an individual within the group will be eaten.

Sociality offers several benefits to animals reproduction. It facilitates encounters between males and females, which, for solitary animals, may consume much time and energy. Sociality also helps synchronize reproductive behavior through the mutual stimulation that individuals have on one another. Among colonial birds the sounds and displays of courting individuals set in motion prereproductive endocrine changes in other individuals. Because there is more social stimulation, large colonies of gulls produce more young per nest than do small colonies. Furthermore, parental care that social animals provide their offspring increases survival of the brood (Figure 38-12). Social living provides opportunities for individuals to give aid and to share food with young other than their own. Such interactions within a social network have produced some intricate cooperative behavior among parents, their young, and their kin.

Of the many other advantages of social organization noted by behaviorists, we will mention only a few in this brief treatment: cooperation in hunting for food; huddling for mutual protection from severe weather; opportunities for division of labor, which is especially well developed in the social insects with their caste systems; and the potential for learning and transmitting useful information through the society.

Observers of a seminatural colony of macaque monkeys in Japan recount an interesting example of acquiring and passing tradition in a society. The macaques were provisioned with sweet potatoes and wheat at a feeding station on the beach of an island colony. One day a young female

Figure 38-12
An infant yellow baboon (*Papio cyanocephalus*) "jockey rides" its mother. Later, as the infant is weaned, the mother-infant bond weakens and the infant will be refused rides.

Figure 38-13
Japanese macaque washing sweet potatoes. The tradition began when a young female named Imo began washing sand from the potatoes before eating them. Younger members of the troop quickly imitated the behavior.

named Imo was observed washing the sand off a sweet potato in seawater. The behavior was quickly imitated by Imo's playmates and later by Imo's mother. Still later when the young members of the troop became mothers they waded into the sea to wash their potatoes; their offspring imitated them without hesitation. The tradition was firmly established in the troop (Figure 38-13).

Some years later, Imo, an adult, discovered that she could separate wheat from sand by tossing a handful

of sandy wheat in the water; allowing the sand to sink, she could scoop up the floating wheat to eat. Again, within a few years, wheat-sifting became a tradition in the troop.

Imo's peers and social inferiors copied her innovations most readily. The adult males, her superiors in the social hierarchy, would not adopt the practice but continued laboriously to pick wet sand grains off their sweet potatoes and scout the beach for single grains of wheat.

Social living also has some disadvantages as compared with a solitary existence for some animals. Species that survive by camouflage from potential predators profit by being dispersed. Large predators benefit from a solitary existence for a different reason, their requirement for a large supply of prey. Thus there is no overriding adaptive advantage to sociality that inevitably selects against the solitary way of life. It depends on the ecological situation.

Aggression and Dominance

Many animal species are social because of the numerous benefits that sociality offers. Sociality requires cooperation. At the same time animals, like governments, tend to look out for their own interests. In short, they are in competition with one another because of limitations in the common resources that all require for life. Animals may compete for food, water, sexual mates, or shelter when such requirements are limited in quantity and are therefore worth a fight.

Much of what animals do to resolve competition is called **aggression,** which we may define as an offensive physical action, or threat, to force others to abandon something they own or might attain. Many behaviorists consider aggression part of a somewhat more inclusive interaction called **agonistic** (Gr. contest) behavior, referring to any activity related to fighting, whether it be aggression, defense, submission, or retreat.

Contrary to the widely held notion that aggressive behavior aims at the destruction or at least defeat of an opponent, most aggressive encounters are duels that lack the violence that we usually associate with fighting. Many species possess specialized weapons such as sharpened teeth, beaks, claws, or horns that are used for protection from, or predation on, other species. Although potentially dangerous, such weapons are seldom used in any severely damaging way against members of *their own species.*

Animal aggression within the species seldom results in injury or death because animals have evolved many symbolic **ritualized displays** that carry mutually understood meanings. A ritualized display is a behavior that has been modified through evolution to make it increasingly effective in serving a communicative function. Through **ritualization,** simple movements or traits become more intensive, conspicuous, or precise, and acquire the function of a signal. The result of such intensification is to reduce the possibility of misunderstanding. Fights over mates, food, or territory become ritualized jousts rather than bloody, no-holds-barred battles. When fiddler crabs spar for territory, their large claws usually are only slightly opened, Even in intense fighting when the claws are used, the crabs grasp each other in a way that prevents reciprocal injury. Rival male poisonous snakes engage in stylized bouts by winding themselves together; each attempts to butt the other's head with its own until one becomes so fatigued that it retreats. The rivals never bite each other. Many species of fish contest territorial boundaries with lateral displays, the males puffing themselves to look as threatening as possible. The encounter is usually settled when either animal perceives itself obviously inferior, folds up its fins, and swims away. Rival giraffes engage in largely symbolic "necking" matches in which two males standing side by side wrap and unwrap their necks around each other (Figure 38-14). Neither uses its potentially lethal hooves on the other, and neither is injured.

Thus animals fight as though programmed by rules that prevent serious injury. Fights between rival bighorn rams are spectacular to watch, and the sound of clashing horns may be heard for hundreds of meters (Figure 38-15). But the skull is so well protected by the massive horns that injury occurs only by accident. Nevertheless, despite these constraints, aggressive encounters on occasion can be true fights to the death. If African male elephants are unable to resolve dominance conflicts painlessly with ritual postures, they may resort to incredibly violent battles, with each trying to plunge its tusks into the most vulnerable parts of the opponent's body.

More commonly, however, the loser of a ritualized encounter may simply run away, or signal defeat by a specialized subordination ritual. If it becomes evident to him that he is going to lose anyway, he profits by communicating his submission as quickly as possible, thereby avoiding the cost of a real thrashing. Such submissive displays that signal the end of a fight may be almost the opposite of

Figure 38-14
Male Masai giraffes. *Giraffa camelopardalis,* fight for social dominance. Such fights are largely symbolic, seldom resulting in injury.

Figure 38-15
Male bighorn sheep *Ovis canadensis,* fight for social dominance during the breeding season.

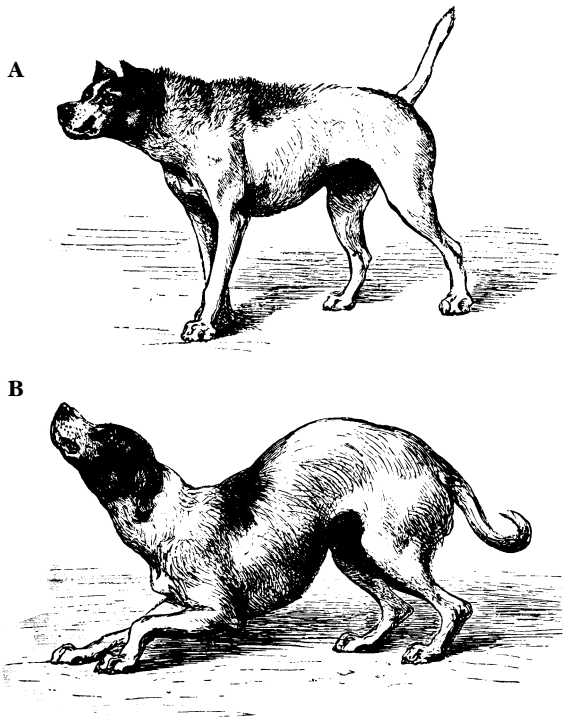

Figure 38-16
Darwin's principle of antithesis as exemplified by the postures of dogs. **A,** A dog approaches another dog with hostile, aggressive intentions. **B,** The same dog is in a humble and conciliatory state of mind. The signals of aggressive display have been reversed.

threat displays (Figure 38-16). In his book *Expression of the Emotions in Man and Animals* (1872), Charles Darwin described the seemingly opposite nature of threat and appeasement displays as the "principle of antithesis." The principle remains accepted by animal behaviorists today.

The winner of an aggressive competition is dominant to the loser, the subordinate. For the victor, dominance means enhanced access to all contested resources that contribute to reproductive success: food, mates, and territory. In a social species, dominance interactions often take the form of a dominance hierarchy. One animal at the top wins encounters with all other members in the social group; the second in rank wins all but those with the top-ranking individual.

Such a simple, ordered hierarchy was first observed in chickens by Schjelderup-Ebbe, who called the hierarchy a "peck-order." Once social ranking is established, actual pecking diminishes and is replaced by threats, bluffs, and bows. Top hens and cocks get unquestioned access to feed and water, dusting areas, and the roost. The system works because it reduces social tensions that would constantly surface if animals had to fight all the time over social position.

However, not all dominance hierarchies have clear-cut dominant and subordinate individuals. In some hierarchies, dominant animals are frequently challenged by subordinates.

The subordinates in any social order may be expendable. In many systems they never get a chance to reproduce, and when times get difficult they are often the first to die. During times of food scarcity, death of weaker members helps to protect the resource for stronger members. Rather than sharing food, the excess population is sacrificed. This sacrifice is not viewed by contemporary behaviorists as resulting from some direct, purposeful process ensuring "good for the species"; it is a *consequence* of the individual advantage that the stronger, dominant individuals possess during such circumstances.

Territoriality

Territorial ownership is another facet of sociality in animal populations. A territory is a fixed area from which intruders *of the same species* are excluded. This exclusion involves defending the area from intruders and spending long periods of time being conspicuous on the site. Territorial defense has been observed in numerous animals: insects, crustaceans, fishes, amphibians, lizards, birds, and mammals, including humans.

Sometimes the space defended moves with the individual. Individual distance, as it is called, can be observed as the spacing between swallows or pigeons on a wire, gulls lined up on the beach, or people lined up for a bus.

Territoriality is generally an alternative to dominance behavior, although both systems may be observed operating in the same

species. A territorial system may work well when the population is low, but it may break down with increasing population density and be replaced with dominance hierarchies in which all animals occupy the same space.

Like every other competitive endeavor, territoriality carries both costs and advantages. It is beneficial when it ensures access to limited resources, *unless* the territorial boundaries cannot be maintained with little effort. The presumed benefits of a territory are, in fact, numerous: uncontested access to a foraging area; enhanced attractiveness to females thus reducing the problems of pair-bonding, mating, and rearing the young; reduced disease transmission; reduced vulnerability to predators. But the advantages of holding a territory begin to wane if the individual must spend most of the time in boundary disputes with neighbors.

Most of the time and energy required for territoriality are expended when the territory is first established. Once the boundaries are located they tend to be respected, and aggressive behavior diminishes as territorial neighbors come to recognize each other. Indeed, neighbors may look so peaceful that an observer who was not present when the territories were established may conclude (incorrectly) that the animals are not territorial. A "beachmaster" sea lion (that is, a dominant male with many females) seldom quarrels with his neighbors who have their own territories to defend. However, he must be constantly vigilant against bachelor bulls who challenge the beachmaster for mating privileges.

Birds are conspicuously territorial. Most male songbirds establish territories in the early spring and defend these vigorously against all males of the same species during spring and summer when mating and nesting are at their height. A male song sparrow, for example, has a territory of approximately three-fourths of an acre. In any given area, the number of song sparrows remains approximately the same each year. The population remains stable because the young occupy territories of adults that die or are killed. Any surplus in the song sparrow population is excluded from territories and thus not able to mate or nest.

Figure 38-17
Gannet nesting colony. Note precise spacing of nests with each occupant just beyond pecking distance of its neighbors.

Sea birds such as gulls, gannets, boobies, and albatrosses occupy colonies that are divided into very small territories just large enough for nesting (Figure 38-17). The territories of these birds cannot include their fishing grounds, since they all forage in the sea where the food is always shifting in location and shared by all.

Territorial behavior is not as prominent with mammals as it is with birds. Mammals are less mobile than birds, making it more difficult for them to patrol a territory for trespassers. Instead, many mammals have **home ranges** (p. 626). A home range is the total area an individual traverses in its activities. It is not an exclusive, defended preserve but overlaps with the home ranges of other individuals of the same species.

For example, home ranges of baboon troops overlap extensively, although a small part of each range becomes the recognized territory of each troop for its exclusive use. Home ranges may shift considerably with the seasons. A baboon troop may have to shift to a new range during the dry season to obtain water and better grass. Elephants, before their movements were restricted by humans, made long seasonal migrations across the African savanna to new feeding ranges. However, the home ranges established for each season are remarkably consistent in size.

Mating Systems

Animals display a diversity of mating systems. Behavioral ecologists generally classify mating systems by the degree to which males and females associate during mating. **Monogamy** is an association between one male and one female at a time. **Polygamy** is a general term that incorporates all multiple mating systems where females and males may have more than one mate. **Polygyny** refers to a male that mates with more than one female. **Polyandry** is a system in which a female mates with more than one male. There are specific types of polygyny. **Resource defense polygyny** occurs when males gain access to females indirectly by holding critical resources. For example, female bullfrogs prefer to mate with males who are larger and older. These males defend territories of higher quality than smaller males because their territories have better temperature regimes for tadpoles to grow or because they are free of predatory leeches. **Female defense polygyny** occurs when females aggregate and, consequently, are defendable. Thus, when female elephant seals occupy a small island, dominant males can defend and gain access to them for mating relatively easily (Figure 38-18). This situation was previously known as a "harem." **Male dominance polygyny** occurs when females select mates from aggregations of males. For example, some animals form **leks.** A lek is a communal display ground where males congregate to attract and court females. Females choose and mate with the

Figure 38-18
Two elephant seals, *Mirounga angustirostris,* fight to establish dominance. Males are much larger than females in this highly polygynous society.

Figure 38-19
Male sage grouse, *Centrocercus urophasianus*, displaying at its lek.

male having the most attractive qualities (Figure 38-19). Leks characterize some birds, including prairie chickens and sage grouse. In these systems, sexual selection (p. 127) is often intense, resulting in evolution of bizarre courtship rituals and exaggerated morphological traits.

Altruistic Behavior and Kin Selection

If, as Darwin suggested, animals should behave selfishly and strive to produce as many offspring as possible, why do some animals help others at some risk to themselves? Why do some individuals show utmost cooperation with members of their social group and even forego breeding themselves? Why do some individuals appear to sacrifice themselves so that other members of their group can survive? Until the mid 1960s, scientists had trouble explaining in Darwinian terms how such **altruistic behavior** could persist in a population.

Most instances of altruistic behaviors were explained using a **group-selection** argument. Group selectionists suggested that animals that helped others or that failed to mate did so for the benefit of the other members of the group. Therefore, such behaviors produce increased survivorship of groups whose members behaved altruistically. According to proponents of this argument, selection occurs at the level of the group, not at the level of the individual as Darwin suggested. However, the group-selection argument as originally proposed by V. C. Wynne-Edwards in 1962 has been rejected by the vast majority of behavioral ecologists for a number of reasons.

For example, if in a social group there were randomly distributed genes for a risky altruistic behavior, such as giving calls to warn others of predators, those lacking such genes would flourish. They would be warned with no risk to themselves; their chances of reproduction would be greater and, in time, the "selfish" alleles would eliminate the altruistic ones from the group's gene pool.

In 1964, W. D. Hamilton, based largely on his studies of insects, proposed a new way to explain altruistic behavior by modifying Darwin's original concept of fitness. He reasoned that fitness is measured not just by the number of offspring produced but by the increase or decrease in particular alleles in the gene pool. Thus, an individual may act altruistically, even at great risk, if it helps increase representation of its alleles in the gene pool. Alleles are shared by all relatives, including parents and offspring, brothers and sisters, cousins and other relations. Alleles that influence altruistic behavior among relatives would persist in future generations. Since the most closely related animals share the most genes by common descent, we expect that altruistic behavior would be most common among closely related individuals. Thus, if everything else were equal, brothers who on average share half their alleles would be more likely to aid one another than they would a cousin who shares on average only 25% of their alleles. Hamilton's hypothesis based on this genetic explanation for altruism and cooperation is called **kin selection.** Essentially, kin selection is the selection of genes by individuals

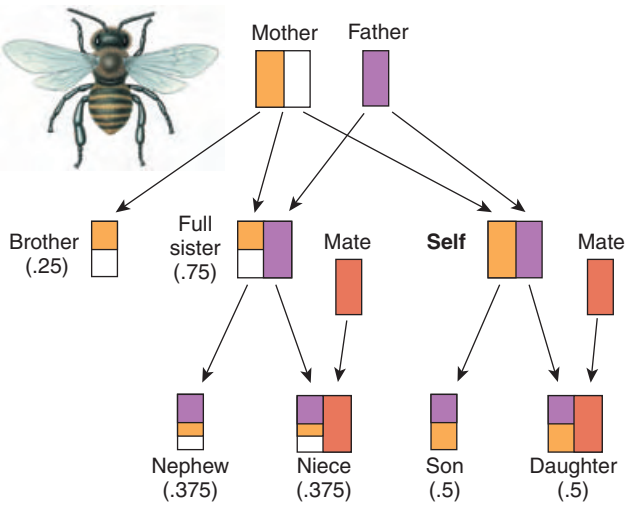

Figure 38-20

Haplodiploidy in honey bees, showing degrees of relatedness of a female worker bee (labeled SELF) to individuals she might raise. In honey bees, as in other haplodiploid animals, diploid females develop from fertilized eggs, and males develop from unfertilized eggs. Each daughter of a male gets all his genes (purple bar) and full sisters receive an identical one half of their genome from the same father. Open bars represent other, unrelated alleles. Because full sisters also share half the genes they receive from their common mother (yellow bar), the relatedness of SELF to a full sister is 0.75, the average of 0.5 and 1.0. (In a diploid-diploid system as in humans, the relatedness of siblings is 0.5 because both paternally and maternally inherited genes have a 50% chance of being present in a sibling.) Note that relatedness of female workers to a brother is only 0.25, because brothers are fatherless.

Figure 38-21

Belding's ground squirrel, *Spermophilus beldingi,* gives an alarm call to warn of the approach of a predator. This risky behavior endangers the callers more than noncallers.

assisting the survival and reproduction of individuals who possess the same genes by common descent.

Hamilton's hypothesis revolutionized evolutionary and behavioral biology. The main criterion of Darwinian fitness is the relative number of an individual's alleles that are passed to future generations. Hamilton, however, developed the concept of **inclusive fitness,** which is the relative number of an individual's alleles that are passed on to future generations either as a result of an individual's own reproductive success *or that of related individuals*. Thus, kin selection and inclusive fitness may be able to explain many altruistic behaviors that have perplexed biologists for many years.

A good example of altruism and kin selection in nature is the remarkable cooperation and coordination among eusocial insects such as ants, bees, and wasps. Through haplodiploidy (p. 139), where males are haploid and females are diploid, sisters are genetically related on average by 75% rather than 50% (Figure 38-20). Sisters are more closely related to each other than to their own daughters! Therefore, they cooperate with other members of their social group, forego breeding themselves and aid the queen to produce more sisters who are more closely related (75% related) than potential offspring (50% related).

Female Belding's ground squirrels, found in the High Sierra of California, give alarm calls when a predator approaches (Figure 38-21). Alarm calling warns other members of the social group and is risky to the alarm caller. However, the benefits to alarm calling outweigh the risks because alarm callers are warning *related* individuals. Thus, alarm-calling behavior, even if it is risky, may be favored by selection if it increases inclusive fitness of the caller.

Kinship theory suggests that animals may evolve an ability to recognize categories of relatives so that cooperation or aid-giving behavior will be directed more efficiently toward relatives. Although kin recognition behavior was discussed by Hamilton, little was known about it until almost 20 years after he wrote his seminal papers. Through a number of experimental studies we now know that a variety of species can discriminate between kin and non-kin. Such species are found among invertebrates, including isopods and insects, and vertebrates, including fishes, frog and toad tadpoles, birds, squirrels, and monkeys. Some species can even discriminate between full siblings and half-siblings and between cousins and unrelated individuals. Thus, some species have a finely tuned ability to identify relatives of various degrees of relatedness. The cues used in kin recognition vary from species to species. Birds use vocalizations whereas many other species use chemical cues.

Animal Communication

Only through communication can one animal influence the behavior of another. Compared with the enormous communicative potential of human speech, however, nonhuman communication is severely restricted. Animals

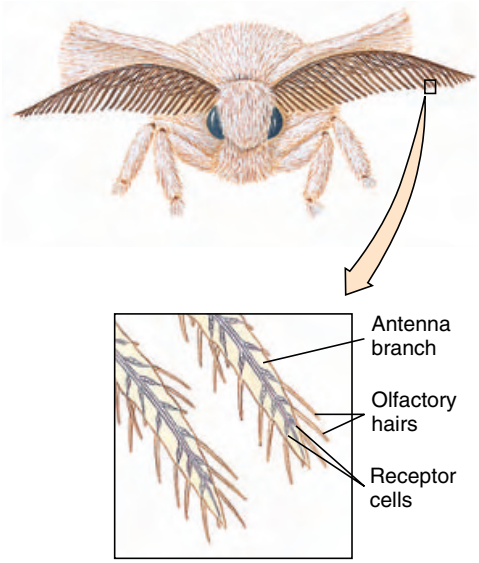

Figure 38-22
Large antennae of a male silkworm moth *Bombyx mori;* these are especially sensitive to the sex attractant (pheromone) released by the female moth.

may communicate by sounds, scents, touch, and movement. Indeed any sensory channel may be used, and in this sense animal communication has richness and variety.

Unlike our language, which is composed of words with definite meanings that may be rearranged to generate an almost infinite array of new meanings and images, communication of other animals consists of a limited repertoire of signals. Typically, each signal conveys one and only one message. These messages cannot be divided or rearranged to construct *new kinds* of information. A single message from a sender may, however, contain several bits of relevant information for a receiver.

The song of a cricket announces to an unfertilized female the species of the sender (males of different species have different songs), his sex (only males sing), his location (source of the song), and social status (only a male able to defend the area around his burrow sings from one location). This information is crucial to the female and accomplishes a biological function. But there is no way for the male to alter his song to provide additional information concerning food, predators, or habitat, which might improve his mate's chances of survival and thus enhance his own fitness.

Chemical Sex Attraction in Moths

Mate attraction in silkworm moths illustrates an extreme case of stereotyped, single message communication that has evolved to serve a single biological function: mating. Virgin female silkworm moths have special glands that produce a chemical sex attractant to which males are sensitive. Adult males smell with their large bushy antennae, covered with thousands of sensory hairs that function as receptors (Figure 38-22). Most of these receptors are sensitive to the chemical attractant **bombykol** (a complex alcohol named after the silkworm *Bombyx mori*) and to nothing else.

To attract males, females merely sit quietly and emit a minute amount of bombykol, which is carried downwind. When a few molecules reach a male's antennae, he is stimulated to fly upwind in search of the female. His search is at first random, but, when by chance he approaches within a few hundred yards of the female, he encounters a concentration gradient of the attractant. Guided by the gradient, he flies toward the female, finds her, and copulates with her.

In this example of chemical communication the attractant bombykol, a *pheromone* (p. 738), serves as a signal to bring the sexes together. Its effectiveness is ensured because natural selection favors the evolution of males with antennal receptors sensitive enough to detect the attractant at great distances (several miles). Males with a genotype that produces a less sensitive sensory system fail to locate a female and thus are reproductively eliminated from the population.

Language of Honey Bees

One of the most sophisticated and complex of all nonhuman communication systems is the symbolic language of bees. Honey bees are able to communicate the location of food resources when these sources are too distant to be located easily by individual bees. They communicate by dances, which are mainly of two forms. The form having the most informational richness is the **waggle dance** (Figure 38-23). Bees most commonly execute these dances when a forager has returned from a rich source, carrying either nectar in her stomach or pollen grains packed in basketlike spaces formed by hairs on her legs. The waggle dance is roughly in the pattern of a figure-eight made against the vertical surface on the comb inside the hive. One cycle of the dance consists of three components: (1) a circle with a diameter about three times the length of the bee, (2) a straight run while waggling the abdomen from side to side and emitting a pulsed, low-frequency sound, and (3) another circle, turning in the opposite direction from the first. This dance is repeated many times with the circling alternating clockwise and counterclockwise.

The significance of the bee dances was discovered in 1943 by German zoologist Karl von Frisch, one of the recipients of the 1973 Nobel Prize. Despite detailed and extensive experiments by von Frisch and others that supported his original interpretations of the honey bee dances, the experiments have been criticized, especially by American biologist Adrian Wenner, who suggests that the correlation between dance symbolism and food location is accidental. He argued that foraging bees bring back odors characteristic of the food source, and that recruits are stimulated by dance to search for flowers bearing those odors. Wenner, with P. H. Wells, has reviewed his studies as a scientific autobiography and polemic (*Anatomy of a controversy: the question of a language among bees,* 1990, Columbia University Press). Wenner and Wells' assertions have generated strong controversy and have stimulated more rigorously controlled research on the bee dances. Recently, researchers have constructed a robot bee that can be moved through the waggle dance while producing the dance song with vibrating metal "wings." When operated in a hive, the computer-directed robot successfully recruited attending bees to visit preselected food dishes outside the hive that had

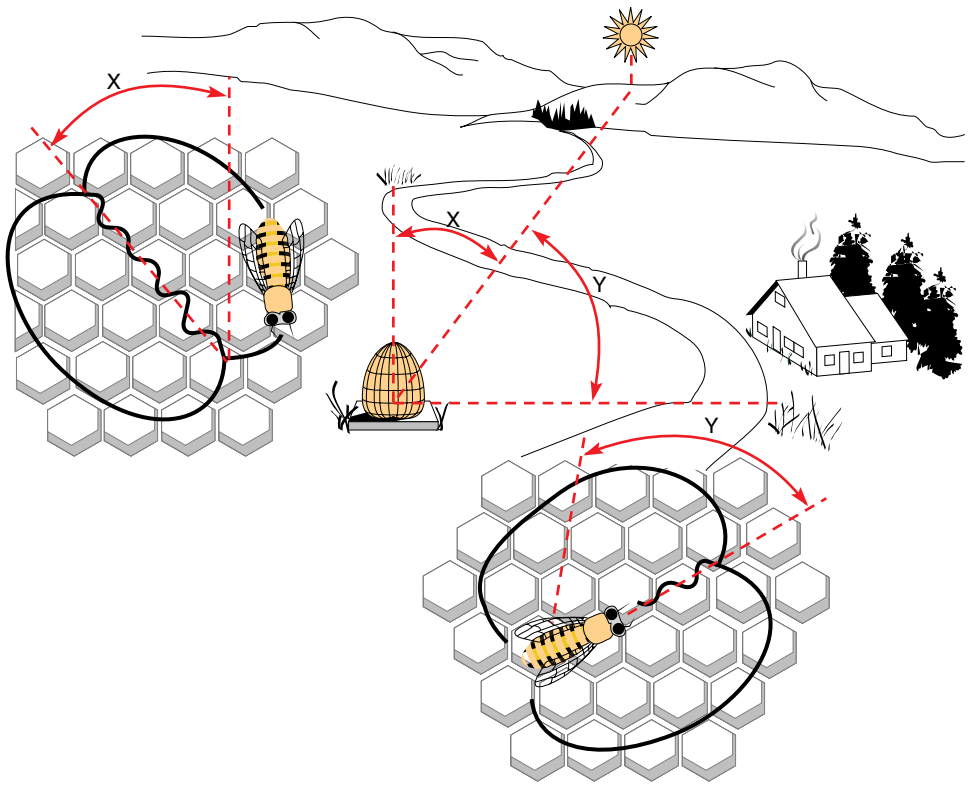

Figure 38-23
Waggle dance of the honey bee used to communicate both the direction and distance of a food source. The straight run of the waggle dance indicates direction according to the position of the sun (angles *X* and *Y*).

never been visited previously. These experiments provide convincing evidence that the bee dances do communicate both direction and distance information to foraging bees.

The straight, waggle run is the important informational component of the dance. Waggle dances are performed almost always in clear weather, and the direction of the straight run is related to the position of the sun. If the forager has located food directly toward the sun, she will make her waggle run straight upward over the vertical surface of the comb. If food was located 60 degrees to the right of the sun, her waggle run is 60 degrees to the right of vertical. We see then that the waggle run points at the same angle relative to the vertical as the food is located relative to the sun.

Distance of the food source is also coded into bee dances. If the food is close to the hive (less than 50 m), the forager employs a simpler dance called the **round dance.** The forager simply turns a complete clockwise circle, then turns, and completes a counterclockwise circle, a performance that is repeated many times. Other workers cluster around the scout and become stimulated by the dance as well as by the odor of nectar and pollen grains from flowers she has visited. The recruits then fly out and search in all directions but do not stray far. The round dance carries the message that food is to be found in the vicinity of the hive.

If the food source is farther away, round dances become waggle dances, which provide both distance and directional information. The tempo of the waggle dance is related inversely to the food's distance. If the food is about 100 m away, each figure-eight cycle lasts about 1.25 seconds; if 1000 m away, it lasts about 3 seconds; and if about 8 km (5 miles) away, it lasts 8 seconds. When food is plentiful, the bees may not dance at all. But when food is scarce, the dancing becomes intense, and other workers cluster around the returning scouts and follow them through the dance patterns.

Communication by Displays

A display is a kind of behavior or series of behaviors that serves a communicative purpose. The release of sex attractant by the female moth and the dances of bees just described are examples of displays; so are alarm calls of herring gulls, songs of the white-crowned sparrow, courtship dances of the sage grouse, and "eyespots" on the hind wings of certain moths that are exposed quickly to startle potential predators.

The elaborate pair-bonding displays of blue-footed boobies (Figure 38-24) are performed with maximum intensity when the birds come together after a period of separation. The male at right in the illustration is sky pointing: the head and tail are pointed skyward and the wings are swiveled forward in a seemingly impossible position to display their glossy upper surfaces to the female. This display is accompanied by a high-piping whistle. The female at left, for her part, is parading. She steps with exaggerated slow deliberation, lifting each brilliant blue foot in turn, as though holding it aloft momentarily for the male to admire. Such highly personalized displays, performed with droll solemnity, appear comical, even inane to the observer. Indeed the boobies, whose name is derived from the Spanish word "bobo" meaning clown, presumably were so designated for their amusing antics.

The exaggerated nature of the displays ensures that the message is not missed or misunderstood. Such displays are essential to establish and maintain a strong pair bond between male and female. This requirement also explains the repetitious nature of displays that follow one another throughout courtship and until laying of eggs. Redundancy of displays maintains a state of mutual stimulation between male and female, ensuring the degree

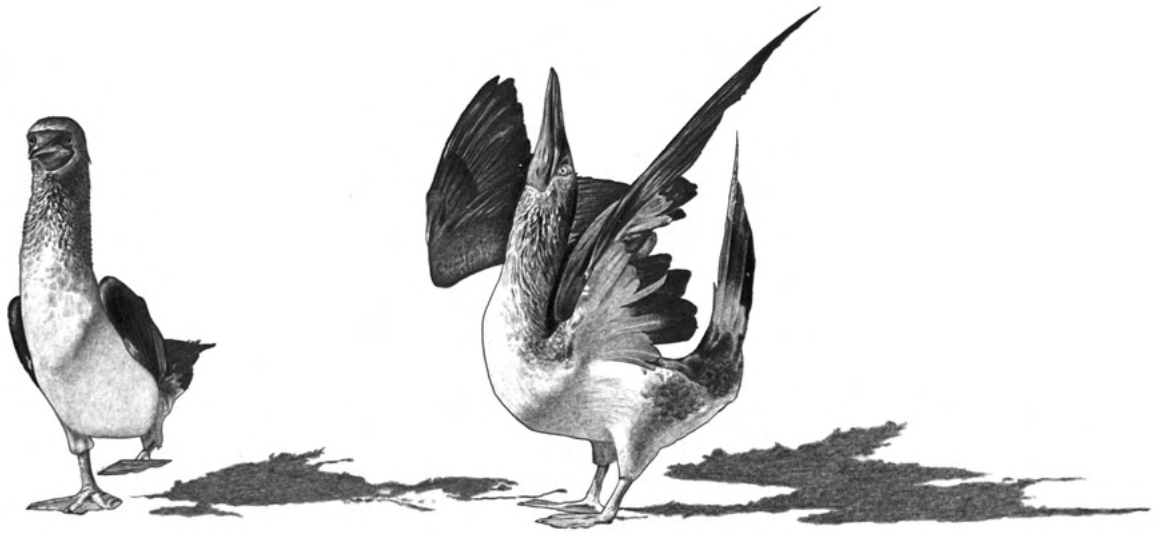

Figure 38-24

A pair of Galápagos blue-footed boobies, *Sula nebouxii,* display to each other. The male (*right*) is sky pointing; the female (*left*) is parading. Such vivid, stereotyped, communicative displays serve to maintain reciprocal stimulation and cooperative behavior during courtship, mating, nesting, and care of the young.

of cooperation necessary for copulation and subsequent incubation and care of the young. A sexually aroused male has little success with an indifferent female.

Communication between Humans and Other Animals

One uncertainty in studies of animal communication is understanding what sensory channel an animal is using. The signals may be visual displays, odors, vocalizations, tactile vibrations, or electrical currents (as, for example, among certain fishes). Even more difficult is establishing two-way communication between humans and other animals since the investigator must translate meanings into symbols that the animal can understand. Furthermore, people are poor social partners for most other animals.

Animal Cognition

One of the most fascinating subjects in animal behavior deals with animal intelligence and awareness. Animal cognition is a general term for mental function, including perception, thinking, and memory. Many biologists believe that mental processes of animals may be similar to those of humans. Recent studies on animal cognition with nonhuman primates and African Grey parrots have yielded fascinating results.

In the late 1960s Beatrix and Allen Gardner of the University of Nevada in Reno began using American Sign Language (ASL) to train a chimpanzee named Washoe to communicate with her hands the same way that deaf people do. By age five Washoe could sign 132 words, which she could put into strings forming sentences and phrases. She could answer questions, make suggestions, and convey moods. In one session, when asked what a swan was, Washoe answered "water bird." Washoe also taught signs to other chimpanzees. At first, signs were used as play but soon the chimpanzees used them to make spontaneous requests to trainers such as "drink," "tickle," and "hug." Similar work has been done with other primates including gorillas, orangutans, and pygmy chimpanzees.

Irene Pepperberg of the University of Arizona has worked for years with an African Grey parrot named Alex. Because parrots can vocalize like humans, Pepperberg was able to communicate with Alex using human vocal language. Over the years Alex learned a number of attributes including colors, shapes, and materials for more than 100 objects. Alex not only can identify objects by colors and shape, but can also distinguish the difference between two objects. Thus, if Alex is given two objects of the same color but one larger than the other, he could state that the difference between them was "size." Alex can also count and relate to the trainer how many objects of each particular category are present.

Conscious awareness is also part of cognition. Donald Griffin wrote two books suggesting that many animals are capable of self-awareness and can think and reason. The ability of apes, parrots, and other animals to use language-related skills is significant because it tells us about their cognitive abilities and we can begin to communicate with them. The possibility that animals may have thinking processes similar to humans and that they have a conscious awareness has shed new light on animal behavior studies and added new significance to our studies of animals in general. Studies of animal cognition remain highly controversial.

The animal behaviorist Irven DeVore reported how choosing the proper channel for dialogue can have more than academic interest:*

> One day on the savanna I was away from my truck watching a baboon troop when a young

*DeVore, Irven. The marvels of animal behavior. 1972. Washington, D.C., National Geographic Society.

juvenile came and picked up my binoculars. I knew if the glasses disappeared into the troop they'd be lost, so I grabbed them back. The juvenile screamed. Immediately every adult male in the troop rushed at me—I realized what a cornered leopard must feel like. The truck was 30 or 40 feet away. I had to face the males. I started smacking my lips very loudly, a gesture that says as strongly as a baboon can, "I mean you no harm." The males came charging up, growling, snarling, showing their teeth. Right in front of me they halted, cocked their heads to one side—and started lip-smacking back to me. They lip-smacked. I lip-smacked, "I mean you no harm." "I mean *you* no harm." It was, in retrospect, a marvelous conversation. But while my lips talked baboon, my feet edged toward the truck until I could leap inside and close the door.

The study of animal communication has made great strides in recent years, buoyed by the assimilation of a wealth of facts and information about communication in many species. The animal world is filled with communication. In recognizing that reasoning and insight are not required for effective, highly organized behavior, we should not conclude that other animals are, as Descartes proclaimed in the seventeenth century, nothing more than machines.

Summary

Animal behavior has emerged as a scientific discipline from three different experimental approaches. Comparative psychology emphasizes the identification of mechanisms controlling behavior, using relatively few species, with the intent that these mechanisms might have wide applicability among animals. Ethology is the study of behavior, both innate and learned, of animals in their natural habitats. Behaviorists have shown that behavioral traits have evolutionary histories and evolve by natural selection. Sociobiology aims to understand how and why social behavior in animals has evolved. Both ethology and sociobiology distinguish between studies that focus on the mechanisms of behavior (proximate causation) and those that focus on function or evolution of behavior (ultimate causation).

Students of animal behavior have observed and cataloged many behavioral patterns of animals that are highly predictable and almost invariable in performance. Often these patterns are triggered, or "released," by specific, and usually simple, environmental stimuli, called sign stimuli. Although such formalized behaviors may be released inappropriately at times, they are efficient and enable the animal to respond rapidly. The development of behavioral patterns depends on an interaction between an organism and the environment in which the animal lives. For this reason, behavioral scientists prefer not to describe behaviors—those that are largely invariable in their performance—as "instinctive" or "innate."

Behavior may be modified by learning through experience. Two simple kinds of learning behavior are habituation, which is the reduction or elimination of a behavioral response in the absence of any reward or punishment; and sensitization, in which a repeated stimulus increases the strength of a behavioral response. The gill-withdrawal reflex of the marine mollusc *Aplysia* is described as a protective response that can be modified experimentally to show either habituation or sensitization. The modification of the alarm response of herring gull chicks is another example of habituation. Another form of learning is imprinting, the lasting recognition bond that forms early in life between the young of many social animals and their mothers.

Social behavior is behavior arising from interactions of members of a species with one another. In social organizations, animals tend to remain together, communicate with each other, and usually resist intrusions by "outsiders." The advantages of sociality include cooperative defense from predators, cooperative searching for food, improved reproductive performance and parental care of the young, and transmission of useful information through the society. Because social animals compete with one another for resources (such as food, sexual mates, and shelter), conflicts are often resolved by a form of overt hostility called aggression. Most aggressive encounters between conspecifics are stylized bouts involving more bluff than intent to injure or kill. Dominance hierarchies, in which a priority of access to common resources is established by aggression, are common in social organizations. Territoriality is an alternative to dominance. A territory is a defended area from which intruders of the same species are excluded.

Mating systems include monogamy, the mating of an individual with only one partner of the opposite sex each breeding season; and polygamy, the mating of an individual with two or more partners in a breeding season. Two forms of polygamy are polygyny, the mating of a male with more than one female; and polyandry, the mating of a female with more than one male. Several types of polygyny are recognized.

A behavior in which one animal may reduce it own fitness to increase the fitness of others is called altruistic behavior. Examples are risky behaviors such as one member of a social group warning others of a predator, and cooperative behavior among social insects in which an individual may sacrifice itself to benefit the colony. The favored explanation of altruism is kin selection, in which the recipient of an altruistic act is sufficiently closely related to the altruist that the recipient's survival would benefit the genes shared with the altruist.

Communication, often considered the essence of social organization, is the means by which animals influence the behavior of other animals, using sounds, scents, visual displays, touch, or other sensory signals. As compared with the richness of human language, animals communicate with a very limited repertoire of signals. One of the most famous examples of animal communication is that of the symbolic dances of honey bees. Birds communicate by calls and songs and, especially, by visual displays. By ritualization, simple movements have evolved to become conspicuous signals having definite meanings.

Review Questions

1. How do experimental approaches of comparative psychology and ethology differ? Comment on the aims and methods employed by each.
2. Egg-retrieval behavior of greylag geese is an excellent example of a highly predictable behavior. Interpret this behavior within the framework of classical ethology, using these terms: releaser, sign stimulus, and stereotyped behavior. Interpret the territorial defense behavior of male three-spined sticklebacks in the same context.
3. The idea that behavior must be *either* innate or learned has been called a "nature versus nurture" controversy. What reasons are there for believing that such a strict dichotomy does not exist?
4. Two kinds of simple learning are habituation and imprinting. Distinguish between these two types of learning, and offer an example of each.
5. Some strains of bees show hygienic behavior by uncapping cells containing larvae infected with a bacterial disease called foulbrood and removing the dead larvae from the hive. What is the evidence that this behavior is transmitted by two independently segregating genes?
6. Discuss the advantages of sociality for animals. If social living has so many advantages, why do many animals successfully live alone?
7. Suggest why aggression, which might seem counterproductive, exists among social animals.
8. What is the selective advantage to the winner, as well as to the loser, that aggressive encounters within species for social dominance are usually ritualized displays or symbolic fights rather than unrestrained fights to the death?
9. Of what use is a territory to an animal, and how is a territory established and kept? What is the difference between territory and home range?
10. Polygyny is a form of polygamy in which a male mates with more than one female. Explain how three forms of polygyny differ from each other: resource defense polygyny, female defense polygyny, and male dominance polygyny.
11. Give an example of an altruistic behavior and explain how such behavior conflicts with Darwin's expectation that animals will act selfishly to produce as many offspring as possible.
12. Earlier explanations of altruistic behavior as a form of group selection have been supplanted by Hamilton's hypothesis of kin selection. What distinguishes kin selection and how does it accord with the notion of inclusive fitness, the relative number of an individual's alleles that pass to the next generation?
13. Comment on the limitations of animal communication as compared to those of human communication.
14. The dance language used by returning forager honey bees to specify the location of food is an example of remarkably complex communication among "simple" animals. How is direction and distance information coded into the waggle dance of the bees? What is the purpose of the round dance?
15. What is meant by "ritualization" in display communication? What is the adaptive significance of ritualization?
16. Early efforts by humans to communicate vocally with chimpanzees were almost total failures. Recently, however, researchers have learned how to communicate successfully with apes. How was this task accomplished?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Ethology. University of Georgia Ethology and Animal Behavior resources. Includes electronic journals, directories, and many links.

Animal Behavior Society. Documents on the value of the study of animal behavior, lists of institutions with departments specializing in animal behavior, educational activities, the Animal Behavior Society newsletter, research reports, and interesting new information about animal behavior.

Center for Integrative Study of Animal Behavior. Programs in animal behavior, research articles, computer archives for the study of animal behavior, and articles from the Animal Behavior Bulletin are featured at this site.

Animal Behavior and Welfare Sites. Many links to a variety of subjects relating to animal behavior.

Animal Behavior Resources on the Internet. A wealth of information on animal behavior societies, resources, programs, mailing lists, and research results.

OLC Student Center Website

PART FIVE

The Animal and Its Environment

39 The Biosphere and Animal Distribution **40** Animal Ecology

Arctic ground squirrel.

CHAPTER

39

The Biosphere and Animal Distribution

Spaceship earth.

Spaceship Earth

All life is confined to a thin veneer of the earth called the **biosphere.** From the first remarkable photographs of earth taken from the *Apollo* spacecraft, revealing a beautiful blue and white globe lying against the limitless backdrop of space, viewers were struck and perhaps humbled by our isolation and insignificance in the enormity of the universe. The phrase "spaceship earth" became a part of our vocabulary, and the realization evolved that all the resources we will ever have for sustaining life are restricted to a thin layer of land and sea and a narrow veil of atmosphere above it. We could better appreciate just how thin the biosphere is if we could shrink the earth and all of its dimensions to a 1 m sphere. We would no longer perceive vertical dimensions on the earth's surface. The highest mountains would fail to penetrate a thin coat of paint applied to our shrunken earth; a fingernail's scratch on the surface would exceed the depth of the ocean's deepest trenches.

Earth's biosphere and the organisms in it have evolved together. In the continuous interchange between organism and environment, both have been altered, and a favorable relationship preserved. Earth's biosphere, with its living and nonliving components, is not a static thing but has undergone an evolution in every way as dramatic as the evolution of the animal kingdom. Today the biosphere is changing rapidly under the impact of humans, one of the greatest agents of biotic disturbance the earth has ever known. Only the historical bombardment of the earth by asteroids has produced a greater disturbance of the earth's biota. ■

In a universe of billions of stars, our earth is a small planet circling an ordinary star. Thousands of other stars are like our sun with planetary systems that conceivably could support life. Yet, of all these, our planet is the only one that we *know* supports life. Until proven otherwise, the earth is unique, a true wonder of an infinite universe.

What makes earth an especially fit environment for life? Most biologists would agree that foremost is the presence of liquid water on the earth's surface. Water, with its many extraordinary physical properties (p. 28) provided the medium for the origin of life and bestowed on earth a moderate climate suitable for life's continued evolution. Many other properties of earth make it optimal for life. Among these are a steady supply of light and heat from an unfailing sun; a suitable range of temperature for life, neither too hot nor too cold; a supply of the major and minor elements required by living matter; and a gravity force strong enough to hold an extensive gaseous atmosphere.

The many properties that make the earth wonderfully suitable for life were first recognized and examined in detail by Lawrence J. Henderson (1878 to 1942) in his book *The Fitness of the Environment,* published in 1913. The profound insights of this distinguished Harvard biochemist and physiologist were remarkable, appearing as they did before ecology had become a science. His insightful understanding of reciprocity between organism and environment has become a principle that underlies all ecological science. Henderson's book deserves a broader appreciation than it has received; it is, for example, seldom mentioned in ecology textbooks.

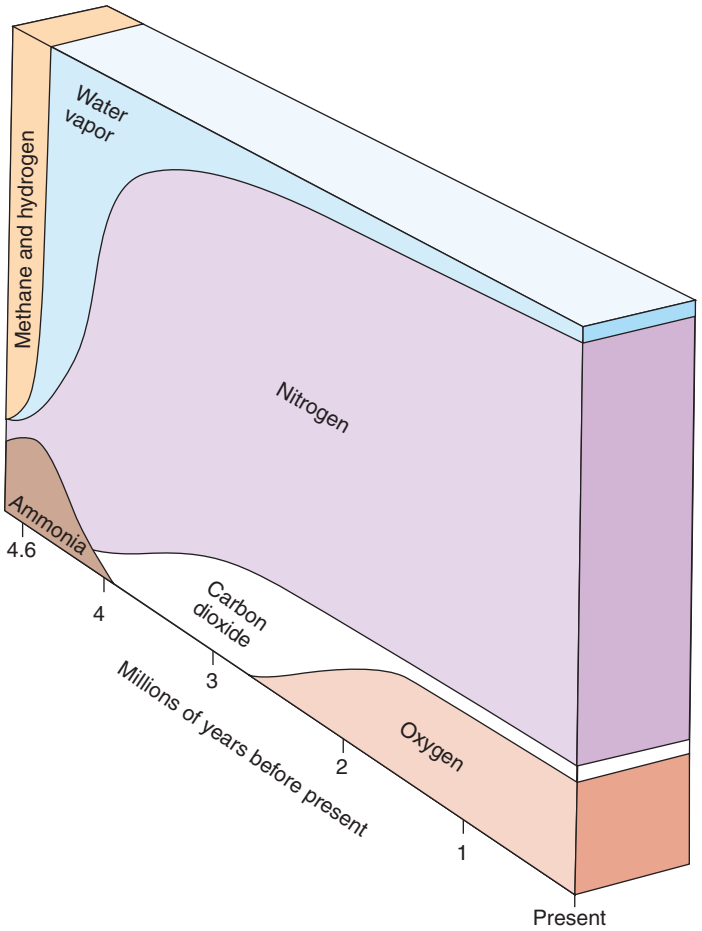

Figure 39-1
Changing composition of earth's atmosphere over time. The primitive atmosphere formed as hydrogen, methane, and ammonia. Hydrogen, too light to be held by the earth's gravitational field, was lost to space. Nitrogen, carbon dioxide, sulfur dioxide, and water vapor emitted from volcanoes replaced the remaining primitive gases. The first free oxygen was formed by solar radiation acting on water molecules (photochemical dissociation) in the atmosphere. When oxygen-producing plants appeared 3 to 3.5 billion years ago atmospheric oxygen gradually rose to its present level approximately 400 million years ago.

An organism and its environment share a reciprocal relationship. The environment is modified by organisms, and populations of organisms are modified by the evolutionary process to adapt them to the environment and its changes. As an open system, an animal is forever receiving and giving off materials and energy. Building materials for life are obtained from the physical environment, either directly by producers such as green plants or indirectly by consumers that return inorganic substances to the environment by excretion or by decay and disintegration of their bodies.

A living form is a transient link that is built of environmental materials, which are then returned to the environment to be used again in the re-creation of new life. Life, death, decay, and re-creation have been the cycle of existence since life began.

The primitive earth of 4.5 billion years ago, barren, stormy, and volcanic with a reducing atmosphere of ammonia, methane, and water (Figure 39-1), was wonderfully fit for the prebiotic syntheses that led to life's beginnings. Yet, it was totally unsuited, indeed lethal, for the kinds of living organisms that inhabit the earth today, just as early forms of life could not survive in our present environment. The appearance of free oxygen in the atmosphere, produced largely if not almost entirely by life, is an example of the reciprocity between organism and environment. Although oxygen was at first poisonous to early forms of life, its gradual accumulation from photosynthesis over the ages forced protective biochemical alterations to appear that led eventually to complete dependence on oxygen by most organisms. As living organisms adapt and evolve, they act on and produce changes in their environment. In so doing they must themselves change.

Distribution of Life on Earth

Biosphere and Its Subdivisions

The biosphere as usually defined is the thin outer layer of the earth capable of supporting life. It is probably best viewed as a global system that includes all life on earth and the physical environments in which living organisms exist and interact. The nonliving subdivisions of the biosphere include the lithosphere, hydrosphere, and atmosphere.

The **lithosphere** is the rocky material of the earth's outer shell and is the ultimate source of all mineral elements required by living organisms. The **hydrosphere** is the water on or near the earth's surface, and it extends into the lithosphere and the atmosphere. Water is distributed over the earth by a global hydrological cycle of evaporation, precipitation, and runoff. Five-sixths of the evaporation is from the ocean, and more water is evaporated from the ocean than is returned to it by precipitation. Oceanic evaporation therefore provides much of the rainfall that supports life on land. The gaseous component of the biosphere, the **atmosphere,** extends to some 3500 km above the surface of the earth, but all life is confined to the lowest 8 to 15 km (troposphere). The screening layer in the atmosphere of oxygen-ozone is concentrated mostly between 20 and 25 km. The main gases present in the troposphere are (by volume) nitrogen, 78%; oxygen, 21%; argon, 0.93%; carbon dioxide, 0.03%; and variable amounts of water vapor.

Atmospheric oxygen has originated almost entirely from photosynthesis. As discussed in Chapter 2, the primitive earth contained a reducing atmosphere devoid of oxygen. When oxygen-producing photosynthesis appeared about 3 billion years ago (Figure 39-1), oxygen gradually began to accumulate in the atmosphere. It is believed that by the mid-Paleozoic era, some 400 million years BP, the oxygen concentration had reached its present level of about 21%. Since then, oxygen consumption by animals and plants has approximately equaled oxygen production. The present surplus of free oxygen in the atmosphere resulted from fossilization of plants before they could decay or be consumed by animals. As these vast stores of fossil fuels are burned by our industrialized civilization, the oxygen surplus that accumulated over the ages conceivably could be depleted. Fortunately, depletion is unlikely for two reasons: (1) most of the total fossilized carbon is in the form of noncombustible shales and rocks, and (2) the oxygen reserves in the atmosphere and in the oceans are so enormous that the supply could last thousands of years even if all photosynthetic replenishment suddenly were to cease.

The rapid input of carbon dioxide into the atmosphere from the burning of fossil fuels may significantly affect the earth's heat budget. Much of the sun's short-wave light energy absorbed by the earth's surface reradiates as longer-wave infrared heat energy (Figure 39-2). Materials in the atmosphere, especially carbon dioxide and water vapor, impede this heat loss and allow the atmosphere to warm up. This heating of the atmosphere is called the "greenhouse effect," since the atmosphere acts to trap reradiated heat from the earth in much the same way the glass of a greenhouse traps heat reradiated by the plants and soil inside. While the greenhouse effect provides conditions essential for all life on earth, there is concern that the gradual accumulation of carbon dioxide could lead to an increase in the temperature of the biosphere as a whole (Figure 39-3).

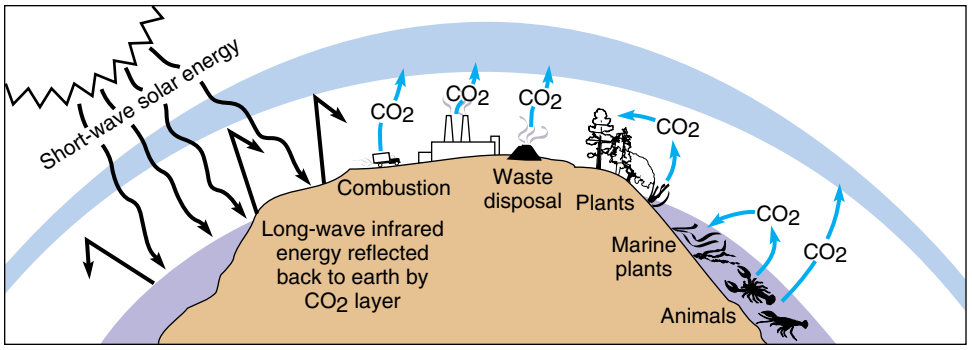

Figure 39-2
"Greenhouse effect." Carbon dioxide and water vapor in the atmosphere are transparent to sunlight but absorb heat energy reradiated from the earth, leading to warming of atmospheric air.

The concern over the long-range effects of increasing atmospheric carbon dioxide, primarily from the burning of fossil fuel, stems not from mere conjecture. Atmospheric carbon dioxide increased from about 280 parts per million (ppm) before the Industrial Revolution to an average 365 ppm today and is increasing at a rate of 1.3 ppm per year. It is expected to exceed 600 ppm in the next century. In the past century global temperature has increased 0.4° C and most experts agree that it will have increased 2° to 6° C when carbon dioxide and other heat-trapping greenhouse gases have doubled in the next century. If computer models are correct, rising global temperature will raise the sea level with gradual melting of the earth's ice caps (sea level has already risen 5 cm over the past century), alter crop yields, forests, and water supplies, and expand the world's desert—all of which would profoundly impact the earth's habitability.

Terrestrial Environments: Biomes

A biome is a major biotic unit bearing a characteristic and easily recognized array of plant life. Botanists long ago recognized that the terrestrial environment of the earth could be divided into large units having a distinctive vegetation, such as forests, prairies, and deserts. Animal distribution has always been more difficult to map, because plant and animal distributions do not

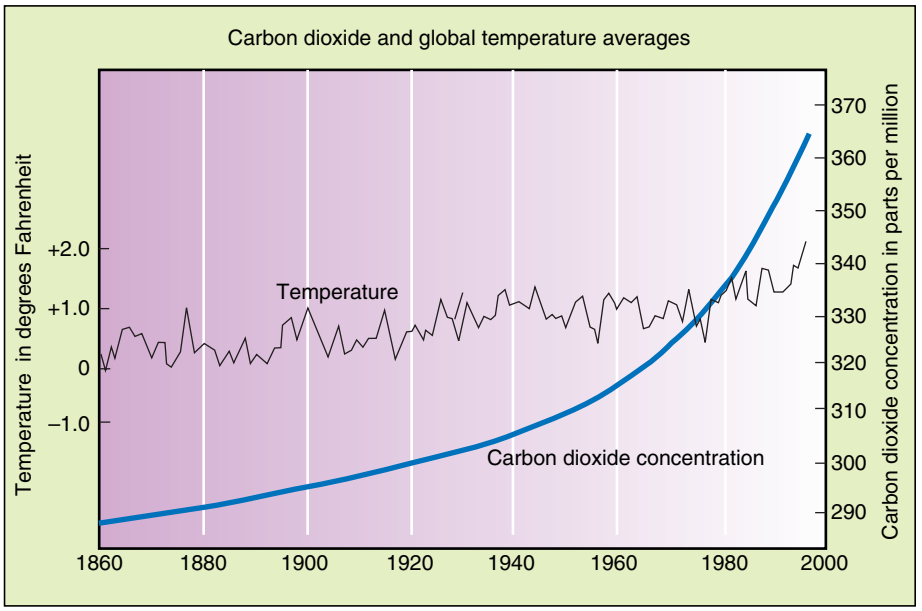

Figure 39-3

Rise in global atmospheric carbon dioxide and global temperature averages for the past 140 years. Data points before 1958 come from analysis of air trapped in bubbles in glacial ice from sites around the world. Atmospheric carbon dioxide has climbed steadily for more than a century while the earth's temperature has followed a more erratic upward trend.

Figure 39-4

Major biomes of North America. Boundaries between biomes are not distinct as shown but grade into one another over broad areas.

exactly coincide. Over time zoogeographers came to accept plant distributions as the basic biotic units and recognized biomes as distinctive combinations of plants and animals. A biome is therefore identified by its dominant plant formation (Figure 39-4), but, since animals depend on plants, each biome supports a characteristic fauna.

Each biome is distinctive, but its borders are not. Anyone who has traveled across North America knows that plant communities grade into one another over broad areas. The moist deciduous forests of the Appalachians give way gradually to the drier oak forests of the upper Mississippi Valley, and then to oak woodlands with grassy understory. This yields to tall and mixed prairies (now corn and wheatlands), then to desert grasslands, and finally to desert shrublands. The indistinct boundaries where the dominant plants of adjacent biomes are mixed together form an almost continuous gradient called an **ecocline.** Thus biomes are in some sense abstractions, a convenient way for us to organize our concepts about different communities. Nevertheless, anyone can distinguish a grassland, deciduous forest, coniferous forest, or shrub desert by the dominant plants in each. And we can make reasonable assumptions about the kinds of animals that live in each biome.

Distinctiveness of a biome is determined mainly by climate, the characteristic pattern of rainfall and temperature of each region, and the solar radiation it receives. Global variation in climate arises from uneven heating of the atmosphere by the sun. Because of the lower angle of the sun's rays striking higher latitudes, atmospheric heating is less there than at the equator (Figure 39-5). Air warmed at the equator rises and moves toward the poles. It is replaced by cold air moving away from the poles at lower levels. This pattern is complicated by the earth's rotation, which produces a Coriolis effect that deflects moving air to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Air circulation in each hemisphere is

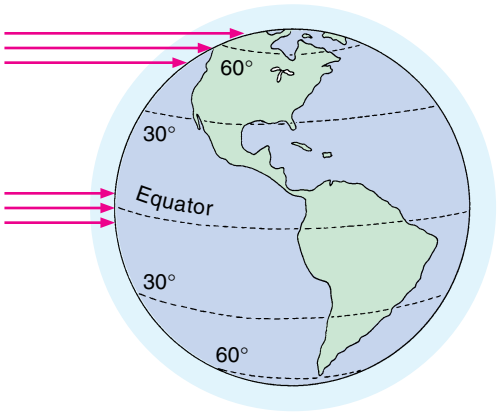

Figure 39-5
The earth's climate is determined by differential solar radiation between the higher latitudes and equator. Solar energy is spread across a much larger, slanting surface area at high latitudes than is an equivalent amount of energy at the equator.

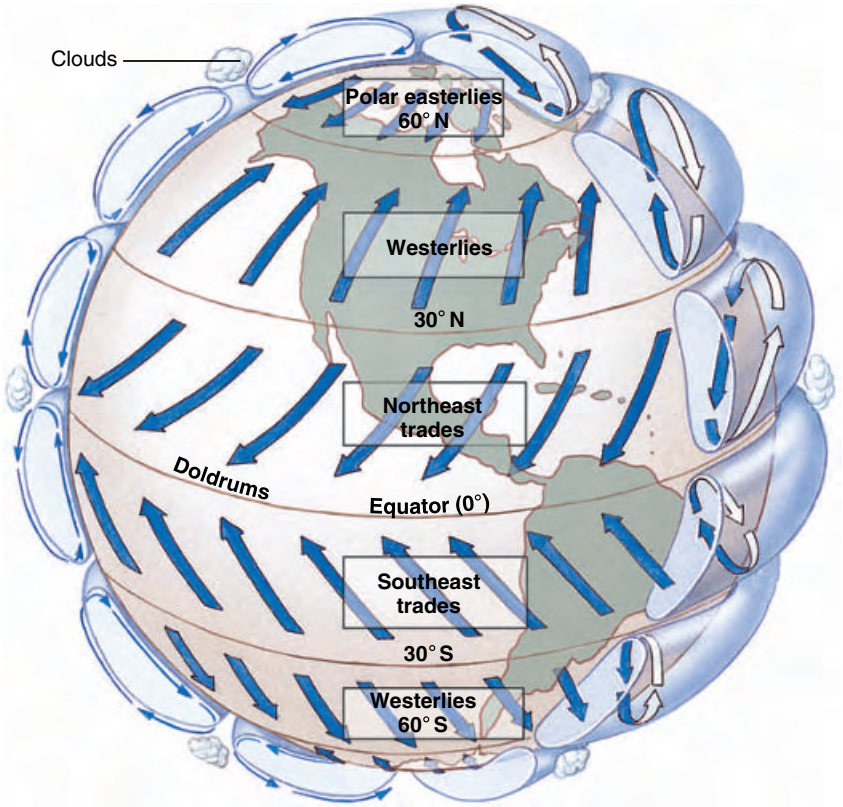

Figure 39-6
The earth as a heat engine. As the result of unequal heating across the earth's surface, together with other factors such as the earth's rotation, circulation of the oceans, and presence of landmasses, the earth acts like a giant heat engine that imposes a complex patchwork of climates on the earth. See text for explanation.

broken into three latitudinal zones, called cells (Figure 39-6). In the Northern Hemisphere, for example, hot moist air at the equator cools and condenses as it rises, providing rainfall for the lush vegetation of the equatorial rain forests. Warm air then flows northward at high levels, cools, and sinks at 20° to 30° latitude. This air is very dry, having lost its moisture at the equator. As it heats it takes up even more moisture, causing intense evaporation at the earth's surface and producing a subtropical belt of deserts centered between 15° and 30° north (deserts of the American southwest, Saharan Africa, Arabian Peninsula, and India). The air then flows southward toward the equator, picking up moisture as it moves across the ocean, and being deflected to the right as the northeast trade winds. The cycle in this cell is completed when the air, now laden with moisture, reaches the equator.

A second circulation cell between 30° and 60° north arises when cool air sinking at around 30° moves northward at the surface. At 50° to 60° north it encounters cold air moving south from the North Pole, producing an unstable stormy area with abundant precipitation. The warmer air from the south is deflected upward and turns south at high altitude to complete the second cell. A third, polar cell forms when cold, southward-moving Arctic air returns to the pole at high altitude.

The principal terrestrial biomes are temperate deciduous forest, temperate coniferous forest, tropical forest, grassland, tundra, and desert. In this brief survey, we will refer especially to the biomes of North America and will consider predominant features of each.

Temperate Deciduous Forest

The temperate deciduous forest, best developed in eastern North America, encompasses several forest types that change gradually from the northeast to the south. Deciduous, broad-leaved trees such as oak, maple, and beech that shed their leaves in winter predominate. Seasonal aspects are better defined in this biome than in any other. The deciduous habit is an adaptation of dormancy for low-energy levels from the sun in winter and freezing winter temperatures. In summer, the relatively dense forests form a closed canopy that creates deep shade below. Consequently there has been a selection for understory plants that grow rapidly in the spring and flower early before the canopy develops. The mean annual precipitation is relatively high (75 to 125 cm, or 30 to 50 inches), and rain falls periodically throughout the year. Mean annual temperatures range between 5° and 18° C (41° to 65° F).

Animal communities in deciduous forests respond to seasonal change in various ways. Some, such as the insect-eating warblers, migrate. Others, such as woodchucks, hibernate during winter months. Others that are unable to escape survive by using available food (for example, deer) or stored food supplies (for example, squirrels). Hunting and habitat loss have eliminated virtually all the large carnivores that once roamed eastern

Figure 39-7
A bull moose browses on dwarf birch in the coniferous forest biome. Note shedding of antler skin ("velvet"), signifying that antler growth is complete and that breeding season is approaching.

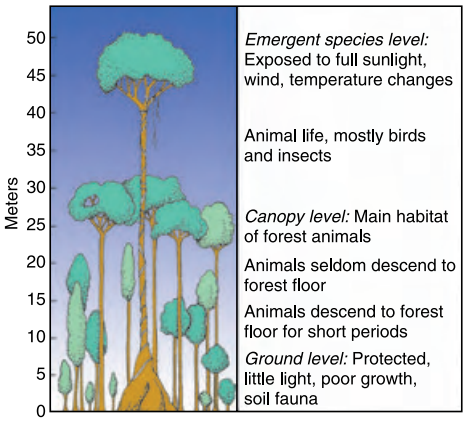

Figure 39-8
Profile of tropical forest, showing stratification of animal and plant life into six strata. The animal biomass is small compared with the biomass of the trees.

forests, such as mountain lions, bobcats, and wolves. Deer, on the other hand, thrive in second-growth forests under protection of strict hunting management. Insect and invertebrate communities are abundant in deciduous forests because decaying logs and forest floor litter provide excellent shelter.

Heavy exploitation of the deciduous forests of North America began in the seventeenth century and reached a peak in the nineteenth century. Logging removed nearly all of the once-magnificent stands of temperate hardwoods. With the opening of the prairie for agriculture, many eastern farms were abandoned and allowed to return gradually to deciduous forests.

Coniferous Forest

In North America coniferous forests form a broad, continuous, continent-wide belt stretching across Canada and Alaska, and south through the Rocky Mountains into Mexico. This biome continues across northern Eurasia, making it one of the largest plant formations on earth. It is dominated by evergreens—pine, fir, spruce, and cedar—which are adapted to withstand freezing and take full advantage of short summer growing seasons. Conical trees with their flexible branches shed snow easily. The northern area is the **boreal** (northern) **forest,** often called **taiga** (a Russian word, pronounced "tie-ga"). The taiga is dominated by white and black spruce, balsam, subalpine fir, larch, and birch. Mean annual precipitation is less than 100 cm (40 inches) and the average temperature ranges from −5° to +3° C (23° to 37° F).

In the central region of North America, the taiga merges into **lake forest,** dominated by white pine, red pine, and eastern hemlock. However, most of this forest was destroyed by exploitive logging and was replaced by shrubby second growth, which still characterizes much of Michigan, Wisconsin, southern Ontario, and Minnesota today. The large **southern evergreen forests** occupy much of the southeastern United States. The last old growth coniferous forests of the Pacific northwest are rapidly falling to commercial logging.

Mammals of the boreal and lake coniferous forests are deer, moose (Figure 39-7), elk, snowshoe hare, a variety of rodents, carnivores such as wolves, foxes, wolverines, lynxes, weasels, and martins, and the omnivorous bears. They are adapted physiologically or behaviorally for long, cold, snowy winters. Common birds are chickadees, nuthatches, warblers, and jays. One bird, the red crossbill, has a beak specialized for picking seeds from cones. Mosquitoes and flies are pests to both animals and humans in this biome. Southern coniferous forests lack many mammals found in the north, but they have more snakes, lizards, and amphibians.

Tropical Forest

The worldwide equatorial belt of tropical forests is an area of high rainfall (more than 200 cm [80 inches] per year), high humidity, relatively high and constant temperatures averaging more than 17° C (63° F), and little seasonal variation in day length. These conditions have nurtured luxurious, uninterrupted growth that reaches its greatest intensity in rain forests. In sharp contrast to temperate deciduous forests, dominated as they are by relatively few tree species, tropical forests contain thousands of species, none of which is dominant. A single hectare typically contains 50 to 70 tree species as compared with 10 to 20 tree species in an equivalent area of hardwood forest in the eastern United States. Climbing plants and epiphytes are common among the trunks and limbs. A distinctive feature of tropical forests is stratification of life into six, and occasionally as many as eight, feeding strata (Figure 39-8).

Insectivorous birds and bats occupy the air above the canopy; below it birds, fruit bats, and mammals feed on leaves and fruit. In the middle zones are arboreal mammals (such as monkeys and tree sloths), numerous birds, insectivorous bats, insects, and amphibians. A middle zone of climbing animals, such as squirrels and civets, range up and down the trunks, feeding from all strata. On the ground are large mammals lacking climbing ability, such as the large rodents of South America (for example, capybara, paca, and agouti) and members of the pig family. Finally, a mixed group of small insectivorous, carnivorous, and herbivorous animals searches the litter and lower tree trunks for food. No other biome can match tropical forests in incredible variety of animal species. Food webs are intricate and notoriously difficult for ecologists to unravel.

Tropical forests, especially the enormous expanse centered in the Amazon Basin, are the most seriously threatened of forest ecosystems. Large areas are being cleared for agriculture by "slash-and-burn" methods, but, because of low soil fertility, farms are soon abandoned. It may seem paradoxical that a biome as luxuriant as a tropical forest should have poor soil. This occurs because nutrients released by decomposition are rapidly recycled by plants, leaving no reservoir of humus. In many areas, once the plants are removed, the soil rapidly becomes a hard, bricklike crust called **laterite.** Tropical plants cannot recolonize such areas.

Each month an area of undisturbed tropical forest the size of Massachusetts is converted to other uses. Unlike forest clearing in temperate zones, which made possible sustained, productive agriculture, tropical soils quickly become depleted, forcing farmers to move on to clear more forest. Other pressures on tropical forests include logging by multinational timber companies, which cut large tracts of timber to make furniture for developed countries, and clearing of land for cattle ranching.

Figure 39-9
Bison grazing on a short-grass prairie.

Grassland

The North American prairie biome is one of the most extensive grasslands in the world, extending from the Rocky Mountain edge on the west to the eastern deciduous forest on the east, and from northern Mexico in the south to the Canadian provinces of Alberta, Saskatchewan, and Manitoba in the north. The original grassland associations of plants and animals have been almost completely destroyed by humans. The prairies today have been transformed into the most productive agricultural region in the world, dominated by monocultures of cereal grains. In grazing lands virtually all the major native grasses have been replaced by alien species. Vast areas of Arizona and New Mexico have been converted from lush grasslands to parched desert by more than a century of livestock overgrazing. Of the once dominant herbivore, bison (Figure 39-9), very few survive, but jackrabbits, prairie dogs, ground squirrels, and antelope remain. Mammalian predators include coyotes, ferrets, and badgers, although, of these, only coyotes are common. Rainfall on the North American prairie ranges from about 80 cm (31 inches) in the east to 40 cm (16 inches) in the west. Average annual temperatures range between 10° and 20° C (50° to 68° F).

Tundra

The tundra is characteristic of severe, cold climatic regions, especially treeless Arctic regions and high mountaintops. Plant life must adapt itself to a short growing season of about 60 days and to a soil that remains frozen for most of the year. Average annual precipitation is usually less than 25 cm (10 inches) and the annual temperature averages about −10° C (14° F).

Most tundra regions are covered with bogs, marshes, ponds, and a spongy mat of decayed vegetation, although high tundras may be covered only with lichens and grasses. Despite the thin soil and short growing season, vegetation of dwarf woody plants, grasses, sedges, and lichens may be quite profuse. Plants of the alpine tundra of high mountains, such as the Rockies and Sierra Nevadas, differ from the Arctic tundra in some respects. Characteristic animals of the Arctic tundra are the lemming, caribou (Figure 39-10), musk-ox, arctic fox, arctic hare, ptarmigan, and (during the summer) many migratory birds.

Desert

Deserts are arid regions where rainfall is low (less than 25 cm [10 inches] a year), and water evaporation is high. The North American desert is of two parts,

Figure 39-10
A large male caribou on the Alaskan tundra. The gregarious caribou travel in large herds, feeding in summer on grasses, dwarf willow, and birch, but in winter almost exclusively on lichen.

the hot deserts of the southwest (Mohave, Sonoran, and Chihuahuan) and the cool, high desert in the rain shadow of the High Sierras and the Cascade mountains. Desert plants, such as thorny shrubs and cacti, have reduced foliage, drought-resistant seeds, and other adaptations for conserving water. Many large desert animals have developed remarkable anatomical and physiological adaptations for keeping cool and conserving water (p. 679). Most smaller animals avoid the most severe conditions by living in burrows or developing nocturnal habits. Mammals found there include mule deer, peccary, cottontail, jackrabbit, kangaroo rat, and ground squirrel. Typical birds are roadrunner, cactus wren, turkey vulture, and burrowing owl. Reptiles are numerous, and a few species of toads are common. Arthropods include a great variety of insects and arachnids.

Deserts are expanding rapidly. Between 1882 and 1952 the area of the earth's land surface occupied by desert increased from an estimated 9.4 to 23.3%. Since 1965, 650,000 km^2 of grazing land was added to the Sahara Desert of Africa, the largest desert on earth, because of an extended drought combined with overgrazing by livestock.

Aquatic Environments

Inland Waters

Of all the water in the world, a mere 2.5% is fresh water. Most fresh water is contained in polar ice caps, or stored underground in aquifers and soil moisture, leaving only 0.01% of the world's inland waters available as habitat for aquatic life. Yet a quarter of the world's vertebrates and nearly half of its fishes live in these fragile "islands" of water—water that must also supply human needs for irrigation, drinking water, hydroelectric power, and waste disposal.

Inland waters are divided broadly into running-water, or **lotic** (L. *lotus,* action of washing) habitats, and standing-water, or **lentic** (L. *lentus,* slow) habitats. Lotic habitats follow a gradient from mountain brooks to streams and rivers. Brooks and streams with high-velocity water flow are high in dissolved oxygen because of their turbulence. Energy input is chiefly in the form of organic detritus washed from adjacent terrestrial areas. More slowly moving rivers have less dissolved oxygen and more floating algae and plants. Their fauna is tolerant of lower oxygen concentration.

Lentic habitats, such as ponds and lakes, tend to have still lower concentrations of oxygen, particularly in the deeper areas. Animals living on the bottom or on submerged vegetation **(benthos)** include snails and mussels, crustaceans, and a wide variety of insects. Many swimming forms, called **nekton,** are found in lakes and larger ponds. Depending on the nutrients available, a large contingent of small floating or weakly swimming plants and animals **(plankton)** may occur. Ponds and lakes have short lifespans—a few hundred to many thousands of years depending on size and rate of sedimentation—and undergo great physical change as they age. The Great Lakes of North America, which occupy depressions gouged out by the glacial advances of the Pleistocene epoch, became ice free about 5000 years ago.

A striking exception to the short lifetimes of most lakes is Lake Baikal in southern Siberia. This enormous lake, 1741 m deep (more than 1 mile), is by far the oldest lake in the world, dating from at least the Paleocene—more than 60 million years BP. The speciation of sculpins in Lake Baikal is illustrated in Figure 6-20, p. 118.

Many freshwater habitats have been severely damaged by human pollution such as dumping of toxic industrial wastes and enormous quantities of sewage. Of the Great Lakes, Lake Erie has been the most seriously affected by the inflow of large amounts of nitrates and phosphates. These nutrients fertilize the lake, creating huge blooms of algae that die and sink to the bottom to decompose and rob the lake of oxygen. As a result, all levels of aquatic life are adversely affected.

Oceans

By almost any measure, oceans represent by far the largest portion of the earth's biosphere. They cover 71% of the earth's surface to an average depth of 3.75 km (2.3 miles), with their greatest depths reaching to more than 11.5 km (7.2 miles) below sea level. The marine world is relatively uniform as compared with land, and in many respects it is less demanding on life

forms. However, the evident monotony of the ocean's surface belies the variety of life below. Oceans are the cradle of life, and this is reflected by the variety of organisms living there—more than 200,000 species of unicellular forms, plants, and animals. The vast majority of these forms, about 98%, live on the seabed **(benthic);** only 2% live freely in the open ocean **(pelagic).** Of the benthic forms, most occur in the intertidal zone or shallow depths of the oceans. Less than 1% live in the deep ocean below 2000 m.

The most productive areas are concentrated along continental margins and a few areas where the waters are enriched by organic nutrients and debris lifted by upwelling currents into the sunlit, or **photic,** zone, where photosynthetic activity occurs. With certain notable exceptions (see box in Chapter 40, p. 834), all life below the photic zone must be supported by the light "rain" of organic particles from above.

Life in the ocean is divided into regions, or provinces, each with its own distinctive life forms (Figures 39-11 and 39-12). The **littoral,** or **intertidal,** zone, where sea and land meet, is paradoxically both the harshest and the richest of all marine environments. It, as well as the animals living there, is subjected to pounding surf, sun, wind, rain, extreme temperature fluctuations, erosion, and sedimentation. Yet because of the diversity of available habitats and the bounteous supply of nutrients, animals such as barnacles, snails, chitons, limpets, mussels, sea urchins, sea stars, and many others flourish there. Below the littoral zone is the **sublittoral,** or **subtidal** zone, which is always submerged. It also supports a rich variety of animal life, as well as forests of brown algae.

An **estuary** is a semienclosed transition zone where fresh water flows into the sea. Despite an unstable salinity caused by the variable entry of fresh water, the estuary is a nutrient-rich habitat that supports a diverse fauna.

The **neritic,** or shallow water, zone surrounds the continents and extends to the edge of the continental shelf—approximately to a depth of 200 m (Figure 39-11). This zone is more productive than the open ocean because it benefits from nutrients delivered by rivers and by upwelling at the edge of the continental shelf. Algal growth is prolific, which in turn supports a diverse animal life, including most of the world's fisheries.

Areas of **upwelling,** although small and restricted to a few regions, are vital sources of nutrient renewal for the surface photic zone. Some of the world's most productive fisheries are—or were—centered on upwelling regions. Before its collapse in 1972, the Peruvian anchovy fishery, which depended on the Peru Current, provided 22% of all fish caught in the world! Earlier, the California sardine fishery and the Japanese herring fishery, both fisheries of upwelling regions, were intensively harvested to the point of collapse and have never recovered. The world's fisheries today are seriously imperiled due to overfishing, degradation of fish habitats by trawling, wasteful fishing methods, and marine pollution. Some of the world's greatest fishing grounds, such as the Grand Banks and Georges Banks of eastern North America, have been fished to total collapse. As our demand for food from the sea rises, fish are being extracted much faster than fish populations can reproduce.

The vast open ocean is known as the **pelagic** realm (Figure 39-12). Despite its size (comprising 90% of the total oceanic area), the pelagic realm is relatively impoverished biologically because, as organisms die, they sink out of the photic zone, carrying nutrients into the bathypelagic zone where they are immobilized. However, in areas of upwelling and where oceanic

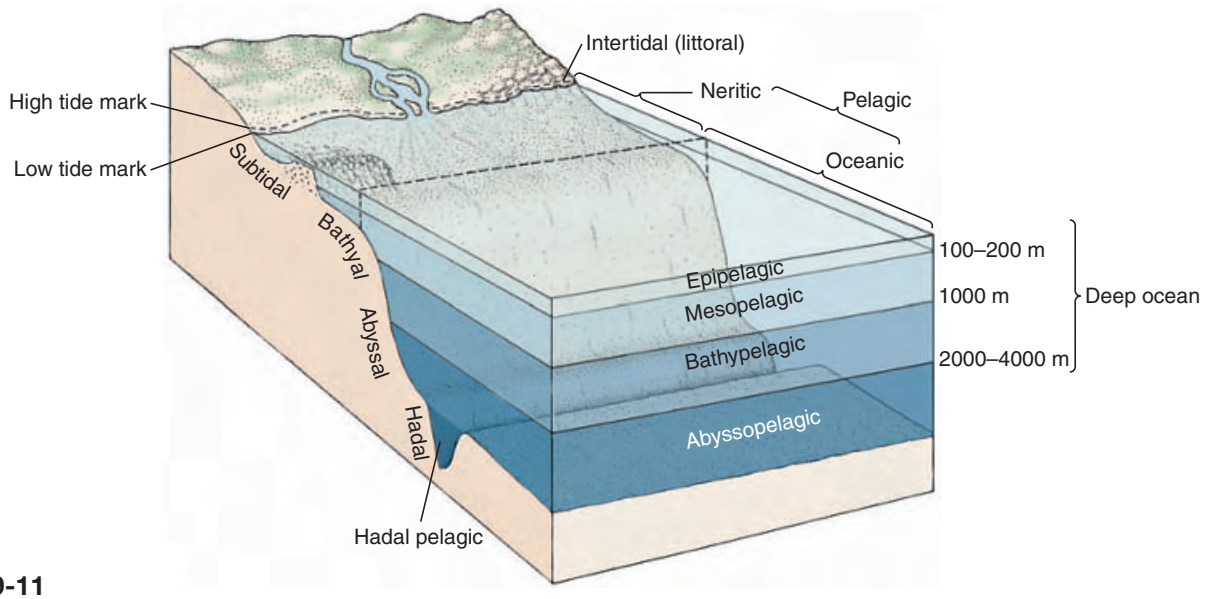

Figure 39-11
Major marine zones.

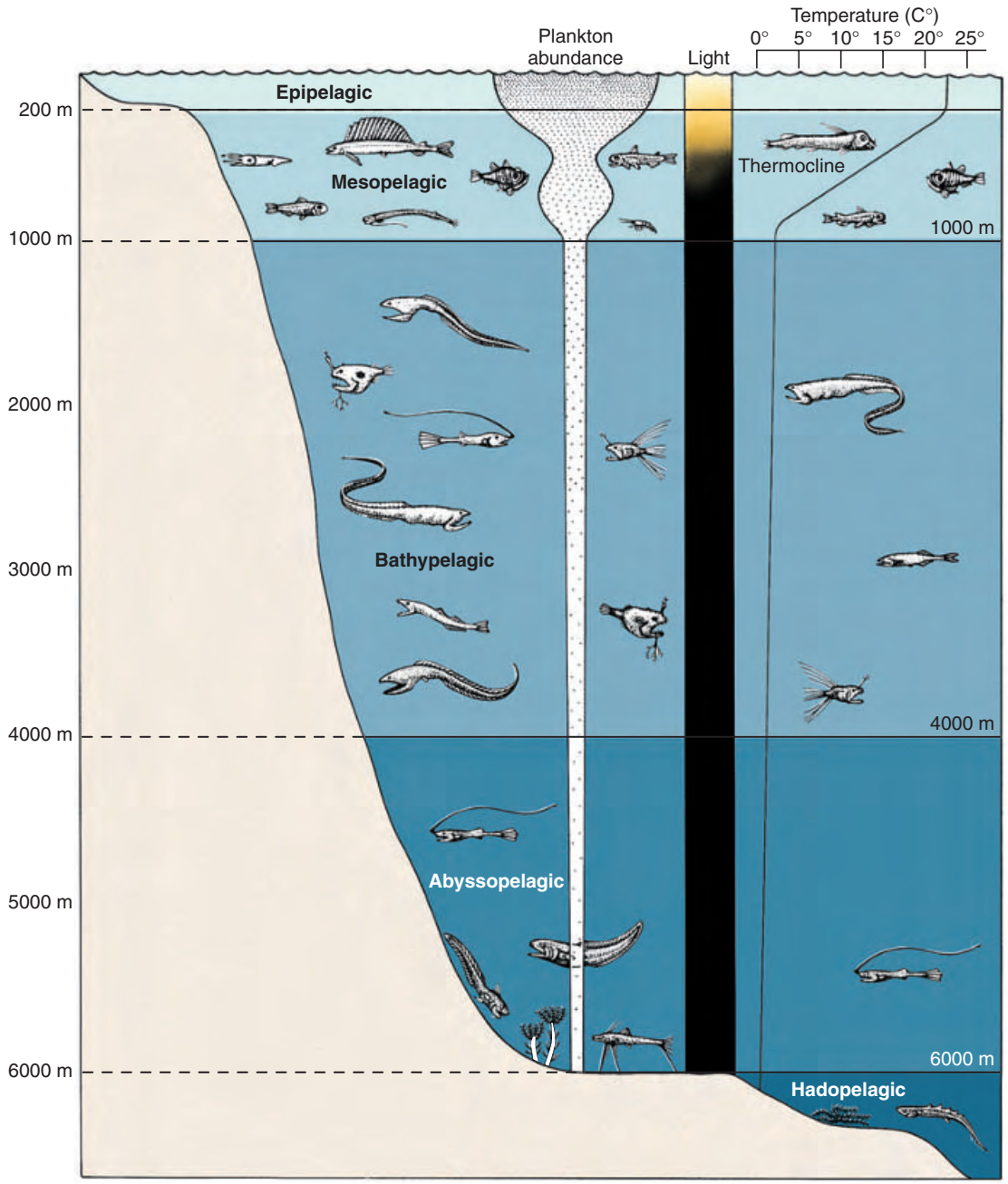

Figure 39-12

Life of the pelagic zones. Each zone supports a distinct community of organisms. Animals in zones below the mesopelagic depend on the meager rain of food that sinks out of the epipelagic and mesopelagic zones.

currents converge, nutrients are replenished and productivity may be high. The enormously productive polar seas are an example. Before their populations were overexploited by humans, baleen whales probably consumed around 77 million tons of Antarctic krill (a shrimplike animal, Figure 19-27, p. 405) per year, far more than the entire catch of all fish, crustaceans, and molluscs taken by all the world's fishing fleet in any single year. The enormous krill population was sustained by phytoplankton, the base of the food chain (p. 836), which in turn flourished because of the abundance of nutrients in the Antarctic sea.

Below the surface, or **epipelagic,** layers of the pelagic realm are the great ocean depths, characterized by enormous pressure, perpetual darkness, and a constant temperature near 0° C. It remained a world unknown to humans until recently, when baited cameras, bathyscaphs, and deep-water trawls have been lowered to view and sample the ocean bottom. There are several distinct habitats in the ocean depths (Figure 39-12). The **mesopelagic** is the "twilight zone,"

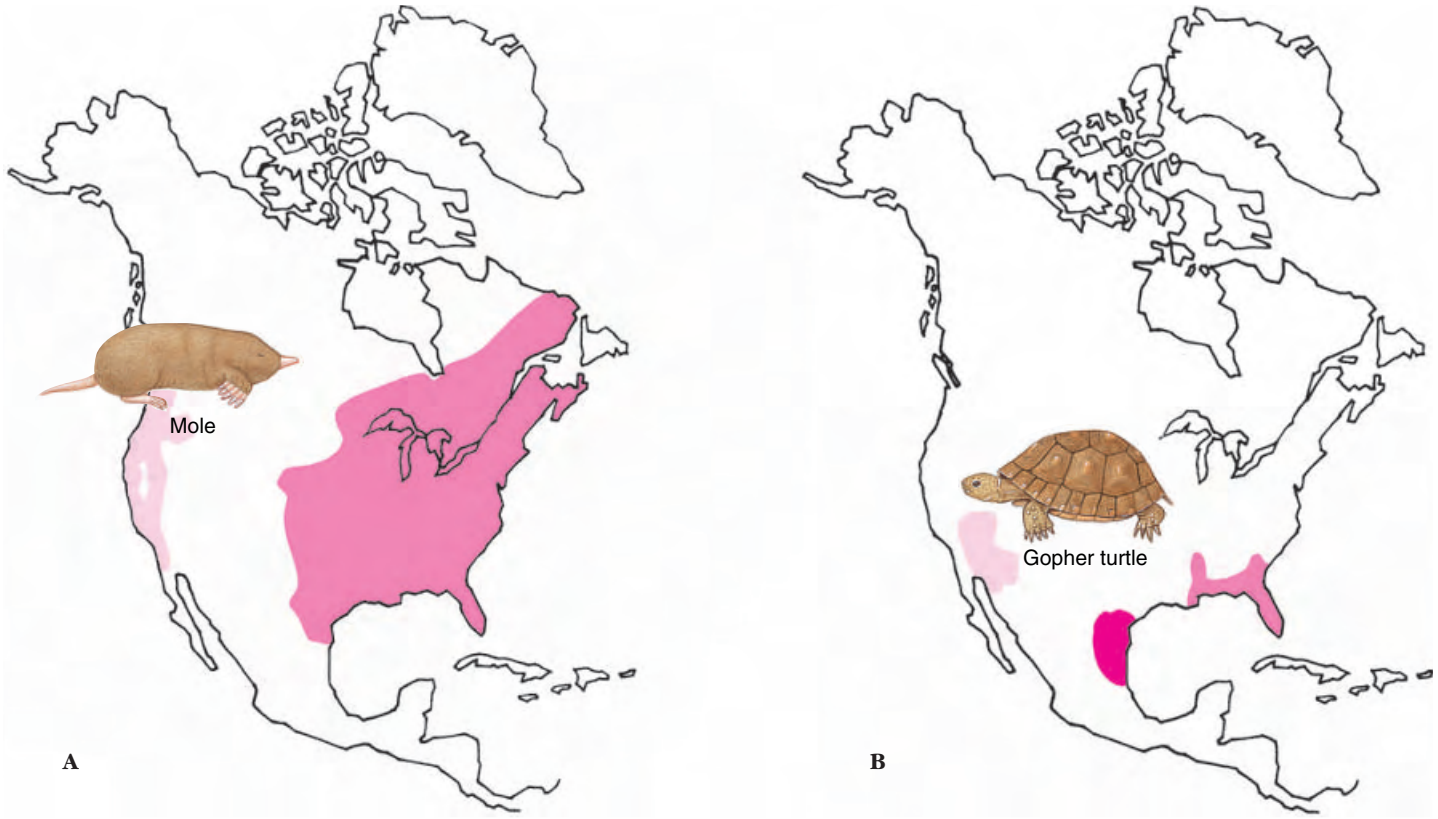

Figure 39-13
Disjunct distributions in North America. **A,** Moles of the family Talpidae probably entered North America across the Bering land bridge that once joined North America and Asia during the Tertiary period. Eastern and western populations are now separated by the Rocky Mountains. **B,** Gopher turtles of the genus *Gopherus* are now separated into three fully isolated populations.

which receives dim light and supports a varied community of animals. Below the mesopelagic is a world of perpetual darkness, divided into three depth zones as shown in Figure 39-12: bathypelagic, abyssopelagic, and hadopelagic. Deep-sea forms depend on that meager portion of the gentle rain of organic debris from above that escapes consumption by organisms in the water column. On the sea floor exists the benthos, represented by sea anemones, sea urchins, crustaceans, polychaete worms, and fishes—indeed nearly all major metazoan groups. Most are deposit feeders characterized by very slow growth (because of scarcity of food) and long lives.

Recently self-contained benthic communities of animals that are completely independent of solar energy and the rain of organic debris from above were discovered adjacent to vents of hot water issuing from rifts in the ocean floor (see box in Chapter 40, p. 834).

Animal Distribution (Zoogeography)

The study of zoogeography tries to explain why animals are distributed as they are, their patterns of dispersal, and the factors responsible for their dispersal. Most animals typically occupy limited geographic areas. Humans, however, and creatures such as house mice and cockroaches that share human habitations, are able to live almost anywhere on earth. It is not always easy to explain why animals are distributed as they are, since similar habitats on separate continents may be occupied by quite different kinds of animals. A particular species may be absent from a region that supports similar animals because of barriers that prevent it from getting there or because established populations of other animals prevent it from colonizing.

Thus we would like to discover why animals are found where they are or are not found where one thinks they ought to be. Usually this means studying the past. The fossil record plainly shows that animals once flourished in regions from which they are now absent. Extinction has played a major role, but many groups left descendants that migrated to other regions and survived. For example, ancestors of camels originated in North America, where their fossils are found. They spread during the Pleistocene epoch by way of Alaska to Eurasia and Africa, where they are represented today by true camels, and to South America, where their descendants survive as llamas, alpacas, guanacos and vicuñas. (The Pleistocene began

about 1.7 million years BP and ended about 11 thousand years BP; see the geological time table on the back inside-cover.) Then camels became extinct in North America about 10,000 years BP at the close of the Ice Age. Thus the history of an animal species or its ancestor must be known before one can understand why it lives where it does. The earth's surface is undergoing constant change. Many areas that are now land were once covered with seas; fertile plains may be claimed by advancing desert; impassable mountain barriers may arise where none existed before; or inhospitable ice fields may retreat before a warmer climate to be replaced by forests. Geological change has been responsible for much of the alteration in animal (and plant) distribution and has been a powerful influence in shaping organic evolution.

Disjunct Distributions

A major problem for zoogeographers is to explain the numerous instances of discontinuous or **disjunct distributions:** closely related species living in widely separated areas of a continent, or even the world (Figure 39-13). How could a group of animals become so dispersed geographically? There are two possible ways for a disjunct distribution to arise. Either a population moves from its place of origin to a new location **(dispersal),** traversing intervening territory that is unsuited for long-term colonization, or the environment changes, breaking a once continuously-distributed species into geographically separated populations **(vicariance).** Vicariance may involve climatic changes that contract and fragment the areas of habitat favorable for a species, or it may involve physical movement of landmasses or waterways that carry different populations of a species away from each other.

Distribution by Dispersal

By dispersal, animals spread into new localities from their places of origin. Dispersal involves *emigration* from one region and *immigration* into another. Dispersal is a *one-way,* outward movement that must be distinguished from *periodic* movement back and forth between two localities, such as seasonal migration of many birds. Dispersing animals may move actively under their own power, or they may be passively dispersed by wind, by floating or rafting on rivers, lakes, or the sea, or by hitching rides on other animals. Animals are expected to expand their geographic distributions in this manner across all favorable habitat that is accessible to them. For example, as the last Pleistocene glaciers retreated northward, habitats favorable for many temperate species became available on formerly glaciated territory in North America, Europe, and Asia. Species that originated immediately south of the glaciated territory prior to glacial retreat then expanded northward as new habitats appeared. Because the reproductive rate of animal populations is great, there is a continuous pressure on populations to expand across all favorable habitats.

Dispersal easily explains the movement of animal populations into favorable habitats that are geographically adjacent to their places of origin. This movement produces an expanded but geographically continuous distribution. Can dispersal also explain the origins of geographically disjunct distributions? For example, flightless ratite birds (Figure 39-14) inhabit disjunct landmasses primarily of the Southern Hemisphere including Africa, Australia, Madagascar, New Guinea, New Zealand, and South

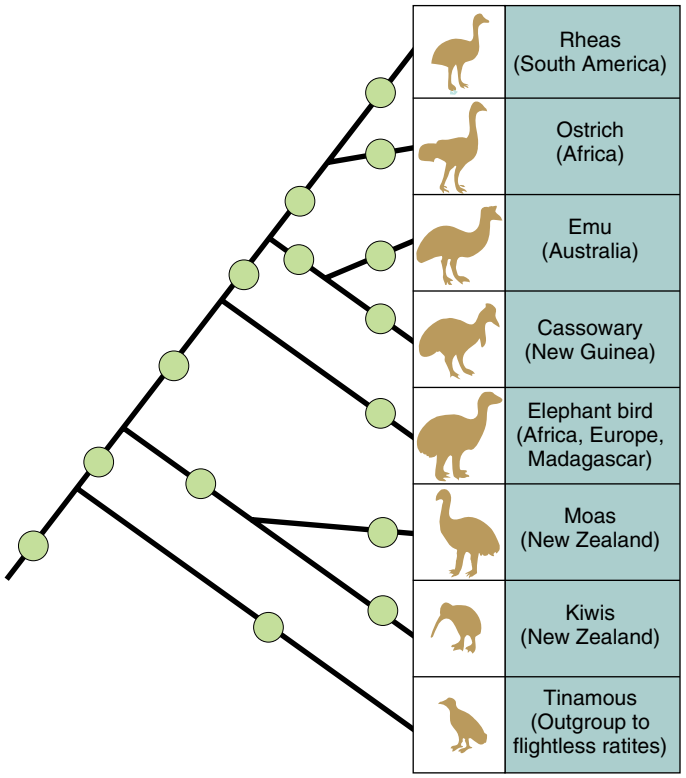

Figure 39-14

The phylogenetic relationships inferred for flightless birds (Chapter 6, pp. 114–115). Vicariance biogeography proposes that these flightless species descended from an ancestral species that was widespread in the Southern Hemisphere when Africa, Australia, Madagascar, New Guinea, New Zealand, and South America were connected. By moving apart, these landmasses fragmented both themselves and the flightless populations they contained. If the vicariance hypothesis is correct, the phylogenetic branching sequence inferred for the allopatric flightless species reflects the sequence by which their landmasses broke apart from each other. This hypothesis is tested by looking for similar phylogenetic patterns in other groups of animals and plants whose ancestral populations would have been fragmented by the same geological events. The widespread geographic distribution of the elephant bird suggests that it has dispersed following the fragmentation of landmasses.

America. These landmasses are separated from each other by ocean, a very strong barrier to ratite dispersal. To explain this distribution by dispersal, one must postulate a **center of origin** from which the group dispersed to reach all of the widely separated landmasses on which it is now found. Because ratites do not fly, a dispersalist hypothesis requires intermittent, passive rafting of individuals across the ocean. Is this hypothesis reasonable? We know from studies of the Galápagos Islands and Hawaii (Chapter 6) that occasional, long-distance dispersal of terrestrial animals and plants across oceans does occur. This is the only way that terrestrial animals could colonize islands produced by oceanic volcanoes. For flightless birds and many other discontinuously distributed animals, however, there is an alternative to the hypothesis that disjunct distribution was produced by dispersal over unfavorable habitat. This is the hypothesis of vicariance (L. *vicarius,* a substitute).

Distribution by Vicariance

Disjunct distributions of animals may be created by physical changes in the environment that cause formerly continuous habitats to become disjunct. Areas that were once joined may become separated by barriers that are effectively impenetrable for many animals that inhabit them. The study of fragmentation of biotas in this manner is called **vicariance biogeography.** At the species level, "vicariance" is often used as a synonym of "allopatry," which is simply a distribution of populations in geographically separated areas p. 116–117. Lava flows from a volcano may cause a formerly continuous forest to become separated into geographically discontinuous patches, thereby breaking many species of plants and animals into geographically isolated populations.

Perhaps the most dramatic vicariant phenomenon in the earth's history is continental drift, through which a once continuous landmass was sequentially broken into continents and islands separated by ocean (see the following text). All terrestrial and freshwater animal species that had spread across the initially continuous landmass became sequentially fragmented into many populations on different continents and islands separated by ocean. Vicariance by continental drift gives us another hypothesis for explaining the disjunct distribution of flightless birds; they may descend from an ancestral species that was widespread in the Southern Hemisphere when Africa, Australia, Madagascar, New Guinea, New Zealand, and South America were in closer contact than they are today. When these landmasses moved apart across the ocean, the ancestral species would have fragmented into disjunct populations that evolved independently, producing the diversity of forms that we observe today.

How do we test hypotheses of vicariance biogeography? Reconstructing past histories of environmental changes might seem impossible, but we do have a very powerful method for testing such hypotheses, and it is based on the systematic methods presented in Chapter 10.

Suppose that the different species of flightless birds evolved allopatrically as continental drifting sequentially broke their terrestrial environment into isolated pieces. If we construct a cladogram or phylogenetic tree of these birds as shown in Figure 39-14, the earliest divergence should correspond to the first vicariant event that fragmented their common ancestral species. All subsequent branching events on the tree should correspond sequentially to subsequent vicariant events that fragmented major lineages further. Our tree hypothetically reconstructs the history of vicariant events for the group. If we erase the names of the species from the terminal branches of the tree and replace them with the geographic areas in which each species is found, we have a hypothesis for the sequential separation of the different geographic areas. We can test this vicariant hypothesis further by identifying other groups of terrestrial organisms that have different species in each of the same geographic areas as flightless birds. If our hypothesis is correct, these groups were fragmented geographically by the same vicariant events that fragmented the flightless birds. We therefore predict that the cladogram or phylogenetic trees constructed for species in the other groups will show the same branching pattern as the flightless bird tree when we replace the species names with those of the areas they inhabit. If this hypothesis is confirmed, we have a **general area cladogram** that depicts the history of fragmentation of the different geographic areas studied. This general area cladogram can be investigated further using geological and climatic studies.

In many groups of organisms, it is likely that both vicariant and dispersal events have contributed to the evolution of disjunct distributional patterns. Methods of vicariance biogeography will be very useful for finding such cases. Indeed, the cladogram of flightless birds is not just a simple grouping of birds that inhabit nearby areas. We can ask whether any branches on a cladogram representing a particular group of species are inconsistent with the general area cladogram for geographic areas that the species inhabit. Suppose that the cladogram for a particular taxon is consistent with the area cladogram except for placement of a single branch. We explain most of the geographic disjunctions within the taxon by vicariance but look for dispersal to explain the single branch that is not compatible with the general area cladogram. In this way, we can focus our study of dispersal on specific cases in which it is most likely to have occurred.

Continental Drift Theory

It is no accident that the current enthusiasm for vicariance biogeography coincides with the recent acceptance of the continental drift theory by geologists. The continental drift theory is not new (it was proposed in 1912 by the German meteorologist Alfred Wegener), but it remained controversial and largely

neglected until the newly proposed theory of **plate tectonics** provided a mechanism to account for drifting continents (unfortunately, Wegener did not live to see his hypothesis accepted). According to the theory of plate tectonics (tectonics means "deforming movement"), the earth's surface is composed of 6 to 10 rocky plates, about 100 km thick, that shift about on a more malleable underlying layer. Wegener proposed that the earth's continents had been drifting like rafts following the breakup of a single great landmass called Pangaea ("all land"). According to recent workers who have considerably revised Wegener's dating, the original breakup of Pangaea occurred approximately 200 million years ago. Two great supercontinents were formed: a northern Laurasia and a southern Gondwana, separated from each other by the Tethys Sea (Figure 39-15). At the end of the Jurassic period, some 135 million years ago, the supercontinents began to fragment and drift apart. Laurasia split into North America, most of Eurasia, and Greenland. Gondwana split into South America, Africa, Madagascar, Arabia, India, Southeast Asia, Australia, and Antarctica. This theory is supported by the appearance of fit between the continents, by airborne paleomagnetic surveys, by seismographic studies, by the presence of mid-ocean ridges where the tectonic plates are born, and by a wealth of biological data.

Continental drift explains several otherwise puzzling distributions of animals, such as the similarity of invertebrate fossils in Africa and South America, as well as certain similarities in present-day faunas at the same latitudes on the two continents. However, the continents have been separated for all of the Cenozoic era and probably for much of the Mesozoic era as well, much too long to explain the distributions of some modern organisms such as placental mammals. Continental drift theory is, nevertheless, enormously useful in explaining interconnections between flora and fauna of the past.

The present distribution of marsupial mammals is an excellent example of the influence of continental breakup. Marsupials appeared in the Middle Cretaceous period, about 100 million years BP, probably in South America. Because South America was at that time connected to Australia through Antarctica (which was then much warmer than it is today), the marsupials spread through all three continents. They also moved into North America, but there they encountered placental mammals, which had dispersed to that continent from Asia. Marsupials evidently could not coexist with placentals, and so became extinct in North America. (North American marsupials today, the opossums, are relatively recent arrivals from South America.) Placentals followed marsupials into South America, but by that time the marsupials had expanded and were too firmly established to be driven into extinction. In the meantime, about 50 million years BP, Australia drifted apart from Antarctica, barring entrance to placentals. Australia remained in isolation, allowing marsupials to diversify into the present rich and varied fauna.

Temporary land bridges also have been important pathways of dispersal. An important and well-established land bridge that no longer exists connected Asia and North America across the Bering Strait. It was across this corridor that the placentals moved from Asia into North America.

Today a land bridge connects North and South America at the Isthmus of Panama. But from the mid-Eocene epoch (50 million years BP) to the end of the Pliocene epoch (3 million years BP), the two continents were completely separated by water. During this long period, the major groups of mammals evolved in distinctive directions on each continent. When the land bridge was reestablished at the end of the Pliocene epoch, a tide of mammals began to flow in both directions (Figure 39-16). This dispersal has been called the "Great American Interchange," one of the most important minglings of distinct continental faunas in the earth's history. For a period both continents gained in mammalian diversity, but the extinction of large numbers of mammals on both continents soon followed. North American carnivores such as raccoons, weasels, foxes, dogs, cats (including sabercats), and bears began preying on South American mammals, which previously had evolved in an environment free of carnivores. Other North American invaders included hoofed mammals (horses, tapirs, peccaries, llamas, deer, antelopes, and mastodonts), rabbits, and several families of rodents. These mammals displaced many South American residents occupying similar habitats. Today nearly half of South American mammals are descendants of recent North American invaders. Only a few South American invaders survived in North America: porcupines, armadillos, and opossums. Several other South American groups, including giant ground sloths, glyptodonts, anteaters, giant aquatic capybaras, toxodonts (rhino-sized plant eaters), and giant armadillos, entered North America but subsequently became extinct there.

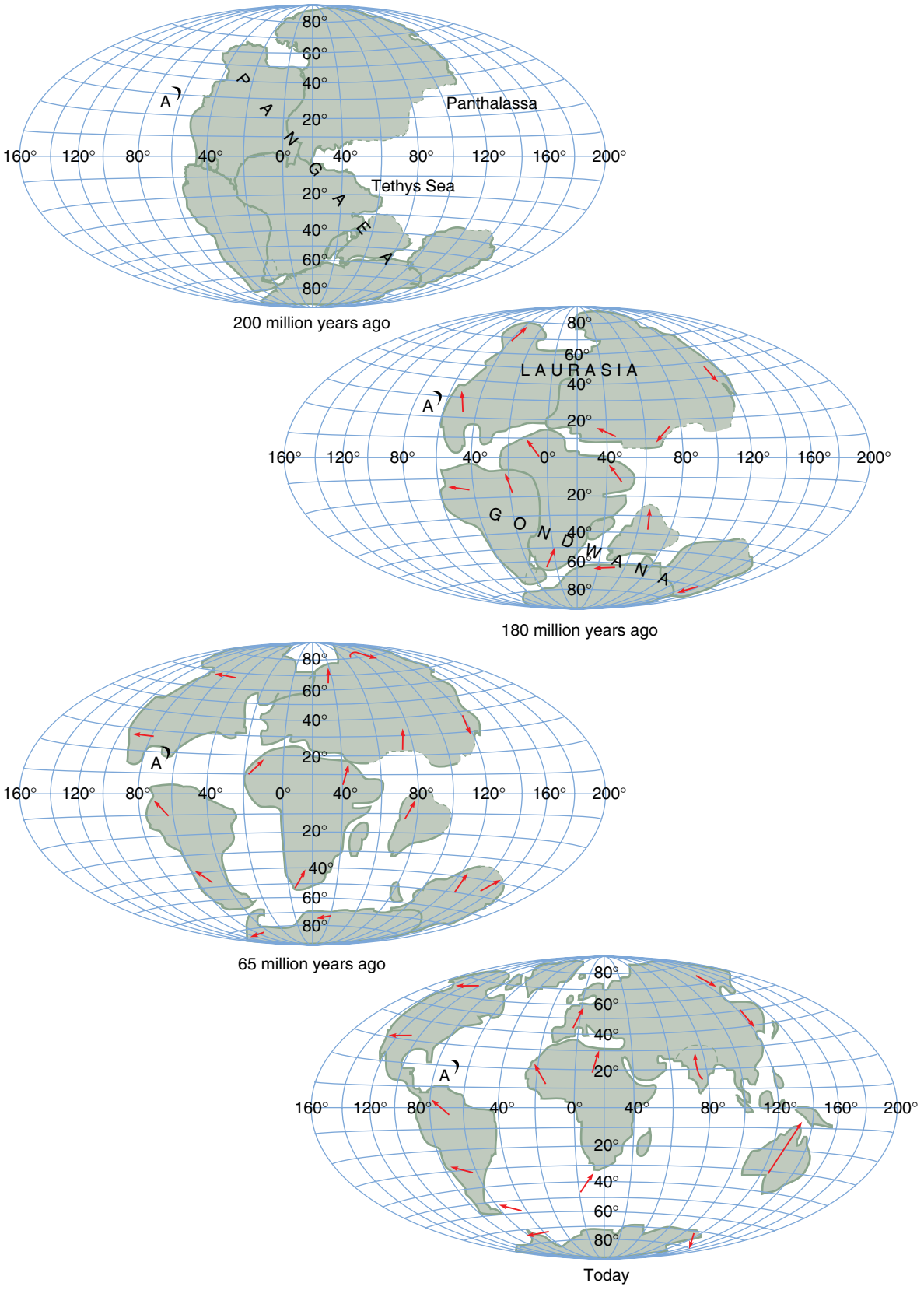

Figure 39-15
Hypothesized drift of continents over the past 200 million years from an original single landmass to their present positions. The universal landmass Pangaea first separated into two supercontinents (Laurasia and Gondwana). These later separated into smaller continents. The arrows indicate vector movements of the continents. The black crescent labeled A is a modern geographical reference point representing the Antilles arc in the West Indies.

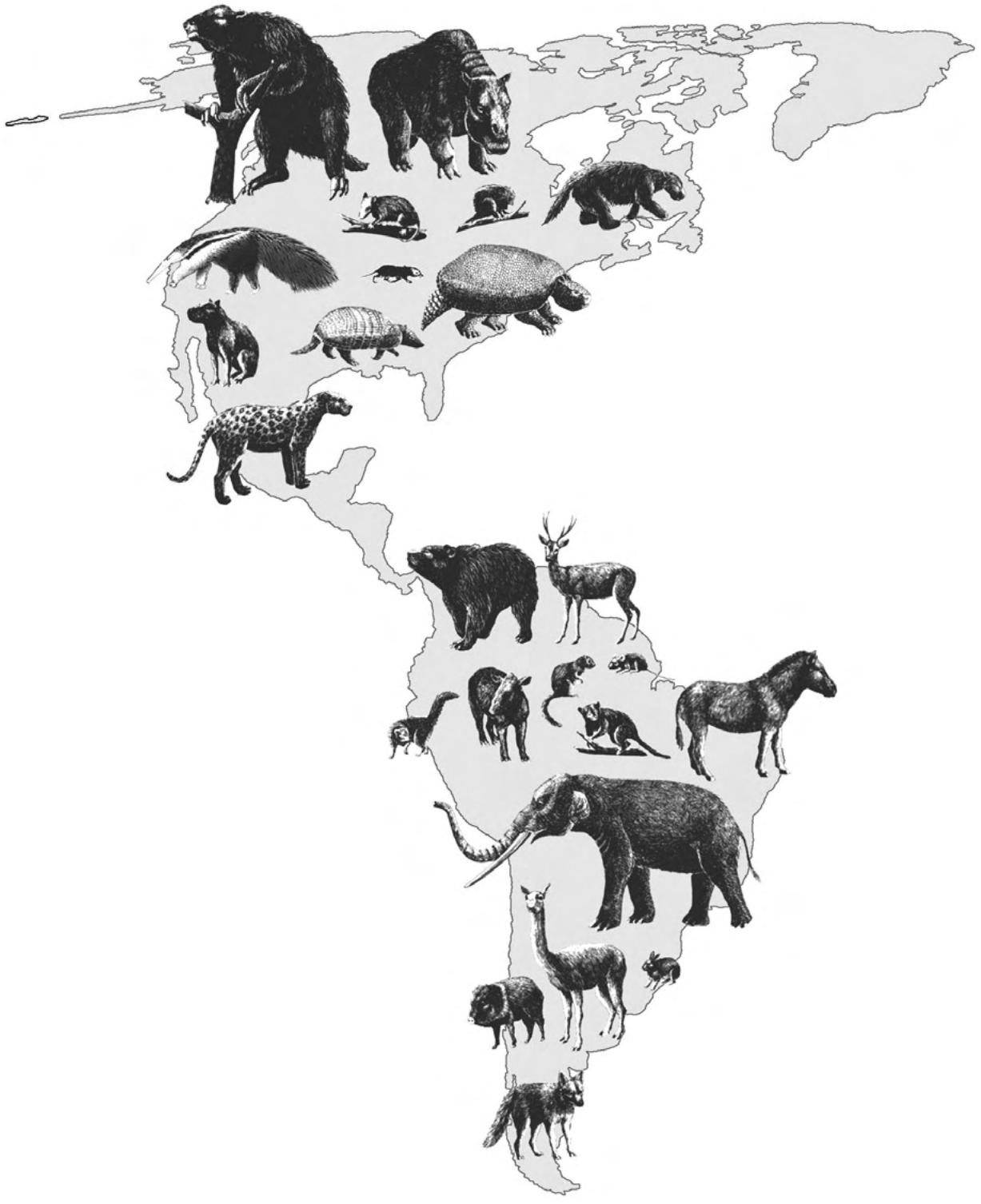

Figure 39-16

The Great American Interchange. The Isthmus of Panama emerged approximately 3 million years ago, permitting the extensive interchange of many families of mammals. At top are representatives of 38 South American genera that walked north across the isthmus. At bottom are representatives of 47 North American genera that migrated to South America. The North American immigrants diversified rapidly after entering South America. South American immigrants to North America diversified little and most became extinct.

Summary

The biosphere is a thin life-containing blanket surrounding the earth. The presence of life on earth is possible because numerous conditions for life are fulfilled on this planet. These include a steady supply of energy from the sun, presence of water, a suitable range of temperatures, the correct proportion of major and minor elements, and the screening of lethal ultraviolet radiation by atmospheric ozone. The earth's environment and living organisms have evolved together, each deeply marking the other.

The biosphere comprises lithosphere, the earth's rocky shell; hydrosphere, the global distribution of water; and atmosphere, the blanket of gas surrounding the earth.

The earth's terrestrial environment is composed of biomes that bear a distinctive array of plant life and associated animal life. Eastern deciduous forest is characterized by distinct seasons and autumn leaf fall. North of the deciduous forest is coniferous forest, which in its northern range is called taiga, an area dominated by needle-leafed trees adapted for heavy snowfall. Animals of the taiga are adapted for long, snowy winters.

The tropical forest is the richest biome, characterized in part by a great diversity of plant species and the vertical stratification of animal habitats. Most tropical forest soils rapidly deteriorate when the forest is removed.

The most modified biome is grassland, or prairie, which has been converted largely to agriculture and grazing. The tundra biome of the far north and the desert biome are both severe environments for animal life, but they are populated nevertheless with organisms that have evolved appropriate adaptations.

Freshwater habitats include rivers and streams (lotic habitats) and ponds and lakes (lentic habitats). All are geologically ephemeral habitats that are strongly influenced by nutrient input.

Oceans occupy 71% of the earth's surface. The photic, or sunlit, zone supports photosynthetic activity by phytoplankton. A rain of nutrients from the photic zone supports the great diversity of life below on the seabed (benthos). The littoral, or tidal, zone is biologically rich but physically harsh. The neritic, or shallow-water, zone overlying the continental shelf is the locus of the world's great fisheries, which are especially productive in areas of upwelling where nutrients are constantly renewed. The open ocean, or pelagic zone, occupies most of the ocean's area but has low biological productivity.

Zoogeography is the study of animal distribution on earth. Animals have become distributed by dispersal, the spread of populations from the centers of origin, and by vicariance, the separation of populations by barriers. Continental drift, now strongly supported by plate tectonic theory, helps explain how animal groups become geographically separated so that evolutionary diversification can occur. It also explains how certain groups, such as marsupial mammals, can become isolated from others. Temporary land bridges have also served as important pathways for animal dispersal.

Review Questions

1. What are the special conditions on earth that make this planet especially fit for life?
2. What is the justification for saying that the earth and life on it have evolved together and that each has deeply influenced the other?
3. What is the biosphere? How would you distinguish between the following subdivisions of the biosphere: lithosphere, hydrosphere, atmosphere?
4. What is the origin of oxygen on earth? What would happen to the earth's supply of oxygen if photosynthesis were suddenly to cease?
5. What is the evidence that increasing carbon dioxide levels in the atmosphere are responsible for the increase in the "greenhouse effect"?
6. What is a biome? Briefly describe six examples of biomes.
7. What are some very productive marine environments, and why are they so productive?
8. What is the source of nutrients for animals living in the deep-sea habitat?
9. What are some reasons why a species may be absent from a habitat or region to which it should adapt well?
10. Define and distinguish between the alternative explanations for disjunct distributions among animals: dispersal and vicariance.
11. Who first proposed the continental drift theory and what finally convinced geologists that the theory was correct?
12. In what way does continental drift help explain the present distribution of marsupial mammals on earth?
13. What was the Great American Interchange, when did it occur, and what were the results?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Biomes, from the University of Texas. Descriptions of biomes, and links.

Biomes. Pictures and descriptions of biomes.

Ecosystems (Biomes) of Our World.

Introduction to Biomes from Radford University.

OLC Student Center Website

CHAPTER

40

Animal Ecology

Talkeetna Mountain Range, Alaska.

Every Species Has Its Niche

The lavish richness of the earth's biomass is organized into a hierarchy of interacting units: an individual organism, a population, a community, and finally an ecosystem, that most bewilderingly complex of all natural systems. Central to ecological study is the habitat, the spatial location where an animal lives. What an animal does in its habitat, its profession as it were, is its niche: how it gets its food, how it arranges for its reproductive perpetuity—in short, how it survives and stays adapted in the Darwinian sense. A niche is a product of evolution and once it is established, no other species in the community can evolve to exploit exactly the same resources. This illustrates the "competitive exclusion principle": no two species will occupy the same niche. Different species are therefore able to form an ecological community in which each has a different role in their shared environment. ■

In the mid-nineteenth century, the German zoologist Ernst Haeckel introduced the term **ecology,** defined as the "relation of the animal to its organic as well as inorganic environment." Environment here includes everything external to the animal but most importantly its immediate surroundings. Although we no longer restrict ecology to animals alone, Haeckel's definition is still basically sound. Animal ecology is now a highly synthetic science that incorporates everything we know about the behavior, physiology, genetics, and evolution of animals to study the interactions between populations of animals and their environments. The major goal of ecological studies is to understand how these diverse interactions determine geographical distributions and abundance of animal populations. Such knowledge is crucial for ensuring continued survival of many populations when their natural environments are altered by human activity.

Not infrequently the word "ecology" is misused as a synonym for environment, which often makes biologists wince. As people concerned about the environment, we can be environmentalists; a person engaged in the scientific study of the relationship of organisms and their environment is an ecologist. He or she is usually an environmentalist too, but environment is not the same as ecology.

The Hierarchy of Ecology

Ecology is studied as a hierarchy of biological systems in interaction with their environments. At the base of the ecological hierarchy is an **organism.** To understand why animals are distributed as they are, ecologists must examine the varied physiological and behavioral mechanisms that animals use to survive, grow, and reproduce. A near-perfect physiological balance between production and loss of heat is required for the success of certain endothermic species (such as birds and mammals) under extreme temperatures as found in the Arctic or a desert. Other species succeed in these situations by escaping the most extreme conditions by migration, hibernation, or torpidity. Insects, fishes, and other ectotherms (animals whose body temperature depends on heat in the environment) compensate for fluctuating temperatures by altering biochemical and cellular processes involving enzymes, lipid organization, and the neuroendocrine system (p. 677). Thus an animal's physiological capacities permit it to live under changing and often adverse environmental conditions. Behavioral responses are important also for obtaining food, finding shelter, escaping enemies and unfavorable environments, finding a mate, courting, and caring for the young. Physiological mechanisms and behaviors that improve adaptability to the environment assist survival of species. Ecologists who focus their studies at the organismal level are called physiological ecologists or behavioral ecologists.

Animals in nature coexist with others of the same species; these groups are known as **populations.** Populations have properties that cannot be discovered from studying individual animals alone, including genetic variability among individuals (polymorphism), growth in numbers over time, and factors that limit the density of individuals in a given area. Ecological studies at the population level help us to predict the future success of endangered species and to discover controls for pest species.

Just as individuals do not exist alone in nature, populations of different species co-occur in more complex associations known as **communities.** The variety of a community is measured as **species diversity.** The populations of species in a community interact with each other in many ways, the most prevalent of which are **predation, parasitism,** and **competition. Predators** obtain energy and nutrients by killing and eating prey. **Parasites** derive similar benefits from their hosts, but usually do not kill the hosts. Competition occurs when food or space are in limited supply and members of different species interfere with each other's use of their shared resources. Communities are complex because all of these interactions occur simultaneously, and their individual effects on the whole structure often cannot be isolated.

Most people are aware that lions, tigers, and wolves are predators, but the world of invertebrates also includes numerous predaceous animals. These predators include unicellular organisms, jellyfish and their relatives, various worms, predaceous insects, sea stars, and many others.

Ecological communities are biological components of the even larger, more complex entities called **ecosystems.** An ecosystem consists of all of the populations in a community together with their physical environment. The study of ecosystems helps us to understand two key processes in nature, the flow of energy and the cycling of materials through biological channels. The largest ecosystem is the **biosphere,** the thin veneer of land, water, and atmosphere that envelopes the great mass of the planet, and that supports all life on earth (see Chapter 39).

Environment and the Niche

An animal's environment is composed of all conditions that directly affect its chances of survival and reproduction. These factors include space, forms of energy such as sunlight, heat, wind and water currents, and also materials such as soil, air, water, and chemicals. The environment also includes other organisms, which can be an animal's food, or its predators, competitors, hosts, or parasites. The environment thus includes both abiotic (nonliving) and biotic (living) factors. Some environmental factors, such as space and food, are utilized directly by an animal, and these are called **resources.**

A resource may be expendable or nonexpendable, depending on how an

animal uses it. Food is expendable, because once eaten it is no longer available. Food therefore must be continuously replenished in the environment. Space, whether total living area or a subset such as the number of suitable nesting sites, is not exhausted by being used, and thus is nonexpendable.

The physical space where an animal lives, and that contains its environment, is its **habitat.** Size of the habitat is variable and depends upon the spatial scale under consideration. A rotten log is a normal habitat for carpenter ants. Such logs occur in larger habitats called forests where deer also are found. However, deer forage in open meadows, so their habitat is larger than the forest. On a larger scale, some migratory birds occupy forests of the north temperate region during summer and move to the tropics during winter. Thus, habitat is defined by the normal activity exhibited by an animal, rather than by arbitrary physical boundaries.

Animals of any species have certain environmental limits of temperature, moisture, and food within which they can grow, reproduce, and survive. A suitable environment therefore must simultaneously meet all requirements for life. A freshwater clam living in a tropical lake could tolerate the temperature of a tropical ocean, but would be killed by the ocean's salinity. A brittle star living in the Arctic Ocean could tolerate the salinity of the tropical ocean but not its temperature. Thus temperature and salinity are two separate dimensions of an animal's environmental limits. If we add another variable, such as pH, we increase our description to three dimensions (Figure 40-1). If we consider all environmental conditions that permit members of a species to survive and multiply, we define the role of that species in nature as distinguished from all others. This unique, multidimensional fingerprint of a species is called its **niche** (opening essay, p. 822). Dimensions of the niche vary among members of a species, making the niche subject to evolution by natural selection. The niche of a species undergoes evolutionary changes over successive generations.

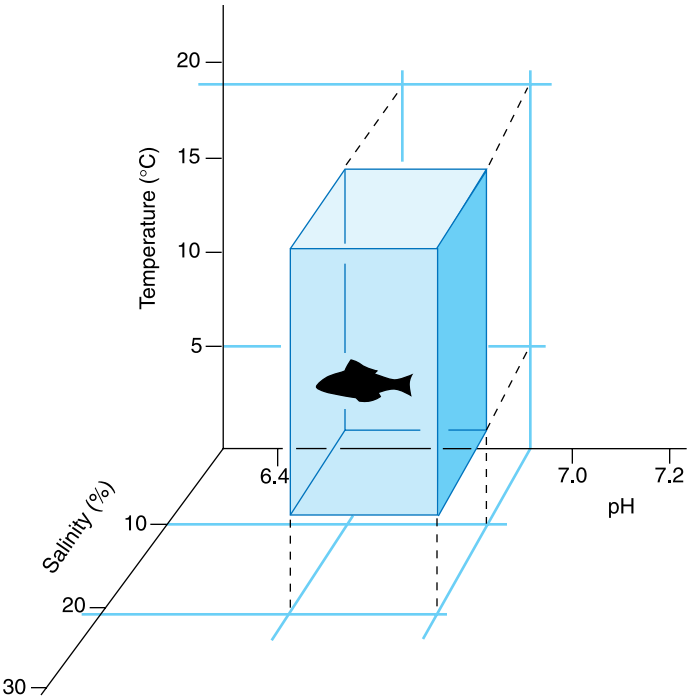


Figure 40-1
Three-dimensional niche volume of a hypothetical animal showing three tolerance ranges. This graphic representation is one way to show the multidimensional nature of environmental relations. This representation is incomplete, however, because additional environmental factors also influence growth, reproduction, and survival.

Animals may be generalists or specialists with respect to tolerance of environmental conditions. For example, most fish are adapted to live in either fresh water or seawater, but not both. However, those that live in salt marshes, such as the minnow *Fundulus heteroclitus,* easily tolerate changes in salinity that occur over tidal cycles in these estuarine habitats as fresh water from the land mixes with seawater. Similarly, whereas most snakes are capable of eating a wide variety of animal prey, others have narrow dietary requirements; for example, the African snake *Dasypeltis scaber* is specialized to eat bird eggs (Figure 34-3, p. 709).

However broad may be the tolerance limits of an animal, it experiences only a single set of conditions at a time. In fact, an animal probably will not experience in the course of its lifetime all environmental conditions that it potentially can tolerate. Thus, we must distinguish an animal's **fundamental niche,** which describes its potential role, and its **realized niche,** the subset of potentially suitable environments that an animal actually experiences.

Populations

Animals exist in nature as members of populations. As we saw in Chapter 6, a population is a reproductively interactive group of animals of a single species (p. 116). A species of animal may comprise a single, cohesive population or may contain many geographically disjunct populations, often called **demes.** Because members of a deme interbreed, they share a common gene pool. Migration of individuals among demes within a species can impart some evolutionary cohesion to the species as a whole.

Each population or deme has a characteristic **age structure, sex ratio,** and **growth rate.** The study of these properties and the factors that influence them is called demography. Demographic characteristics vary according to

the lifestyle of the species under study. For example, some animals (and most plants) are **modular.** Modular animals, such as sponges, corals, and bryozoans, consist of colonies of genetically identical organisms. Reproduction is by asexual **cloning,** as described for hydrozoans in Chapter 13 (p. 260). Most colonies also have distinct periods of gamete formation and sexual reproduction. Colonies propagate also by fragmentation, as seen on coral reefs during severe storms. Pieces of coral may be scattered by wave action on a reef, becoming seeds for formation of a new reef. For these modular animals, age structure and sex ratio are difficult to determine. Changes in colony size can be used to measure growth rate, but counting individuals is more difficult and less meaningful than in **unitary** animals, which are independently living organisms.

Most animals are unitary. However, even some unitary species reproduce asexually. Clonal species are found in many animal groups, including insects, reptiles, and fish. Clonal groups contain only females, which lay unfertilized eggs that hatch into daughters genotypically identical to their mothers. This kind of cloning is called **parthenogenesis** (p. 139). The praying mantid *Bruneria borealis,* common in the southeastern United States, is a parthenogenetic unitary animal.

Most metazoans are biparental (p. 137), and reproduction follows a period of organismal growth and maturation. Each new generation begins with a **cohort** of individuals born at the same time. Of course, individuals of any cohort will not all survive to reproduce. For a population to retain constant size from generation to generation, each adult female must replace herself on average with one daughter that survives to reproduce. If she produces more than one viable female offspring the population will grow; if fewer than one, the population will decline.

Animal species have different characteristic patterns of **survivorship** from birth until death of the last member of a cohort. The three principal types of survivorship are illustrated in Figure 40-2. Curve a, in which all individuals die at the same time, probably occurs only rarely in nature. Curve b, in which the rate of mortality as a proportion of survivors is constant over all ages, is characteristic of some animals that care for their young, such as birds. Human populations generally fall somewhere between curves a and b, depending on the state of nutrition and medical care.

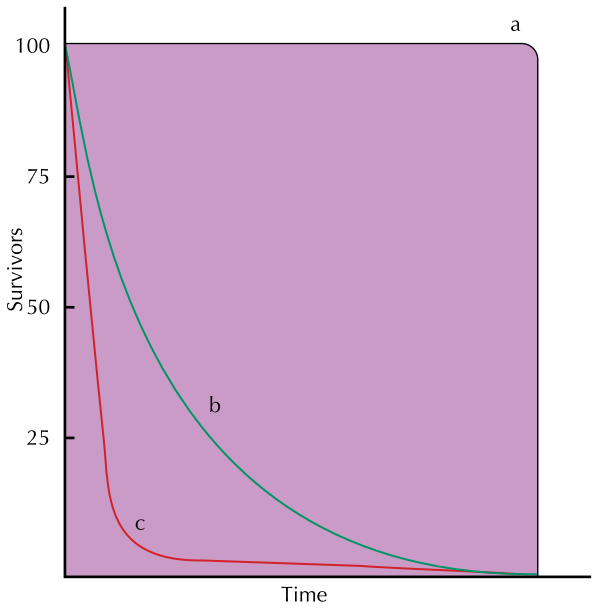


Figure 40-2
Three types of theoretical survivorship curves. See text for explanation.

The survivorship of most invertebrates, and of vertebrates like fish that produce great numbers of offspring, resembles curve c. For example, a mature female marine prosobranch snail, *Ilyanassa obsoleta,* produces thousands of eggs each reproductive period. Zygotes develop into free-swimming planktonic veliger larvae, which can be scattered far from the mother's habitat by oceanic currents. They form part of the plankton and experience high mortality from numerous animals that feed on plankton. Furthermore, the larvae require a specific, sandy-bottomed substrate on which to settle and metamorphose into an adult snail. The probability of a larva surviving long enough to find a suitable habitat is very low, and most of the cohort dies during the veliger stage. We therefore see a rapid drop in survivorship in the first part of the curve. The few larvae that do survive to become snails have improved odds of surviving further, as reflected by the more gentle slope of the curve for older snails. Thus, high reproductive output balances high juvenile mortality in such animals.

Many animals survive to reproduce only once before they die, as seen in many insect species of the temperate zone. Here, adults reproduce before the onset of winter and die, leaving only their eggs to overwinter and repopulate the habitat the following spring. Similarly, Pacific salmon after several years return from the ocean to fresh water to spawn only once, after which all adults of a cohort die. However, other animals survive long enough to produce multiple cohorts of offspring that may mature and reproduce while their parents are still alive and reproductively active. Populations of animals containing multiple cohorts, such as robins, box turtles, and humans, exhibit **age structure.** Analysis of age structure reveals whether the population is actively growing, stable, or declining. Figure 40-3 shows age profiles of two idealized populations. On a global scale, humans exhibit an age structure similar to curve a in Figure 40-2, although age structures vary among regions.

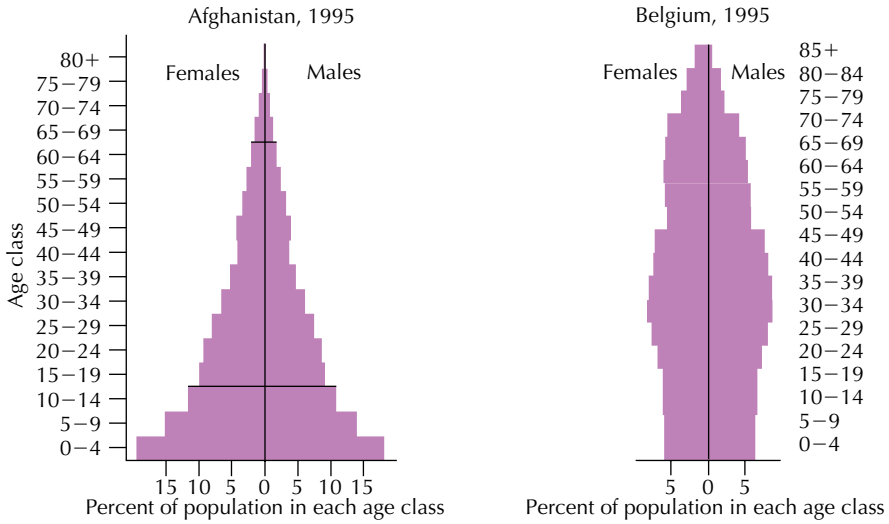


Figure 40-3

Age structure profiles of the human populations of Afghanistan and Belgium in 1995 contrast the rapidly growing, youthful population of Afghanistan with the stable population of Belgium, where the fertility rate is below replacement. Countries such as Afghanistan with a large fraction of the population as children are strained to provide adequate child services. With so many children soon to enter their reproductive years, the population will continue to grow rapidly for many years to come.

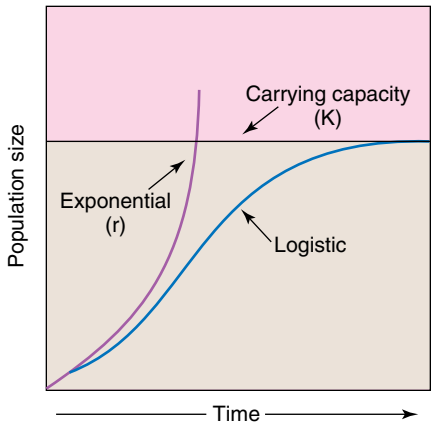


Figure 40-4

Population growth, showing exponential growth of a species in an unlimited environment, and logistic growth in a limited environment.

Population Growth and Intrinsic Regulation

Population growth is the difference between rates of birth and death. As Darwin recognized from the essay of Thomas Malthus (p. 108), all populations have the inherent ability to grow exponentially. This ability is called the **intrinsic rate of increase,** denoted by the symbol **r.** The steeply rising curve in Figure 40-4 shows this kind of growth. If species actually grew in this fashion unchecked, earth's resources soon would be exhausted and mass extinction would follow. A bacterium dividing three times per hour could produce a colony a foot deep over the entire earth after a day and a half, and this mass would be over our heads only one hour later. Animals have much lower potential growth rates than bacteria, but could achieve the same kind of result over a longer period of time, given unlimited resources. Many insects lay thousands of eggs each year. A single codfish may spawn 6 million eggs in a season, and a field mouse can produce 17 litters of five to seven young each year. Obviously, unrestricted growth is not the rule in nature.

Even in the most benign environment, a growing population eventually exhausts food or space. Exponential increases such as locust outbreaks or planktonic blooms in lakes must end when food or space is expended. Actually, among all resources that could limit a population, the one in shortest supply relative to the needs of the population will be depleted before others. This one is termed the **limiting resource.** The largest population that can be supported by the limiting resource in a habitat is called the **carrying capacity** of that environment, symbolized **K.** Ideally, a population will slow its growth rate in response to diminishing resources until it just reaches K, as represented by the sigmoid curve in Figure 40-4. The mathematical expression of exponential and sigmoid (or logistic) growth curves are compared in the box on page 828. Sigmoid growth occurs when there is negative feedback between growth rate and population density. This phenomenon is called density dependence, and is the mechanism for intrinsic regulation of populations. We can compare density dependence by negative feedback to the way endothermic animals regulate their body temperatures when the environmental temperature exceeds an optimum. If the resource is expendable, as with food, carrying capacity is reached when the rate of resource replenishment equals the rate of depletion by the population; the population is then at K for that limiting resource. According to the logistic model, when population density reaches K, rates of birth and death are equal and growth of the population ceases. Thus, a population of grasshoppers in a green meadow may be at carrying capacity even though we see plenty of unconsumed food.

Although experimental populations of protozoa may fit the logistic growth curve closely, most populations in nature tend to fluctuate above and below carrying capacity. For example, after sheep were introduced to Tasmania around 1800, their numbers changed logistically with small oscillations around an average population size of about 1.7 million; we thereby infer the carrying capacity of the environment to be 1.7 million sheep (Figure 40-5A). Ring-necked pheasants introduced on an island in Ontario, Canada exhibited wider oscillations (Figure 40-5B).

Why do intrinsically regulated populations oscillate this way? First, the carrying capacity of an environment can change over time, requiring that a population change its density to track the limiting resource. Second, animals always experience a lag between the time that a resource becomes limited and the time that the

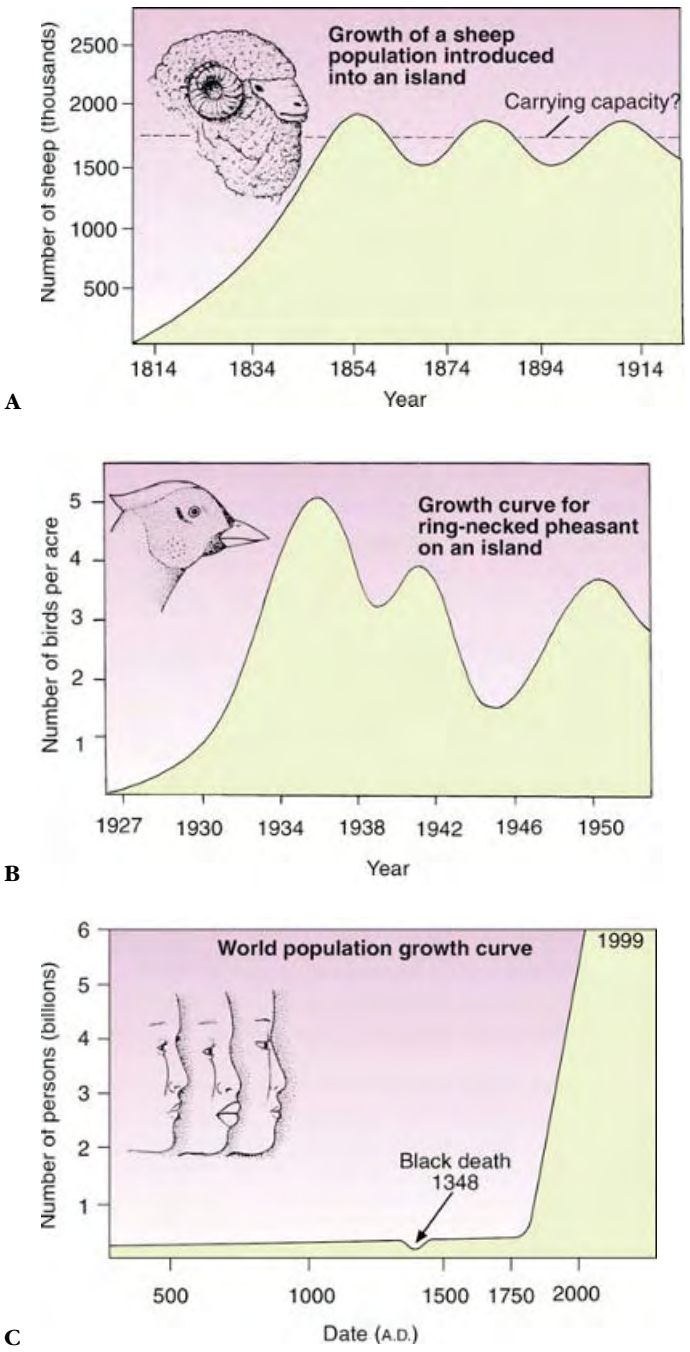


Figure 40-5

Growth curves for sheep **(A),** ring-necked pheasant **(B),** and world human populations **(C)** throughout history. Note that the sheep population on an island is stable because of human control of the population, but the ring-necked pheasant population oscillates greatly, probably because of large changes in carrying capacity. Where would you place the carrying capacity for the human population?

population responds by reducing its rate of growth. Third, **extrinsic** factors occasionally may limit a population's growth below carrying capacity. We consider extrinsic factors below.

On the global scale, humans have the longest record of exponential population growth (Figure 40-5C). Although famine and war have restrained growth of populations locally, the only dip in global human growth resulted from bubonic plague ("black death"), which decimated much of Europe during the fourteenth century. What then is the carrying capacity for the human population? The answer is far from simple, and several important factors must be considered when estimating the human K.

With the development of agriculture, the carrying capacity of the environment increased, and the human population grew steadily from 5 million around 8000 B.C., when agriculture was introduced, to 16 million around 4000 B.C. Despite the toll taken by terrible famines, disease, and war, the population reached 500 million by 1650. With the coming of the Industrial Revolution in Europe and England in the eighteenth century, followed by a medical revolution, discovery of new lands for colonization, and better agriculture practices, the human carrying capacity increased dramatically. The population doubled to 1 billion around 1850. It doubled again to 2 billion by 1927, to 4 billion in 1974, passed 6 billion in October 1999, and is expected to reach 8.9 billion by the year 2030. Thus, the growth has been exponential and remains high (Figure 40-5C).

Recent surveys provide hope that the growth of the human population is slackening. Between 1970 and 2000 the annual growth rate decreased from 1.9% to 1.33%. At 1.33%, it will take nearly 53 years for the world population to double rather than 36.5 years at the higher annual growth rate figure. The decrease is credited to better family planning. Nevertheless, half the global population is under 25 years old and most live in developing countries where access to reliable contraception is limited or nonexistent. Thus, despite the drop in growth rate, the greatest surge in population lies ahead, with a projected 3 billion people added within the next three decades, the most rapid increase ever in human numbers.

Although rapid advancements in agricultural, industrial, and medical technology have undoubtedly increased the earth's carrying capacity for humans, it also has widened the difference between birth and death rates to increase our rate of exponential growth. Each day we add 215,000 people (net) to the approximately 6 billion people currently alive. Assuming that

Exponential and Logistic Growth

We can describe the sigmoid growth curve (see Figure 40-4) by a simple model called the logistic equation. The slope at any point on the growth curve is the growth rate, how rapidly the population size is changing with time. If **N** represents the number of organisms and **t** the time, we can, in the language of calculus, express growth as an instantaneous rate:

dN/dt = the rate of change in the number of organisms per time at a particular instant in time.

When populations are growing in an environment of unlimited resources (unlimited food and space, and no competition from other organisms), growth is limited only by the inherent capacity of the population to reproduce itself. Under these ideal conditions growth is expressed by the symbol **r,** which is defined as the intrinsic rate of population growth per capita. The index **r** is actually the difference between the birth rate and death rate per individual in the population at any instant. The growth rate of the population as a whole is then:

$$dN/dt = rN$$

This expression describes the rapid, **exponential growth** illustrated by the early upward-curving portion of the sigmoid growth curve (see Figure 40-4).

Growth rate for populations in the real world slows as the upper limit is approached, and eventually stops altogether. At this point **N** has reached its maximum density because the space being studied has become "saturated" with animals. This limit is called the carrying capacity of the environment and is expressed by the symbol **K.** The sigmoid population growth curve can now be described by the logistic equation, which is written as follows:

$$dN/dt = rN([K - N]/K)$$

This equation states that the rate of increase per unit of time (dN/dt = rate of growth per capita **(r)** × population size **(N)** × unutilized freedom for growth ([**K − N**]/**K**). One can see from the equation that when the population approaches the carrying capacity, **K − N** approaches 0, dN/dt also approaches 0, and the curve will flatten.

Populations occasionally overshoot the carrying capacity of the environment so that **N** exceeds **K.** The population then exhausts some resource (usually food or shelter). The rate of growth, dN/dt, then becomes negative and the population must decline.

growth remains constant (certainly not a safe assumption, based on the history of human population growth), by the year 2030 more than half a million people will be added each day. In other words, less than ten days will be required to replace all people who inhabited the world in 8000 B.C.

In trying to arrive at an estimate of carrying capacity for the human species, we must consider not only quantity of resources, but quality of life. Approximately 2 billion of the 6 billion people alive today are malnourished. At present 99% of our food comes from the land, and the tiny fraction that we derive from the sea is decreasing due to overexploitation of fish stocks (p. 812). Although there is some disagreement on what would constitute the maximum sustainable agricultural output, scientists do not expect food production to keep pace with population growth.

Extrinsic Limits to Growth

We have seen that the intrinsic carrying capacity of a population for an environment prevents unlimited exponential growth of the population. Population growth also can be limited by extrinsic biotic factors, including predation, parasitism (including disease-causing pathogens), and interspecific competition, or by abiotic influences such as floods, fires, and storms. Although abiotic factors certainly can reduce populations in nature, they cannot truly regulate population growth because their effect is wholly independent of population size; abiotic limiting factors are **density-independent.** A single hailstorm can kill most of the young of wading bird populations, and a forest fire can eliminate entire populations of many animals, regardless of how many individuals there may be.

In contrast, biotic factors can and do act in a **density-dependent** manner. Predators and parasites respond to changes in density of their prey and host populations, respectively, to maintain populations at fairly constant sizes. These sizes are below carrying capacity, because populations regulated by extrinsic factors are not limited by their resources. Competition between species for a common limiting resource lowers the effective carrying capacity for each species below that of either one alone.

Community Ecology

Interactions among Populations in Communities

Populations of animals are part of a larger system, known as the **community,** within which populations of different species interact. The number of species that share a habitat is known as **species diversity.** These species interact in a variety of ways that can be detrimental (−), beneficial (+), or neutral (0) to each species, depending on the nature of the interaction. For instance, we can consider a predator's effect on its prey as (−), because the survival of the prey animal is reduced. However, the same interaction benefits the predator (+) because the food obtained from prey increases the predator's ability to survive and reproduce. Thus, the predatory-prey interaction is + −. Ecologists use this shorthand notation to characterize interspecific interactions because it helps us to view the direction in which the interaction affects each species.

The Biodiversity Crisis

Today, during a period of unprecedented economic prosperity and social progress, we are in the midst of the most serious environmental crisis in our planet's history. An unfortunate reality is that as the economy expands, the ecosystem on which the economy depends does not, leading to an increasingly stressed relationship. The single most direct measure of the planet's health is the status of biodiversity. At unprecedented rates, we are losing its three components: species diversity, genetic diversity, and habitat diversity. These losses arise primarily from habitat destruction, especially rapid destruction of tropical rain forests. Excessive fishing and hunting, illegal pet trade, pollution, and spread of invasive exotic species also contribute to the biodiversity crisis.

Earth's biodiversity provides humans with food and fiber; it underpins our health services (some 25% of drugs prescribed in the United States include chemical compounds from wild organisms); it provides genes for maintaining the vigor of crops and livestock; it provides natural pest control and creates our soils. Loss of keystone species such as African elephants, sea otters, or sea stars means significant changes and lowering of diversity within the ecosystems in which they live. With extinction of animal species we lose beauty and wonder. We will miss the breaching of whales, the howling of wolves, and the grace of cheetahs. Only through significant conservation efforts and through laws that limit environmental degradation will we be able to preserve the planet's biodiversity.

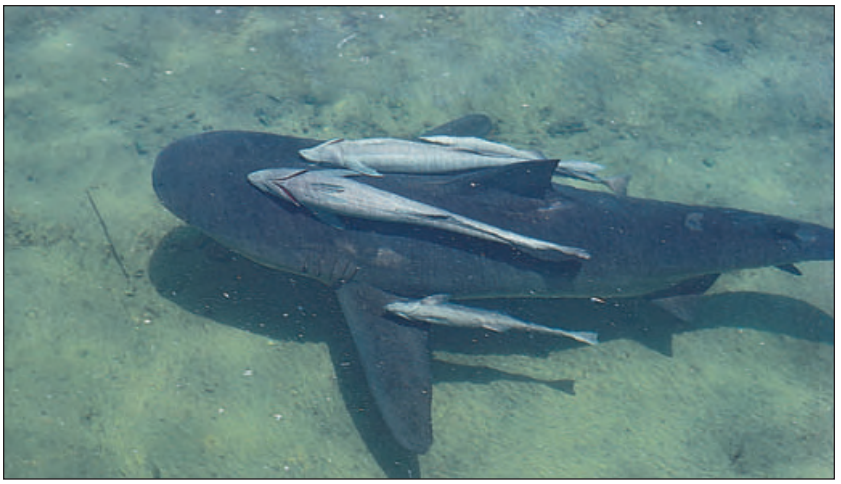


Figure 40-6
Four remoras, *Remora* sp., attached to a shark. Remoras feed on fragments of food left by their shark host, as well as on pelagic invertebrates and small fishes. Although they actually are good swimmers, remoras prefer to be pulled through the water by marine creatures or boats. The shark host may benefit by having embedded copepod skin parasites removed by the remora.

We see other kinds of + − interactions. One of these is **parasitism,** in which the parasite benefits by using the host as a home and source of nutrition, and the host is harmed. **Herbivory,** in which an animal eats a plant, is another + − relationship. **Commensalism** is an interaction that benefits one species and neither harms nor benefits the other (0+). Most bacteria that normally inhabit our intestinal tracts do not affect us (0), but the bacteria benefit (+) by having food and a place to live. A classic example of commensalism is the association of pilot fishes and remoras with sharks (Figure 40-6). These fishes get the "crumbs" remaining when the host shark makes its kill, but we now know that some remoras also feed on ectoparasites of the sharks. Commensalism therefore grades into **mutualism.**

Organisms engaged in mutalism have a friendlier arrangement than commensalistic species, because the fitness of both is enhanced (++). Biologists are finding mutualistic relationships far more common in nature than previously believed (Figure 40-7). Some mutualistic relationships are not only beneficial, but necessary for survival of one or both species. An example is the relationship between a termite and protozoa inhabiting its gut. The protozoa can digest wood eaten by the termite because the protozoa produce an enzyme, lacking in the termite, that digests cellulose; the termite lives on waste products of protozoan metabolism. In return, the protozoa gain a habitat and food supply. Such absolute interdependence among species can be a liability if one of the participants is lost. *Calvaria* trees native to the island of Mauritius have not reproduced successfully for over 300 years, because their seeds germinate only after being eaten and passed through the gut of a dodo bird, now extinct.

Competition between species reduces the fitness of both (−−). Many biologists, including Darwin, considered competition the most common and important interaction in nature. Ecologists have constructed most of their theories of community structure from the premise that competition is the chief organizing factor in species assemblages. Sometimes the effect on one of the species in a competitive relationship is negligible. This condition is called **amensalism,** or **asymmetric competition** (0−). For example, two species of barnacles that commonly occur in rocky intertidal habitats, *Chthamalus stellatus* and *Balanus balanoides,* compete for space. A famous experiment by Joseph Connell* demonstrated that *B. balanoides* excluded *C. stellatus* from a portion of the habitat, while *C. stellatus* had no effect on *B. balanoides.*

We have treated interactions as occurring between pairs of species. However, in natural communities containing populations of many species, a predator may have more than one prey and several animals may compete for the same resource. Thus, ecological

*Connell, J. H. 1961. The influence of interspecific competition and other factors on the distributuion of the barnacle *Chthamalus stellatus.* Ecology **42:**710–723.

Figure 40-7
Among the many examples of mutualism that abound in nature is the whistling thorn acacia of the African savanna and the ants that make their homes in the acacia's swollen galls. The acacia provides both protection for the ants' larvae (*lower photograph of opened gall*) and honeylike secretions used by the ants as food. In turn, the ants protect the tree from herbivores by swarming out as soon as the tree is touched. Giraffes, however, which love the tender acacia leaves, seem immune to the ants' fiery stings.

communities are quite complex and dynamic, a challenge to ecologists who wish to study this level of natural organization.

Competition and Character Displacement

Competition occurs when two or more species share a **limiting resource.** Simply sharing food or space with another species does not produce competition unless the resource is in short supply relative to the needs of the species that share it. Thus, we cannot prove that competition occurs in nature based solely on the sharing of resources. However, we find evidence of competition by investigating the different ways that species exploit a resource.

Competing species may reduce conflict by reducing the overlap of their niches. **Niche overlap** is the portion of the niche's resources shared by two or more species. For example, if two species of birds eat seeds of exactly the same size, competition eventually will exclude one species from the habitat. This example illustrates the principle of **competitive exclusion:** strongly competing species cannot coexist indefinitely. To coexist in the same habitat, species must specialize by partitioning a shared resource and using different portions of it. Specialization of this kind is called **character displacement.**

Character displacement usually appears as differences in organismal morphology or behavior related to exploitation of a resource. For example, in his classic study of the Galápagos finches (p. 119), English ornithologist David Lack noticed that bill sizes of these birds depended on whether they occurred together on the same island (Figure 40-8). On the islands Daphne and Los Hermanos, where *Geospiza fuliginosa* and *G. fortis* occur separately and therefore do not compete with each other, bill sizes are nearly identical; on the island Santa Cruz, where both *G. fuliginosa* and *G. fortis* coexist, their bill sizes do not overlap. These results suggest resource partitioning, because bill size determines the size of seeds selected for food. Recent work by the American ornithologist Peter Grant has confirmed what Lack suspected: *G. fuliginosa* with its smaller bill selects smaller seeds than does *G. fortis* with its larger bill. Where the two species coexisted, competition between them led to evolutionary displacement of the bill sizes to diminish competition. An absence of competition today has been called appropriately "the ghost of competition past."

Character displacement promotes coexistence by reducing niche overlap. When several species share the same general resources by such partioning, they form a **guild.** Just as a guild in medieval times constituted a brotherhood of men sharing a common trade, species in an ecological guild share a common livelihood. The term guild was introduced to ecology by Richard Root in his 1967 paper on niche patterns of the blue-gray gnatcatcher.[†] A classic example of a bird guild is Robert MacArthur's study of a feeding guild consisting of five species of warblers in spruce woods of the northeastern United States.[‡] At first glance, we might ask how five birds, very similar in size and appearance, could coexist by feeding on insects in the same tree. However, on close inspection MacArthur found subtle differences among these birds in sites of foraging (Figure 40-9). One species searched only on outer branches of spruce crowns; another species used the top 60% of the tree's outer and inner branches, although not next to the trunk; another species concentrated on inner branches closer to the trunk; another species used the midsection from the periphery to the trunk; and still another species foraged in the

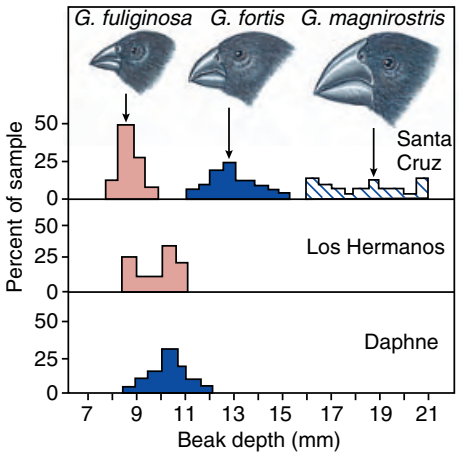


Figure 40-8
Displacement of beak sizes in Darwin's finches from the Galápagos Islands. Beak depths are given for the ground finches *Geospiza fuliginosa* and *G. fortis* where they occur together (sympatric) on Santa Cruz Island and where they occur alone on the islands Daphne and Los Hermanos. *G. magnirostris* is another large ground finch that lives on Santa Cruz.

[†]Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs **37:**317–350.

[‡]MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39:**599–619.

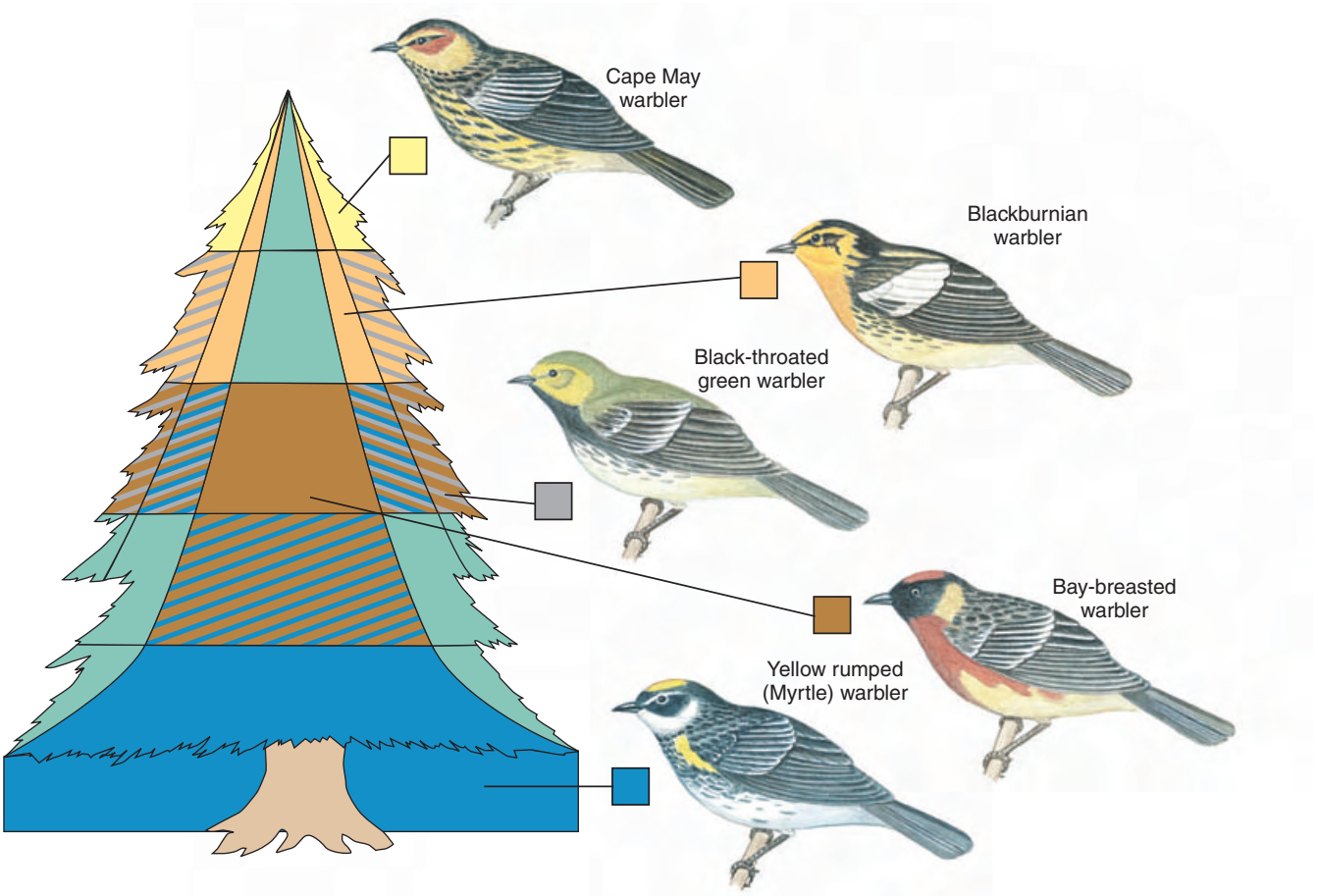


Figure 40-9
Distribution of foraging effort among five species of wood warblers in a northeastern spruce forest. The warblers form a feeding guild.

bottom 20% of the tree. These observations suggest that each warbler's niche within this guild is defined by structural differences in the habitat.

Guilds are not limited to birds. For example, a study done in England on insects associated with Scotch broom plants revealed nine different guilds of insects, including three species of stem miners, two gall-forming species, two that fed on seeds and five that fed on leaves. Another insect guild consists of three species of praying mantids that avoid both competition and predation by differing in sizes of their prey, timing of hatching, and height of vegetation in which they forage.

Predators and Parasites

The ecological warfare waged by predators against their prey causes coevolution: predators get better at catching prey, and prey get better at escaping predators. This is an evolutionary race that the predator cannot afford to win. If a predator became so efficient that it exterminated its prey, the predator species would become extinct. Because most predators feed on more than a single species, specialization on a single prey to the point of extermination is uncommon.

However, when a predator does rely primarily on a single prey species, both populations tend to fluctuate cyclically. First prey density increases, then that of the predator until prey become scarce. At that point, predators must adjust their population size downward by leaving the area, lowering reproduction, or dying. When density of the predator population falls enough to allow reproduction by prey to outpace mortality from predation, the cycle begins again. Thus, populations of both predators and prey show cycles of abundance, but increases and decreases in predator abundance are slightly delayed relative to those of prey because of the time lag in a predator's response to changing prey density. We can illustrate this process in the laboratory with protozoa (Figure 40-10). Perhaps the longest documented natural example of a predator-prey cycle is between Canadian populations of snowshoe hares and lynxes (see Figure 30-27, p. 628).

The war between predators and prey reaches high art in the evolution of defenses by potential prey. Many animals that are palatable escape detection by matching their background, or by resembling some inedible feature of the environment (such as a bird dropping). Such defenses are called cryptic. In contrast to cryptic defenses, animals that are toxic or distasteful to predators actually advertise their strategy with bright colors and conspicuous behavior. These species are protected because predators learn to recognize and to avoid them after one or more distasteful encounters.

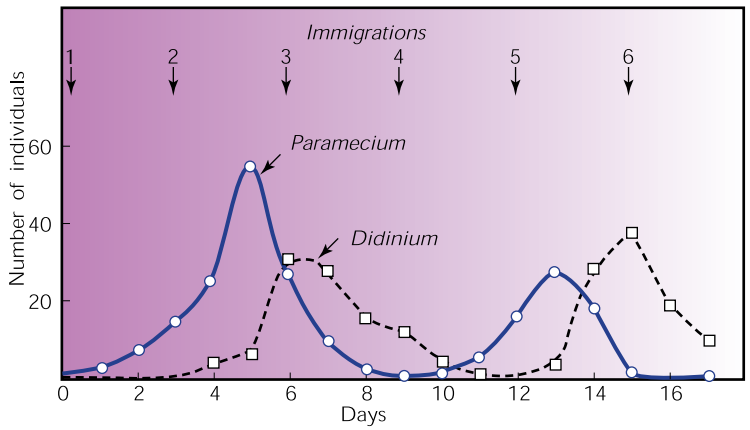


Figure 40-10

Classic predator-prey experiment by Russian biologist G. F. Gause in 1934 shows the cyclic interaction between predator (*Didinium*) and prey (*Paramecium*) in laboratory culture. When the *Didinium* find and eat all the *Paramecium,* the *Didinium* themselves starve. Gause could keep the two species coexisting only by occasionally introducing one *Didinium* and one *Paramecium* to the culture (*arrows*); these introductions simulated migration from an outside source.

A

B

C

Figure 40-11

Artful guises abound in the tropics. **A,** a palatable butterfly (*top photograph*) mimics a poisonous butterfly of a different family (*lower photograph*). **B,** a harmless clearwing moth (*top photograph*) mimics a yellowjacket wasp, which is armed with a stinger (*lower photograph*). Both **A** and **B** are examples of Batesian mimicry. **C,** Two unpalatable tropical butterflies of different families resemble one another, an example of Müllerian mimicry.

When distasteful prey adopt warning coloration, advantages of deceit arise for palatable prey. Palatable prey can deceive potential predators by mimicking distasteful prey. Coral snakes and monarch butterflies are both brightly colored, noxious prey. Coral snakes have a venomous bite, and monarch butterflies are poisonous because caterpillars store poison (cardiac glycoside) from milkweed they eat. Both species serve as **models** for other species, called **mimics,** that do not possess toxins of their own but look like the model species that do (Figure 40-11A and B).

In another form of mimicry, two or more toxic species resemble each other (Figure 40-11C). We can ask why an animal that has its own poison should gain by evolving resemblance to another poisonous animal. The answer is that the predator needs only to experience the toxicity of one species to avoid all similar prey. A predator can learn one warning signal more easily than many!

Sometimes the influence of one population on others is so pervasive that its absence drastically changes the character of the entire community. We call such a population a **keystone species.*** For example, in 1983, a mysterious epidemic swept through Caribbean populations of the sea urchin *Diadema antillarum,* destroying more than 95% of the animals. The immediate effect was on the algal community, no longer grazed by the urchins. In some reefs the algae grew from a thin mat to a thick canopy of altered composition. Both productivity and diversity on the coral reefs declined. *Diadema antillarum* clearly was a keystone predator species for those communities. On the West Coast, the sea star *Pisaster ochraceous* is a keystone species. Sea stars are a major predator of the mussel *Mytilus californianus.* When sea stars were removed experimentally from a patch of Washington State coastline, mussels expanded in members, occupying all space previously used by 25 other

*Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist **103:**91–93.

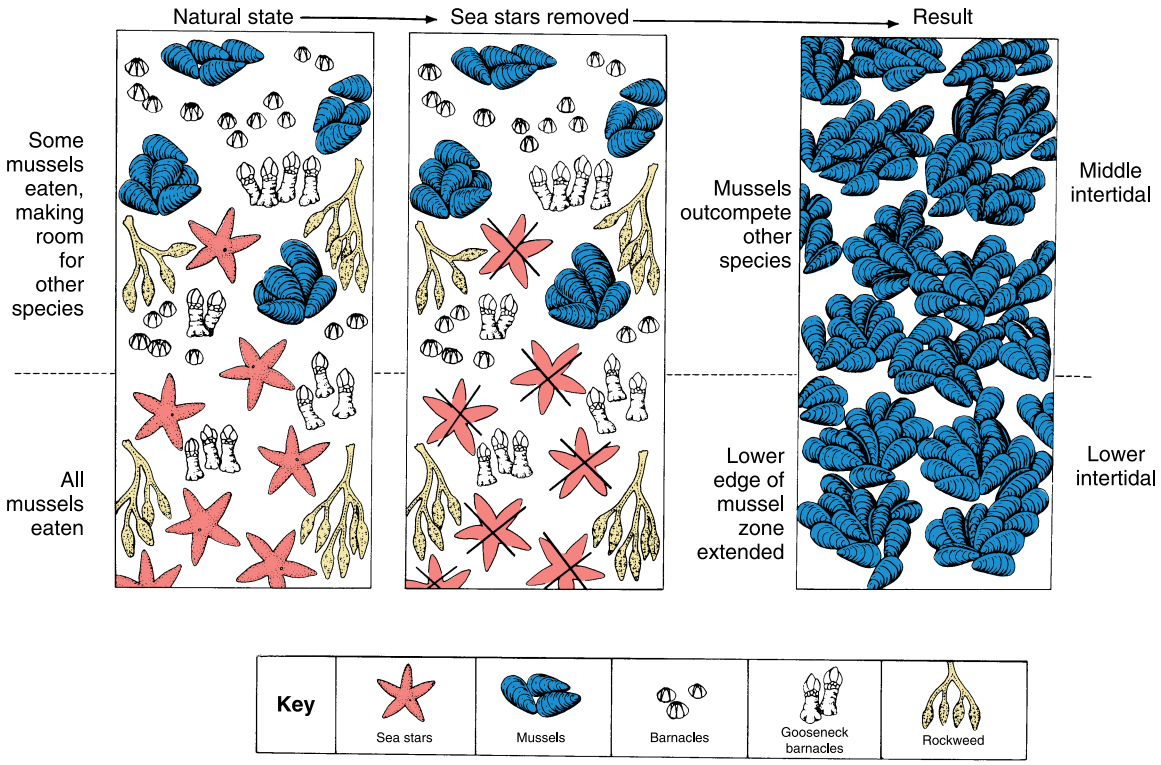


Figure 40-12

The experimental removal of a keystone species, the predatory sea star *Pisaster ochraceus,* from an intertidal community completely changes the structure of the community. With their principal predator missing, mussels form dense beds by outcompeting and replacing other intertidal species.

invertebrate and algal species (Figure 40-12). Keystone predators act by reducing prey populations below the level where resources such as space are limiting. The original notion that all keystone species were predators has been broadened to include any species whose removal causes the extinction of others.

By reducing competition, keystone species allow more species to coexist on the same resource. Consequently they contribute to maintaining diversity in the community. Keystone species can be considered a special case of a more general phenomenon, disturbance. Periodic natural disturbances such as fires and hurricanes also can prevent monopolization of resources and competitive exclusion by a few broadly adapted competitors. Ecologists now believe that disturbances permit more species to coexist in such highly diverse communities as coral reefs and rain forests.

Parasites are often considered freeloaders because they appear to get something from their hosts for nothing. **Ectoparasites** such as ticks and lice infect many different kinds of animals. The host provides nutrition from its body and aids in dispersal of the parasite. However, we must consider that the evolutionary pathway to parasitism from free-living forms often has costs as well as benefits. **Endoparasites** such as tapeworms (see Chapter 14), have lost their ability to choose habitats. Also, because they must move among hosts to complete their life cycle, the chance that a single individual will live to reproduce is very low. The more intermediate hosts involved in a parasite's life cycle, the lower the likelihood of success, and the greater reproductive output must be to balance mortality.

Biologists often are puzzled by the complexity of parasite-host relationships. For example, one of the trematode parasites of the marine gastropod *Ilyanassa obsoleta* actually changes its host's behavior to complete its life cycle. These snails live in sandy-bottomed intertidal habitats in eastern North America. If the snails are exposed to air when the tide recedes, they normally burrow into the sand to avoid desiccation. If, however, a snail is infected with the trematode *Gynaecotyla adunca,* it moves shoreward on high tides preceding low night tides to be left on the beach on the receding tide. Then, as in the legend of the Trojan Horse, the snail sheds cercariae into the sand where they can infect the next intermediate host, a beach-living crustacean. The crustacean may then be eaten by a gull or other shorebird, the definitive hosts for this trematode. The life cycle is completed when the bird defecates into the water, releasing eggs from which hatch the larvae that will infect more snails.

How could this parasite evolve to depend upon the transfer from an aquatic intermediate host to another intermediate host that lives on land? The answer may be that the life cycle of this parasite has been around longer than the crustaceans have occupied land. When the crustacean evolved its terrestrial habit it simply brought the parasite along.

Coevolution between parasite and host may be expected to generate an increasingly benign, less virulent relationship. Selection would favor a benign relationship, because a parasite's fitness is diminished if its host dies. This traditional view has been challenged in recent years. Virulence is correlated, at least in part, with availability of new hosts. When alternative hosts are common and transmission rates are high, a host's life is of less value to a parasite, which may become more virulent.

Ecosystems

Transfer of energy and materials among organisms within ecosystems is the ultimate level of organization in nature. Energy and materials are required to construct and to maintain life, and their incorporation into biological systems is called **productivity.** Productivity is divided into component **trophic levels** based on how organisms obtain energy and materials. Trophic levels are linked together into **food webs** (Figure 40-13), which are pathways for the transfer of energy and materials among organisms within the ecosystem.

Primary producers are organisms that begin productivity by fixing and storing energy from outside the ecosystem. Primary producers usually are green plants that capture solar energy through **photosynthesis** (but see an exception in the box on this page). Powered by solar energy, plants assimilate and organize minerals, water, and carbon dioxide into living tissue. All other organisms survive by consuming this tissue, or by consuming organisms that consumed this tissue. **Consumers** include **herbivores,** which eat plants directly, and **carnivores,** which eat other animals. The most important consumers are **decomposers,** mainly bacteria and fungi that break dead organic matter into its mineral components, returning it to a soluble form that can be used by plants to restart the cycle. Although important chemicals such as nitrogen and carbon are reused endlessly through biological cycling, all energy ultimately is lost from the ecosystem as heat and cannot be recycled. Thus, no ecosystems, including the biosphere of earth, are truly closed.

Life without the Sun

For many years, ecologists believed that all animals depended directly or indirectly on primary production from solar energy. However, in 1977 and 1979, dense communities of animals were discovered living on the sea floor adjacent to vents of hot water issuing from rifts (Galápagos Rift and East Pacific Rise) where tectonic plates on the sea floor are slowly spreading apart. These communities (see photo) included several species of molluscs, some crabs, polychaete worms, enteropneusts (acorn worms), and giant pogonophoran worms. The temperature of seawater above and immediately around vents is 7° to 23° C where it is heated by basaltic intrusions, whereas the surrounding normal seawater is 2° C.

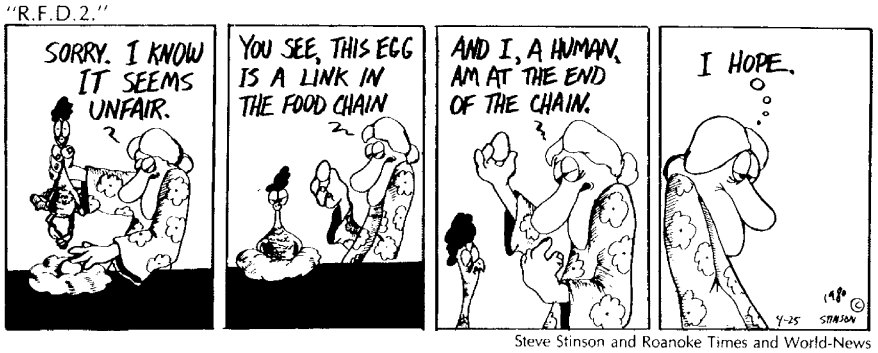
The producers in these vent communities are chemoautotrophic bacteria that derive energy from the oxidation of the large amounts of hydrogen sulfide in the vent water and fix carbon dioxide into organic carbon. Some of the animals in the vent communities—for example, the bivalve molluscs—are filter feeders that ingest the bacteria. Others, such as the giant pogonophoran tubeworms (see p. 442), which lack mouths and digestive tracts, harbor colonies of symbiotic bacteria in their tissues and use the organic carbon that these bacteria synthesize.

A population of giant pogonophoran tubeworms grows in dense profusion near a Galápagos Rift thermal vent, photographed at 2800 m (about 9000 feet) from the deep submersible *Alvin.* Also visible in the photograph are mussels and crabs.

Energy Flow

Every organism in nature has an **energy budget.** Just as we each must partition our income for housing, food, utilities, taxes, and so on, each organism must obtain enough energy to meet its metabolic costs, to grow, and to reproduce.

Ecologists divide the budget into three main components: **gross productivity, net productivity,** and **respiration.** Gross productivity is like gross income; it is the total energy assimilated, analogous to your paycheck before deductions. When an animal eats, food passes through its gut and nutrients are absorbed. Most energy assimilated from these nutrients serves the animal's metabolic demands, which include cellular metabolism and regulation of body heat in endotherms. The energy required for metabolic maintenance is



Steve Stinson and Roanoke Times and World-News

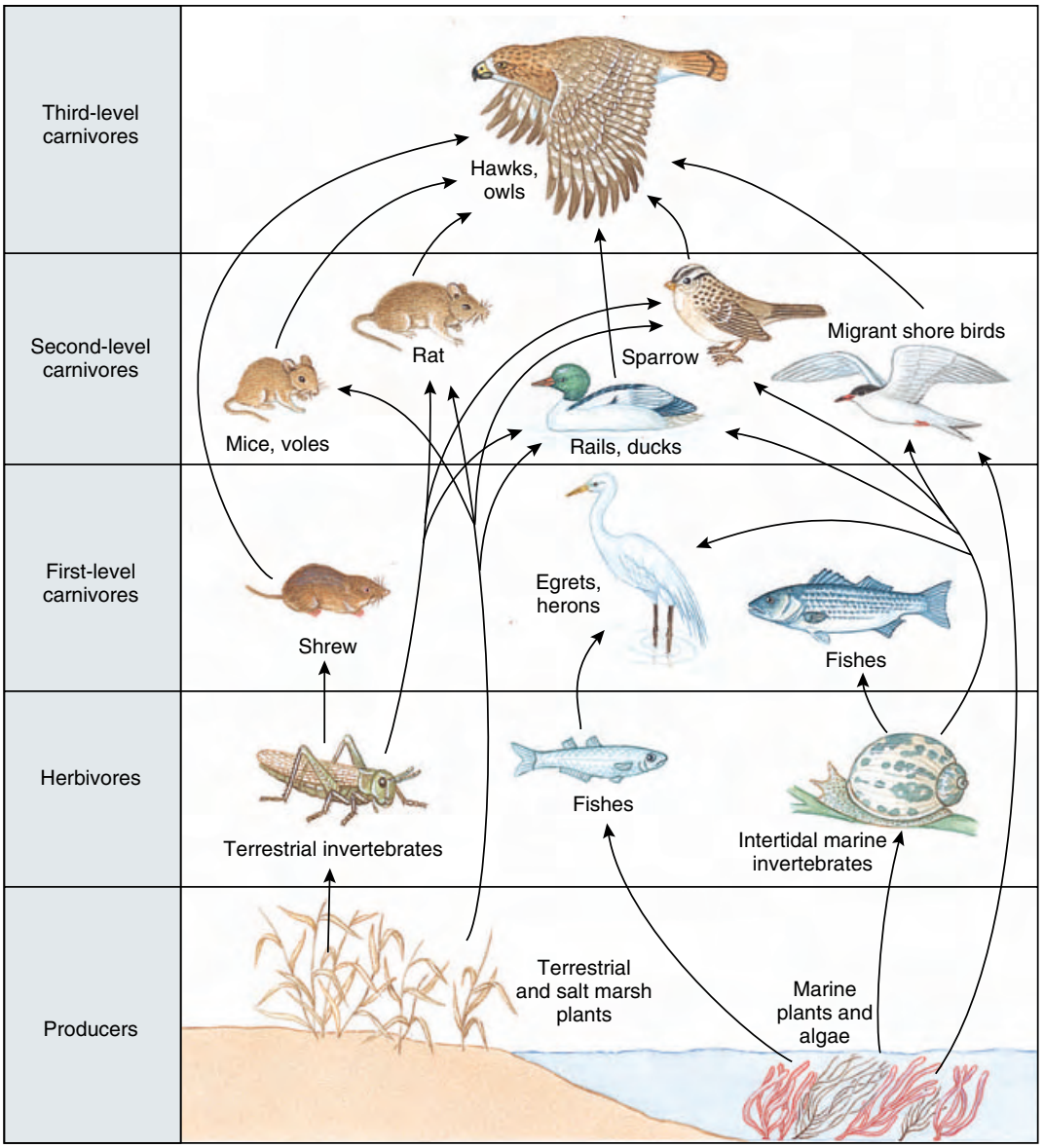


Figure 40-13
Midwinter food web in *Salicornia* salt marsh of San Francisco Bay area.

respiration, which is deducted from gross productivity to arrive at net productivity, an animal's take-home pay. Net productivity is energy stored by the animal in its tissues as **biomass.** This energy is available for growth, and also for reproduction, which is population growth.

The energy budget of an animal is expressed by a simple equation, in which gross and net productivity are represented by $\mathbf{P_g}$ and $\mathbf{P_n}$, respectively, and respiration is **R:**

$$\mathbf{P_n = P_g - R}$$

This equation is a way of stating the first law of thermodynamics (p. 59) in the context of ecology. Its important messages are that the energy budget of every animal is finite and may be limiting, and that energy is available for growth of individuals and populations only after maintenance is satisfied.

The second law of thermodynamics, which states that the total disorder or randomness of a system always increases, is important when we study energy transfers between trophic levels in food webs. Energy for maintenance, R, usually constitutes more than 90% of the assimilated energy (P_g) for animal consumers. More than 90% of the energy in an animal's food is lost as heat, and less than 10% is stored as biomass. Each succeeding trophic level therefore contains only 10% of the energy in the next lower trophic level. Most ecosystems are thereby limited to five or fewer trophic levels.

Our ability to feed a growing human population is influenced profoundly by the second law of thermodynamics (p. 59). Humans, who occupy a position at the end of the food chain, may eat the grain that fixes the sun's energy; this very short chain represents an efficient use of

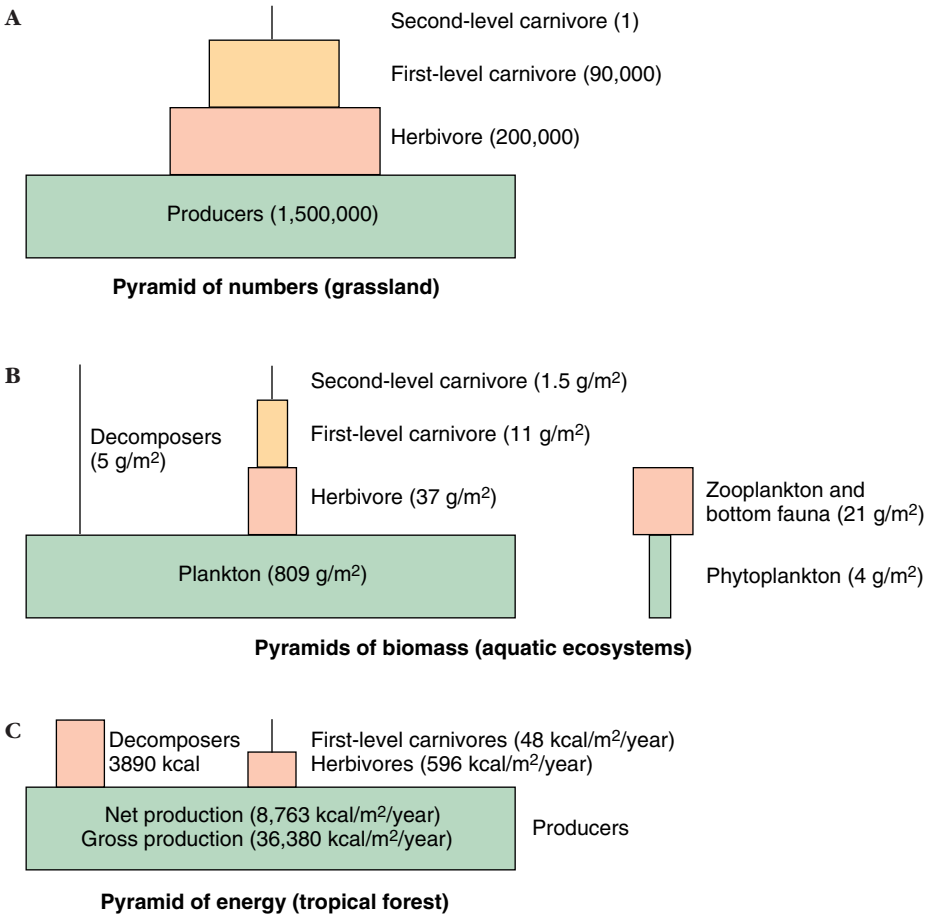


Figure 40-14
Ecological pyramids of numbers, biomass, and energy. Pyramids are generalized, since the area within each trophic level is not scaled proportionally to quantitative differences in units given.

potential energy. Humans also may eat beef from animals that eat grass that fixes the sun's energy; the addition of a trophic level decreases available energy by a factor of 10. Ten times as much plant biomass is needed to feed humans as meat eaters as to feed humans as grain eaters. Consider a person who eats a bass that eats a sunfish that eats zooplankton that eats phytoplankton that fixes the sun's energy. The tenfold loss of energy occurring at each trophic level in this five-step chain requires that the pond must produce 5 tons of phytoplankton for a person to gain a pound by eating bass. If the human population depended on bass for survival, we would quickly exhaust this resource.

These figures must be considered as we look to the sea for food. Productivity of oceans is very low and limited largely to estuaries, marshes, reefs, and upwellings where nutrients are available to phytoplankton producers. Such areas constitute a small part of the ocean. The rest is a watery void.

Marine fisheries supply 18% of the world's protein, but much of this protein is used to feed livestock and poultry. If we remember the rule of 10-to-1 loss in energy with each transfer of material between trophic levels, then use of fish as food for livestock rather than humans is poor use of a valuable resource in a protein-deficient world. Fishes that we prefer to eat include flounder, tuna, and halibut, which are three or four levels up the food chain. Every 125 g of tuna requires one metric ton of phytoplankton to produce. If humans are to derive greater benefit from the oceans as a food source, we must eat more of the less desirable fishes that are at lower trophic levels.

When we examine the food chain in terms of biomass at each level, we can construct **ecological pyramids** either of numbers or of biomass. A pyramid of numbers (Figure 40-14A), also known as **Eltonian pyramid** (after Charles Elton, who first devised the scheme), depicts numbers of organisms that are transferred between each trophic level. This pyramid provides a vivid impression of the great difference in numbers of organisms involved in each step of the chain, and supports the observation that large predatory animals are rarer than the small animals on which they feed. However, a pyramid of numbers does not indicate actual mass of organisms at each level.

The concepts of food chains and ecological pyramids were invented and first explained in 1923 by Charles Elton, a young ecologist at Oxford University. Working for a summer on a treeless arctic island, Elton watched arctic foxes as they roamed, noting what they ate and, in turn, what their prey had eaten, until be was able to trace the complex cycling of nitrogen in food throughout the animal community. Elton realized that life in a food chain comes in discrete sizes, because each form had evolved to be much bigger than the thing it eats. He thus explained the common observation that large animals are rare while small animals are common.

More instructive are pyramids of biomass (Figure 40-14B), which depict the total bulk, or "standing crop," of organisms at each trophic level. Such pyramids usually slope upward because mass and energy are lost at each transfer. However, in some aquatic ecosystems in which the producers are algae, which have short life spans and rapid turnover, the pyramid is inverted. Algae can tolerate heavy exploitation by the zooplankton consumers. Therefore, the base of the pyramid (biomass of phytoplankton) is smaller than the biomass of zooplankton it supports. We could liken this inverted pyramid to a person who weighs far more than the food in a refrigerator, but who can be sustained

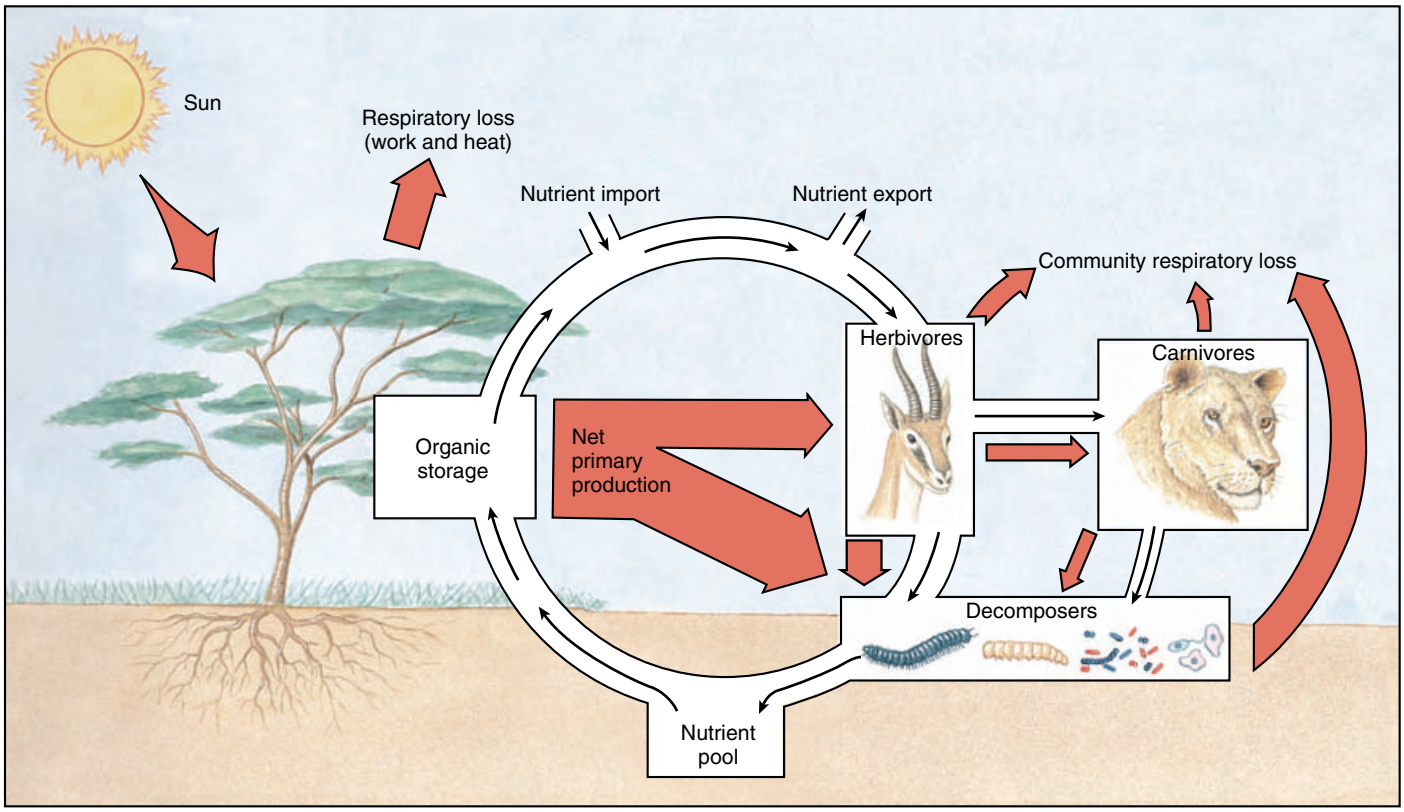


Figure 40-15
Nutrient cycles and energy flow in a terrestrial ecosystem. Note that nutrients are recycled, whereas energy flow (*red*) is one way.

from the refrigerator because the food is constantly replenished.

A third type of pyramid is a pyramid of energy, which shows rate of energy flow between levels (Figure 40-14C). An energy pyramid is never inverted because energy transferred from each level is less than what was put into it. A pyramid of energy gives the best overall picture of community structure because it is based on production. In the example above, productivity of phytoplankton exceeds that of zooplankton, even though biomass of phytoplankton is less than biomass of zooplankton (because of heavy grazing by the zooplankton consumers).

Nutrient Cycles

All elements essential for life are derived from the environment, where they are present in air, soil, rocks, and water. When plants and animals die and their bodies decay, or when organic substances are burned or oxidized, elements and inorganic compounds essential for life processes (nutrients) are released and returned to the environment. Decomposers fulfill an essential role in this process by feeding on the remains of plants and animals and on fecal material. The result is that nutrients flow in a perpetual cycle between biotic and abiotic components of the ecosystem. Nutrient cycles are often called **biogeochemical cycles** because they involve exchanges between living organisms (bio-) and rocks, air, and water of the earths' crust (geo-). Continuous input of energy from the sun keeps nutrients flowing and the ecosystem functioning (Figure 40-15).

We tend to think of biogeochemical cycles in terms of naturally occurring elements, such as water, carbon, and nitrogen. In recent times, however, humans have added synthetic materials to the biosphere that have entered food webs, sometimes with disastrous consequences. Probably the most harmful of these materials, in terms of ecosystemic processes, are pesticides. We currently produce about 2.5 million *tons* of pesticides worldwide, mainly for protection of crops from insects.

Despite such extensive use of poison, more than half of our crops are lost either before or after harvest to pests. The role of pesticides in natural food webs can be insidious for three reasons. First, many pesticides become concentrated as they travel up succeeding trophic levels. The highest concentrations will occur in the biomass of top carnivores such as hawks and owls, diminishing their ability to reproduce. Second, many species that are killed by pesticides are not pests, but merely innocent bystanders, called nontarget species. Nontarget effects happen when pesticides move out of the agricultural field to which they were applied,

through rainwater runoff, leaching through the soil, or dispersal by wind. The third problem is persistence; some chemicals used as pesticides have a long life span in the environment, so that nontarget effects persist long after the pesticides have been applied. Scientists are working to create new pesticides that are more specific in their effects and decompose faster in the environment, but we have a long way to go to limit our warfare against those animals that compete with us for our supply of food.

Summary

Ecology is the study of relationships between organisms and their environments to explain the distribution and abundance of life on earth. The physical space where an animal lives, and that contains its environment, is its habitat. Within the habitat are physical and biological resources that an animal uses to survive and to reproduce, which constitute its niche.

Animal populations consist of demes of interbreeding members sharing a common gene pool. Cohorts of animals have characteristic patterns of survivorship that represent adaptive trade-offs between parental care and numbers of offspring. Animal populations consisting of overlapping cohorts have age structure that indicates whether they are growing, declining, or at equilibrium.

Every species in nature has an intrinsic rate of increase that gives it the potential for exponential growth. The human population is growing exponentially at about 1.33% each year, and is expected to increase from 6 billion to 8.9 billion by the year 2030. Population growth may be regulated intrinsically by the carrying capacity of the environment, extrinsically by competition between species for a limiting resource, or by predators or parasites. Density independent abiotic factors can limit, but not truly regulate, population growth.

Communities consist of populations that interact with one another in any of several ways, including competition, predation, parasitism, commensalism, and mutualism. These relationships are the results of coevolution among populations within communities. Guilds of species avoid competitive exclusion by character displacement, the partitioning of limited resources by morphological specialization. Keystone predators are those that control community structure and reduce competition among prey, which increases species diversity. Parasites and their hosts evolve a benign relationship that ensures their coexistence.

Ecosystems consist of communities and their abiotic environments. Animals occupy the trophic levels of herbivorous and carnivorous consumers within ecosystems. All organisms have an energy budget consisting of gross and net productivity, and respiration. For animals, respiration usually is at least 90% of this budget. Thus, the transfer of energy from one trophic level to another is limited to about 10%, which in turn limits the number of trophic levels in an ecosystem. Ecological pyramids of energy depict how productivity decreases in successively higher trophic levels of food webs.

Ecosystem productivity is a result of energy flow and material cycles within ecosystems. All energy is lost as heat, but nutrients and other materials including pesticides are recycled. No ecosystem, including the global biosphere, is closed because they all depend upon imports and exports of energy and materials from outside.

Review Questions

1. The term ecology is derived from the Greek meaning "house" or "place to live." However, as used by scientists, the term "ecology" is not the same as "environment." What is the distinction between these terms?
2. How would you distinguish between ecosystem, community, and population?
3. What is the distinction between habitat and environment?
4. Define the niche concept. How does the "realized niche" of a population differ from its "fundamental niche"? How does the concept of niche differ from the concept of guild?
5. Populations of independently living (unitary) animals have a characteristic age structure, sex ratio, and growth rate. However, these properties are difficult to determine for modular animals. Why?
6. Explain which of the three survivorship curves in Figure 40-2 best fits the following: (a) a population in which mortality as a proportion of survivors is constant; (b) a population in which there is little early death and most individuals live to old age; (c) a population that experiences heavy mortality of the very young but with the survivors living to old age. Offer an example from the real world of each survivorship pattern.
7. Contrast exponential and logistic growth of a population. Under what conditions might you expect a population to exhibit exponential growth? Why cannot exponential growth be perpetuated indefinitely?
8. Growth of a population may be hindered by either density-dependent or density-independent mechanisms. Define and contrast these two mechanisms. Offer examples of how growth of the human population might be curbed by either agent.
9. Herbivory is an example of an interspecific interaction that is beneficial for the animal (+) but harmful to the plant it eats (−). What are some + − interactions among animal populations? What is the difference between commensalism and mutualism?
10. Explain how character displacement can ease competition between coexisting species.
11. Define predation. How does the predator-prey relationship differ from the parasite-host relationship? Why is the evolutionary race between predator and prey one that the predator cannot afford to win?

12. Mimicry of monarch butterflies by viceroys is an example of a palatable species resembling a toxic one. What is the advantage to the viceroy of this form of mimicry? What is the advantage to a toxic species of mimicking another toxic species?
13. A keystone species has been defined as one whose removal from a community causes the extinction of other species. How does this extinction happen?
14. What is a trophic level, and how does it relate to a food chain?
15. Define *productivity* as the word is used in ecology. What is a primary producer? What is the distinction between gross productivity, net productivity, and respiration? What is the relation of net productivity to biomass (or standing crop)?
16. What is a food chain? How does a food chain differ from a food web?
17. How is it possible to have an inverted pyramid of biomass in which the consumers have a greater biomass than the producers? Can you think of an example of an inverted pyramid of *numbers* in which there are, for example, more herbivores than plants on which they feed?
18. The pyramid of energy has been offered as an example of the second law of thermodynamics (p. 59). Why?
19. Animal communities surrounding deep-sea thermal vents apparently exist in total independence of solar energy. How can this existence be possible?

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

U.S. Fish and Wildlife Service Division of Endangered Species. Shows a map of the United States, listing the number of endangered species ("listed" species) as of May 31, 1999. Some very sobering numbers.

USFWS Division of Endangered Species. An extensive, indexed USFWS site with links to endangered and threatened species, both plants and animal by area or taxonomic group.

USFWS Division of Endangered Species. A listing by state or region of endangered species.

Population Ecology. Online data, information from lecture courses, and the names of organizations, people, and journals involved in population ecology.

The Ecological Society of America Homepage. This large organization has a homepage that will link the user to hundreds of useful sites.

OLC Student Center Website

GLOSSARY

This glossary lists definitions, pronunciations, and derivations of the most important recurrent technical terms, units, and names (excluding taxa) used in the text.

A

abiotic (ā′bī-äd′ik) (Gr. *a,* without, + *biōtos,* life, livable). Characterized by the absence of life.

abomasum (ab′ō-mā′səm) (L. *ab,* from, + *omasum,* paunch). Fourth and last chamber of the stomach of ruminant mammals.

aboral (ab-o′rəl) (L. *ab,* from, + *os,* mouth). A region of an animal opposite the mouth.

abscess (ab′ses) (L. *abscessus,* a going away). Dead cells and tissue fluid confined in a localized area, causing swelling.

acanthodians (a′kan-thō′dē-ənz) (Gr. *akantha,* prickly, thorny). A group of the earliest known true jawed fishes from Lower Silurian to Lower Permian.

acanthor (ə-kan′thor) (Gr. *akantha,* spine or thorn, + *or*). First larval form of acanthocephalans in the intermediate host.

acclimatization (ə-klī′mə-də-zā-shən) (L. *ad,* to, + Gr. *klima,* climate). Gradual physiological adaptation in response to relatively long-lasting environmental changes.

acetabulum (as′ə-tab′ū-ləm) (L. a little saucer for vinegar). True sucker, especially in flukes and leeches; the socket in the hip bone that receives the thigh bone.

acicula (ə-sik′ū-lə) (L. *acicula,* a small needle). Needlelike supporting bristle in parapodia of some polychaetes.

acid A molecule that dissociates in solution to produce a hydrogen ion (H^+).

acinus (as′ə-nəs), pl. **acini** (as′ə-nī) (L. grape). A small lobe of a compound gland or a saclike cavity at the termination of a passage.

acoelomate (ā-sēl′ə-māt′) (Gr. *a,* not, + *koilōma,* cavity). Without a coelom, as in flatworms and proboscis worms.

acontium (ə-kän′chē-əm), pl. **acontia** (Gr. *akontion,* dart). Threadlike structure bearing nematocysts located on mesentery of sea anemone.

acquired immune deficiency syndrome An eventual consequence of infection with the human immunodeficiency virus in which the immune response is severely disabled. The disease is ultimately fatal, and no cure has been discovered.

acrocentric (ak′rō-sen′trək) (Gr. *akros,* tip, + *kentron,* center). Chromosome with centromere near the end.

acron (a′crän) (Gr. *akron,* mountaintop, fr. *akros,* tip). Preoral region of an insect.

actin (Gr. *aktis,* ray). A protein in the contractile tissue that forms the thin myofilaments of striated muscle.

actinotroch (ək-tin′ə-trōk) (Gr. *aktis,* ray, beam, + *trochos,* wheel). Larval form found in Phoronida.

active transport Mediated transport in which a permease transports a molecule across a cell membrane against a concentration gradient; requires expenditure of energy; contrast with **facilitated diffusion.**

adaptation (L. *adaptatus,* fitted). An anatomical structure, physiological process, or behavioral trait that evolved by natural selection and improves an organism's ability to survive and leave descendants.

adaptive radiation Evolutionary diversification that produces numerous ecologically disparate lineages from a single ancestral one, especially when this diversification occurs within a short interval of geological time.

adaptive value Degree to which a characteristic helps an organism to survive and reproduce or lends greater fitness in its environment; selective advantage.

adaptive zone A characteristic reaction and mutual relationship between environment and organism ("way of life") demonstrated by a group of evolutionarily related organisms.

adductor (ə-duk′tər) (L. *ad,* to, + *ducere,* to lead). A muscle that draws a part toward a median axis, or a muscle that draws the two valves of a mollusc shell together.

adenine (ad′nēn, ad′ə-nēn) (Gr. *adēn,* gland, + *ine,* suffix). A purine base; component of nucleotides and nucleic acids.

adenosine (ə-den′ə-sen) **(di-, tri) phosphate** (ADP and ATP). A nucleotide composed of adenine, ribose sugar, and two (ADP) or three (ATP) phosphate units; ATP is an energy-rich compound that, with ADP, serves as a phosphate bond-energy transfer system in cells.

adipose (ad′ə-pōs) (L. *adeps,* fat). Fatty tissue; fatty.

adrenaline (ə-dren′ə-lən) (L. *ad,* to, + *renalis,* pertaining to kidneys). A hormone produced by the adrenal, or suprarenal, gland; epinephrine.

adsorption (ad-sorp′shən) (L. *ad,* to, + *sorbeo,* to absorb). The adhesion of molecules to solid bodies.

aerobic (a-rō′bik) (Gr. *aēr,* air, + *bios,* life). Oxygen-dependent form of respiration.

afferent (af′ə-rənt) (L. *ad,* to, + *ferre,* to bear). Adjective meaning leading or bearing toward some organ, for example, nerves conducting impulses toward the brain or blood vessels carrying blood toward an organ; opposed to **efferent.**

aggression (ə-gres′hən) (L. *aggressus,* attack). An offensive action or procedure.

agonistic behavior (Gr. *agōnistēs,* combatant). An offensive action or threat directed toward another organism.

AIDS See **acquired immune deficiency syndrome.**

alate (ā′lāt) (L. *alatus,* wing). Winged.

albumin (al-byū′mən) (L. *albumen,* white of egg). Any of a large class of simple proteins that are important constituents of vertebrate blood plasma and tissue fluids and also present in milk, whites of eggs, and other animal substances.

alimentary (al′ə-men′tə-rē) (L. *alimentum,* food, nourishment). Having to do with nutrition or nourishment.

allantois (ə-lan′tois) (Gr. *allas,* sausage, + *eidos,* form). One of the extraembryonic membranes of the amniotes that functions in respiration and excretion in birds and reptiles and plays an important role in the development of the placenta in most mammals.

allele (ə-lēl′) (Gr. *allēlōn,* of one another). Alternative forms of genes coding for the same trait; situated at the same locus in homologous chromosomes.

allograft (a′lō-graft) (Gr. *allos,* other, + graft). A piece of tissue or an organ transferred from one individual to another individual of the same species, not identical twins; homograft.

allometry (ə-lom′ə-trē) (Gr. *allos,* other, + *metry,* measure). Relative growth of a part in relation to the whole organism.

allopatric (Gr. *allos,* other, + *patra,* native land). In separate and mutually exclusive geographical regions.

alpha-helix (Gr. *alpha,* first, + L. *helix,* spiral). Literally the first spiral arrangement of the genetic DNA molecule; regular coiled arrangement of polypeptide chain in proteins; secondary structure of proteins.

altricial (al-tri′shəl) (L. *altrices,* nourishers). Referring to young animals (especially birds) having the young hatched in an immature, dependent condition.

alula (al′yə-lə) (L. dim. of *ala,* wing). The first digit or thumb of a bird's wing, much reduced in size.

alveolus (al-vē′ə-ləs) (L. dim. of *alveus,* cavity, hollow). A small cavity or pit, such as a microscopic air sac of the lungs, terminal part of an alveolar gland, or bony socket of a tooth.

ambulacra (am′byə-lak′rə) (L. *ambulare,* to walk). In echinoderms, radiating grooves where podia of water-vascular system characteristically project to outside.

amebocyte (ə-mē′bə-sīt) (Gr. *amoibē,* change, + *kytos,* hollow vessel). Cell in metazoan invertebrate, often functioning in defense against invading particles.

ameboid (ə-mē′boid) (Gr. *amoibē,* change, + *oid,* like). Ameba-like in putting forth pseudopodia.

amictic (ə-mik′tic) (Gr. *a,* without, + *miktos,* mixed or blended). Pertaining to female rotifers, which produce only diploid eggs that cannot be fertilized, or to the eggs produced by such females. Compare with **mictic.**

amino acid (ə-mē′nō) (amine, an organic compound). An organic acid with an amino group (—NH_2). Makes up the structure of proteins.

amitosis (ā′mī-tō′səs) (Gr. *a,* not, + *mitos,* thread). A form of cell division in which mitotic nuclear changes do not occur; cleavage without separation of daughter chromosomes.

amniocentesis (am′nē-ō-sin-tē′səs) (Gr. *amnion,* membrane around the fetus, + *centes,* puncture). Procedure for withdrawing a sample of fluid around the developing embryo for examination of chromosomes in the embryonic cells and other tests.

amnion (am′nē-än) (Gr. *amnion,* membrane around the fetus). The innermost of the extraembryonic membranes forming a fluid-filled sac around the embryo in amniotes.

amniote (am′nē-ōt). Having an amnion; as a noun, an animal that develops an amnion in embryonic life, that is, reptiles, birds, and mammals.

amphiblastula (am′fə-blas′chə-lə) (Gr. *amphi,* on both sides, + *blastos,* germ, + L. *ula,* small). Free-swimming larval stage of certain marine sponges; blastula-like but with only the cells of the animal pole flagellated; those of the vegetal pole unflagellated.

amphid (am′fəd) (Gr. *amphidea,* anything that is bound around). One of a pair of anterior sense organs in certain nematodes.

amphipathic (am-fi-pa′thək) (Gr. *amphi,* on both sides, + *pathos,* suffering, passion). Adjective to describe a molecule with one part soluble in water (polar) and another part insoluble in water (nonpolar).

amplexus (am-plek′səs) (L. embrace). The copulatory embrace of frogs or toads.

ampulla (am-pūl′ə) (L. flask). Membranous vesicle; dilation at one end of each semicircular canal containing sensory epithelium; muscular vesicle above tube foot in water-vascular system of echinoderms.

amylase (am′ə-lās′) (L. *amylum,* starch, + *ase,* suffix meaning enzyme). An enzyme that breaks down starch into smaller units.

anabolism (ə-na′bə-li′zəm) (Gr. *ana,* up, + *bol,* to throw, + *ism,* suffix meaning state of condition). Constructive metabolism.

anadromous (an-ad′rə-məs) (Gr. *anadromos,* running upward). Refers to fishes that migrate up streams from the sea to spawn.

anaerobic (an′ə-rō′bik) (Gr. *an,* not, + *aēr,* air, + *bios,* life). Not dependent on oxygen for respiration.

analogy (L. *analogus,* ratio). Similarity of function but not of origin.

anaphylaxis (an′ə-fə-lax′əs) (Gr. *ana-,* up, + *phylax,* guard). A systemic (whole body) immediate hypersensitivity reaction.

anapsid (ə-nap′səd) (Gr. *an,* without, + *apsis,* arch). Amniotes in which the skull lacks temporal openings, with turtles the only living representatives.

anastomosis (ə-nas′tə-mō′səs) (Gr. *ana,* again, + *stoma,* mouth). A union of two or more blood vessels, fibers, or other structures to form a branching network.

androgen (an′drə-jən) (Gr. *anēr, andros,* man, + *genēs,* born). Any of a group of vertebrate male sex hormones.

androgenic gland (an′drō-jen′ək) (Gr. *anēr,* male, + *gennaein,* to produce). Gland in Crustacea that causes development of male characteristics.

aneuploidy (an′ū-ploid′ē) (Gr. *an,* without, not, + *eu,* good, well, + *ploid,* multiple of). Loss or gain of a chromosome, cells of the organism have one fewer than normal chromosome number, or one extra chromosome, for example, trisomy 21 (Down syndrome).

angiotensin (an′jē-o-ten′sən) (Gr. *angeion,* vessel, + L. *tensio,* to stretch). Blood protein formed from the interaction of renin and a liver protein, causing increased blood pressure and stimulating release of aldosterone and ADH.

Angstrom (after Ångström, Swedish physicist). A unit of one ten-millionth of a millimeter (one ten-thousandth of a micrometer); it is represented by the symbol Å.

anhydrase (an-hī′drās) (Gr. *an,* not, + *hydōr,* water, + *ase,* enzyme suffix). An enzyme involved in the removal of water from a compound. Carbonic anhydrase promotes the conversion of carbonic acid into water and carbon dioxide.

anisogametes (an′īs-ō-gam′ēts) (Gr. *anisos,* unequal, + *gametēs,* spouse). Gametes of a species that differ in form or size.

anlage (än′lä-gə) (Ger. laying out, foundation). Rudimentary form; primordium.

annulus (an′yəl-əs) (L. ring). Any ringlike structure, such as superficial rings on leeches.

antenna (L. sail yard). A sensory appendage on the head of arthropods, or the second pair of the two such pairs of structures in crustaceans.

antennal gland Excretory gland of Crustacea located in the antennal metamere.

anterior (L. comparative of *ante,* before). The head end of an organism, or (as an adjective) toward that end.

anthracosaurs (an-thrak′ə-sors) (Gr. *anthrax,* coal, carbon, + *sauros,* lizard). A group of Paleozoic labyrinthodont amphibians.

antibodies (an′tē-bod′ēz). Proteins (immunoglobulins) in cell surfaces and dissolved in blood, capable of combining with the antigens that stimulated their production.

anticodon (an′tī-kō′don). A sequence of three nucleotides in transfer RNA that is complementary to a codon in messenger RNA.

antigen (an′ti-jən). Any substance capable of stimulating an immune response, most often a protein.

antigenic determinant See **epitope.**

aperture (ap′ər-chər) (L. *apertura* from *aperire,* to uncover). An opening; the opening into the first whorl of a gastropod shell.

apex (ā′peks) (L. summit). Highest or uppermost point; the lower pointed end of the heart.

apical (ā′pə-kl) (L. *apex,* tip). Pertaining to the tip or apex.

apical complex A certain combination of organelles found in the protozoan phylum Apicomplexa.

apocrine (ap′ə-krən) (Gr. *apo,* away, + *krinein,* to separate). Applies to a type of mammalian sweat gland that produces a viscous secretion by breaking off a part of the cytoplasm of secreting cells.

apoptosis (a′pə-tō′səs) (Gr. *apo-,* prefix meaning away from, + *ptōsis,* a falling). Genetically determined cell death, "programmed" cell death.

apopyle (ap′ə-pīl) (Gr. *apo,* away from, + *pylē,* gate). In sponges, opening of the radial canal into the spongocoel.

appendicular (L. *ad,* to, + *pendere,* to hang). Pertaining to appendages; pertaining to vermiform appendix.

arboreal (är-bōr′ē-al) (L. *arbor,* tree). Living in trees.

archaeocytes (ärk′ē-ō-sites) (Gr. *archaios,* beginning, + *kytos,* hollow vessel). Ameboid cells of varied function in sponges.

archenteron (ärk-en′tə-rän) (Gr. *archē,* beginning, + *enteron,* gut). The main cavity of an embryo in the gastrula stage; it is lined with endoderm and represents the future digestive cavity.

archinephros (ärk′ē-nəf′rōs) (Gr. *archaois,* ancient, + *nephros,* kidney). Ancestral vertebrate kidney, existing today only in the embryo of hagfishes.

archosaur (är′kə-sor) (Gr. *archōn,* ruling, + *sauros,* lizard). Advanced diapsid vertebrates, a group that includes the living

crocodiles and the extinct pterosaurs and dinosaurs.

areolar (a-rē′ə-ler) (L. *areola,* small space). A small area, such as spaces between fibers of connective tissue.

arginine phosphate Phosphate storage compound (phosphagen) found in many invertebrates and used to regenerate stores of ATP.

Aristotle's lantern Masticating apparatus of some sea urchins.

arteriole (är-tir′ē-ōl) (L. *arteria,* artery). A small arterial branch that delivers blood to a capillary network.

artery (ärt′ə-rē) (L. *arteria,* artery). A blood vessel that carries blood away from the heart and toward a peripheral cavity.

artiodactyl (är′ti-o-dak′təl) (Gr. *artios,* even, + *daktylos,* toe). One of an order of mammals with two or four digits on each foot.

asconoid (Gr. *askos,* bladder). Simplest form of sponges, with canals leading directly from the outside to the interior.

asexual Without distinct sexual organs; not involving formation of gametes.

assimilation (L. *assimilatio,* bringing into conformity). Absorption and building up of digested nutriments into complex organic protoplasmic materials.

atherosclerosis (a′thə-rō-sklə-rō′səs) (Gr. *athērōma,* tumor full of gruel-like material, + *sklērōs,* hard). Disease characterized by fatty plaques forming in the inner lining of arteries.

atoke (ā′tōk) (Gr. *a,* without, + *tokos,* offspring). Anterior, nonreproductive part of a marine polychaete, as distinct from the posterior, reproductive part (epitoke) during the breeding season.

atoll (ə-tol′) (Maldivian, *atolu*). A coral reef or island surrounding a lagoon.

atom The smallest unit of an element, composed of a dense nucleus of protons and (usually) neutrons surrounded by a system of electrons.

ATP Adenosine triphosphate. In biochemistry, an ester of adenosine and triphosphoric acid.

atrium (ā′trē-əm) (L. *atrium,* vestibule). One of the chambers of the heart; also, the tympanic cavity of the ear; also, the large cavity containing the pharynx in tunicates and cephalochordates.

auricle (aw′ri-kl) (L. *auricula,* dim. of *auris,* ear). One of the less muscular chambers of the heart; atrium; the external ear, or pinna; any earlike lobe or process.

auricularia (ə-rik′u-lar′e-ə) (L. *auricula,* a small ear). A type of larva found in Holothuroidea.

autogamy (aw-täg′ə-me) (Gr. *autos,* self, + *gamos,* marriage). Condition in which the gametic nuclei produced by meiosis fuse within the same organism that produced them to restore the diploid number.

autosome (aw′tə-sōm) (Gr. *autos,* self, + *sōma,* body). Any chromosome that is not a sex chromosome.

autotomy (aw-täd′ə-mē) (Gr. *autos,* self, + *tomos,* a cutting). The breaking off of a part of the body by the organism itself.

autotroph (aw′tə-trōf) (Gr. *autos,* self, + *trophos,* feeder). An organism that makes its organic nutrients from inorganic raw materials.

autotrophic nutrition (Gr. *autos,* self, + *trophia,* denoting nutrition). Nutrition characterized by the ability to use simple inorganic substances for the synthesis of more complex organic compounds, as in green plants and some bacteria.

avicularium (L. *avicula,* small bird, + *aria,* like or connected with). Modified zooid that is attached to the surface of the major zooid in Ectoprocta and resembles a bird's beak.

axial (L. *axis,* axle). Relating to the axis, or stem; on or along the axis.

axocoel (ak′sə-cēl) (Gr. *axon,* an axle, + *koilos,* hollow). The most anterior of three coelomic spaces that appear during larval echinoderm development.

axolotl (ak′sə-lot′l) (Nahuatl, *atl,* water, + *xolotl,* doll, servant, spirit). Larval stage of any of several species of the genus *Ambystoma* (such as *Ambystoma tigrinum*) exhibiting neotenic reproduction.

axon (ak′sän) (Gr. *axōn*). Elongate extension of a neuron that conducts impulses away from the cell body and toward the synaptic terminals.

axoneme (aks′ə-nēm) (L. *axis,* axle, + Gr. *nēma,* thread). The microtubules in a cilium or flagellum, usually arranged as a circlet of nine pairs enclosing one central pair; also, the microtubules of an axopodium.

axopodium (ak′sə-pō′di-um) (Gr. *axon,* an axis, + *podion,* small foot). Long, slender, more or less permanent pseudopodium found in certain sarcodine protozoa. (Also **axopod.**)

B

B cell A type of lymphocyte that is most important in the humoral immune response.

barrier reef A coral reef that runs approximately parallel to the shore and is separated from the shore by a lagoon.

basal body Also known as kinetosome and blepharoplast, a cylinder of nine triplets of microtubules found basal to a flagellum or cilium; same structure as a centriole.

base A molecule that dissociates in solution to produce a hydroxide ion.

basis, basipodite (bā′səs, bā-si′pə-dīt) (Gr. *basis,* base, + *pous, podos,* foot). The distal or second joint of the protopod of a crustacean appendage.

bathypelagic (bath′ə-pe-laj′ik) (Gr. *bathys,* deep, + *pelagos,* open sea). Relating to or inhabiting the deep sea.

benthos (ben′thäs) (Gr. depth of the sea). Organisms that live along the bottom of the seas and lakes; adj., **benthic.** Also, the bottom itself.

bilirubin (bil′ə-ru-bən) (L. *bilis,* bile, + *rubeo,* to be red). A breakdown product of the heme group of hemoglobin, excreted in the bile.

binary fission A mode of asexual reproduction in which the animal splits into two approximately equal offspring.

biogenesis (bī′ō-jen′ə-səs) (Gr. *bios,* life, + *genesis,* birth). The doctrine that life originates only from preexisting life.

biological species concept A reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.

bioluminescence Method of light production by living organisms in which usually certain proteins (luciferins), in the presence of oxygen and an enzyme (luciferase), are converted to oxyluciferins with the liberation of light.

biomass (Gr. *bios,* life, + *maza,* lump or mass). The weight of total living organisms or of a species population per unit of area.

biome (bī′ōm) (Gr. *bios,* life, + *ōma,* abstract group suffix). Complex of plant and animal communities characterized by climatic and soil conditions; the largest ecological unit.

biosphere (Gr. *bios,* life, + *sphaira,* globe). That part of earth containing living organisms.

biotic (bī-äd′ik) (Gr. *biōtos,* life, livable). Of or relating to life.

bipinnaria (L. *bi,* double, + *pinna,* wing, + *aria,* like or connected with). Free-swimming, ciliated, bilateral larva of the asteroid echinoderms; develops into the brachiolaria larva.

biramous (bī-rām′əs) (L. *bi,* double, + *ramus,* a branch). Adjective describing appendages with two distinct branches, contrasted with uniramous, unbranched.

bivalent (bī-vāl′ənt) (L. *bi,* double, + *valen,* strength, worth). The pairs of homologous chromosomes at synapsis in the first meiotic division, a tetrad.

blastocoel (blas′tə-sēl) (Gr. *blastos,* germ, + *koilos,* hollow). Cavity of the blastula.

blastocyst (blast′ō-sist) (Gr. *blastos,* germ, + *kystis,* bladder). Mammalian embryo in the blastula stage.

blastomere (Gr. *blastos,* germ, + *meros,* part). An early cleavage cell.

blastopore (Gr. *blastos,* germ, + *poros,* passage, pore). External opening of the archenteron in the gastrula.

blastula (Gr. *blastos,* germ, + L. *ula,* dim.). Early embryological stage of many animals; consists of a hollow mass of cells.

blending See **polygenic inheritance.**

blepharoplast (blə-fä′rə-plast) (Gr. *blepharon,* eyelid, + *plastos,* formed). See **basal body.**

blood plasma The liquid, noncellular fraction of blood, including dissolved substances.

blood type Characteristic of human blood given by the particular antigens on the

membranes of the erythrocytes, genetically determined, causing agglutination when incompatible groups are mixed; the blood types are designated A, B, O, AB, Rh negative, Rh positive, and others.

Bohr effect A characteristic of hemoglobin that causes it to dissociate from oxygen in greater degree at higher concentrations of carbon dioxide.

boreal (bōr′ē-əl) (L. *boreas,* north wind). Relating to a northern biotic area characterized by a predominance of coniferous forests and tundra.

B.P. Before the present.

brachial (brak′ē-əl) (L. *brachium,* forearm). Referring to the arm.

brachiation (brak′ē-ā′shən) (L. *brachium,* arm). Locomotion by swinging by the arms from one hold to another.

brachiolaria (brak′ē-ō-lār′ē-ə) (L. *brachiola,* little arm, + *aria,* pertaining to). This asteroid larva develops from the bipinnaria larva and has three preoral holdfast processes.

bradyzoite An individual coccidian (a single-celled parasite) such as *Toxoplasma gondii* that is encased in a tissue cyst and divides slowly.

brain hormone See **ecdysiotropin.**

branchial (brank′ē-əl) (Gr. *branchia,* gills). Referring to gills.

bronchiole (bräng′kē-ōl) (Gr. *bronchion,* dim. of *bronchos,* windpipe). Small, thin-walled branch of the bronchus.

bronchus (bräng′kəs) pl. **bronchi** (Gr. *bronchos,* windpipe). Either of two primary divisions of the trachea that lead to the right and left lung.

brown fat Mitochondria-rich, heat-generating adipose tissue of endothermic vertebrates.

buccal (buk′əl) (L. *bucca,* cheek). Referring to the mouth cavity.

budding Reproduction in which the offspring arises as an outgrowth from the parent and is initially smaller than the parent. Failure of the offspring to separate from the parent leads to colony formation.

buffer Any substance or chemical compound that tends to keep pH levels constant when acids or bases are added.

bursa pl. **bursae** (M.L. *bursa,* pouch, purse made of skin). A sac-like cavity. In ophiuroid echinoderms, pouches opening at bases of arms and functioning in respiration and reproduction (genitorespiratory bursae).

C

calciferous glands (kal-si′fə-rəs). Glands in an earthworm that secrete calcium ions into the gut.

calorie (kal′ə-rē) (L. *calere,* to be warm). Unit of heat defined as the amount of heat required to heat 1 g of water from 14.5 to 15.5° C; 1 cal = 4.184 joules in the International System of Units.

calyx (kā-′liks) (L. bud cup of a flower). Any of various cup-shaped zoological structures.

cancellous (kan′səl-əs) (L. *cancelli,* latticework, + *osus,* full of). Having a spongy or porous structure.

capitulum (ka-pi′tə-ləm) (L. small head). Term applied to small, headlike structures of various organisms, including projection from body of ticks and mites carrying mouthparts.

captacula (kap-tak′ū-lə) (L. *captare,* to lie in wait for). Tentacles extending from head of scaphopod molluscs, used in feeding.

carapace (kar′ə-pās) (F. from Sp. *carapacho,* shell). Shieldlike plate covering the cephalothorax of certain crustaceans; dorsal part of the shell of a turtle.

carbohydrate (L. *carbo,* charcoal, + Gr. *hydōr,* water). Compounds of carbon, hydrogen, and oxygen having the generalized formula $(CH_2O)_n$; aldehyde or ketone derivatives of polyhydric alcohols, with hydrogen and oxygen atoms attached in a 2:1 ratio.

carboxyl (kär-bäk′səl) (carbon + oxygen + yl, chemical radical suffix). The acid group of organic molecules (—COOH.)

cardiac (kär′dē-ak) (Gr. *kardia,* heart). Belonging or relating to the heart.

carinate (kar′ə-nāt) (L. *carina,* keel). Having a keel, in particular the flying birds with a keeled sternum for the insertion of flight muscles.

carnivore (kar′nə-vōr′) (L. *carnivorous,* flesh eating). One of the flesh-eating mammals of the order Carnivora. Also, any organism that eats animals. Adj., **carnivorous.**

carotene (kär′ə-tēn) (L. *carota,* carrot, + *ene,* unsaturated straight-chain hydrocarbons). A red, orange, or yellow pigment belonging to the group of carotenoids; precursor of vitamin A.

carrying capacity The maximum number of individuals that can persist under specified environmental conditions.

cartilage (L. *cartilago;* akin to L. *cratis,* wickerwork). A translucent elastic tissue that makes up most of the skeleton of embryos, very young vertebrates, and adult cartilaginous fishes, such as sharks and rays; in higher forms much of it is converted into bone.

caste (kast) (L. *castus,* pure, separated). One of the polymorphic forms within an insect society, each caste having its specific duties, as queen, worker, soldier, and so on.

catabolism (Gr. *kata,* downward, + *bol,* to throw, + *ism,* suffix meaning state of condition). Destructive metabolism; process in which complex molecules are reduced to simpler ones.

catadromous (kə-tad′rə-məs) (Gr. *kata,* down, + *dromos,* a running). Refers to fishes that migrate from fresh water to the ocean to spawn.

catalyst (kad′ə-ləst) (Gr. *kata,* down, + *lysis,* a loosening). A substance that accelerates a chemical reaction but does not become a part of the end product.

caudal (käd′l) (L: *cauda,* tail). Constituting, belonging to, or relating to a tail.

caveolae (ka-vē′ə-lē) (L. *cavea,* a cave, + dim. suffix). The invaginated vesicles and pits in potocytosis.

cDNA See **complementary DNA.**

cecum, caecum (sē′kəm) (L. *caecus,* blind). A blind pouch at the beginning of the large intestine; any similar pouch.

cell-mediated immune response Immune response involving cell surfaces only, not antibody production, specifically the T_H1 arm of the immune response. Contrast **humoral immune response.**

cellulose (sel′ū-lōs) (L. *cella,* small room). Chief polysaccharide constituent of the cell wall of green plants and some fungi; an insoluble carbohydrate $(C_6H_{10}O_5)_n$ that is converted into glucose by hydrolysis.

centriole (sen′trē-ol) (Gr. *kentron,* center of a circle, + L. *ola,* small). A minute cytoplasmic organelle usually found in the centrosome and considered to be the active division center of the animal cell; organizes spindle fibers during mitosis and meiosis. Same structure as basal body or kinetosome.

centrolecithal (sen′tro-les′ə-thəl) (Gr. *kentron,* center, + *lekithos,* yolk, + Eng. *al,* adjective). Pertaining to an insect egg with the yolk concentrated in the center.

centromere (sen′trə-mir) (Gr. *kentron,* center, + *meros,* part). A localized constriction in a characteristic position on a given chromosome, bearing the kinetochore.

centrosome (sen′trə-sōm) (Gr. *kentron,* center, + *sōma*, body). Microtubule organizing center in nuclear division in most eukaryotic cells; in animals and many unicellular organisms it surrounds the centrioles.

cephalization (sef′ə-li-zā-shən) (Gr. *kephale,* head). The process by which specialization, particularly of the sensory organs and appendages, become localized in the head end of animals.

cephalothorax (sef′ə-lä-thō′raks) (Gr. *kephale,* head, + thorax). A body division found in many Arachnida and higher Crustacea, in which the head is fused with some or all of the thoracic segments.

cercaria (ser-kar′ē-ə) (Gr. *kerkos,* tail, + L. *aria,* like or connected with). Tadpolelike larva of trematodes (flukes).

cervical (sər′və-kəl) (L. *cervix,* neck). Relating to a neck.

character (kar′ik-tər). A component of phenotype (including specific molecular, morphological, behavioral or other features) used by systematists to diagnose species or higher taxa, or to evaluate phylogenetic relationships among different species or higher taxa, or relationships among populations within a species.

charging In protein synthesis, a reaction catalyzed by tRNA synthetase, in which an

amino acid is attached to its particular tRNA molecule.

chelicera (kə-lis′ə-rə) pl. **chelicerae** (Gr. *chēlē,* claw, + *keras,* horn). One of a pair of the most anterior head appendages on the members of the subphylum Chelicerata.

chelipeds (kēl′ə-peds) (Gr. *chēlē,* claw, + L. *pes,* foot). Pincerlike first pair of legs in most decapod crustaceans; specialized for seizing and crushing.

chemoautotroph (ke′mō-aw′tō-trōf) (Gr. *chemeia,* transmutation, + *autos,* self, + *trophos,* feeder). An organism utilizing inorganic compounds as a source of energy.

chemotaxis (kē′mō-tak′səs) (Gr. *chēmeia,* an infusion, + *taxō* > *tassō,* to put in order). Orientation movement of cells or organisms in response to a chemical stimulus.

chemotroph (kem′ə-trōf) (Gr. *chēmeia,* an infusion, + *tropē,* to turn). An organism that derives nourishment from inorganic substances without using chlorophyll.

chiasma (kī-az′mə), pl. **chiasmata** (Gr. cross). An intersection or crossing, as of nerves; a connection point between homologous chromatids where crossing over has occurred at synapsis.

chitin (kī′tən) (Fr. *chitine,* from Gr. *chitōn,* tunic). A horny substance that forms part of the cuticle of arthropods and is found sparingly in certain other invertebrates; a nitrogenous polysaccharide insoluble in water, alcohol, dilute acids, and digestive juices of most animals.

chlorocruorin (klō′rō-kroo′ə-rən) (Gr. *chlōros,* light green, + L. *cruor,* blood). A greenish iron-containing respiratory pigment dissolved in the blood plasma of certain marine polychaetes.

chlorogogen cells (klōr′ə-gog-ən) (Gr. *chlōros,* light green, + *agōgos,* a leading, a guide). Modified peritoneal cells, greenish or brownish, clustered around the digestive tract of certain annelids; apparently they aid in elimination of nitrogenous wastes and in food transport.

chlorophyll (klō′rə-fil) (Gr. *chlōros,* light green, + *phyllōn,* leaf). Green pigment found in plants and in some animals; necessary for photosynthesis.

chloroplast (klō′rə-plast) (Gr. *chlōros,* light green, + *plastos,* molded). A plastid containing chlorophyll and usually other pigments, found in cytoplasm of plant cells.

choanocyte (kō-an′ə-sīt) (Gr. *choanē,* funnel, + *kytos,* hollow vessel). One of the flagellate collar cells that line cavities and canals of sponges.

cholinergic (kōl′i-nər′jik) (Gr. *chōle,* bile, + *ergon,* work). Type of nerve fiber that releases acetylcholine from axon terminal.

chorion (kō′rē-on) (Gr. *chorion,* skin). The outer of the double membrane that surrounds the embryo of reptiles, birds, and mammals; in mammals it contributes to the placenta.

choroid (kōr′oid) (Gr. *chorion,* skin, + *eidos,* form). Delicate, highly vascular membrane; in vertebrate eye; the layer between the retina and sclera.

chromatid (krō′mə-tid) (Gr. *chromato,* from *chrōma,* color, + L. *id,* feminine stem for particle of specified kind). A replicated chromosome joined to its sister chromatid by the centromere; separates and becomes daughter chromosome at anaphase of mitosis or anaphase of the second meiotic division.

chromatin (krō′mə-tin) (Gr. *chrōma,* color). The nucleoprotein material of a chromosome; the hereditary material containing DNA.

chromatophore (krō-mat′ə-fōr) (Gr. *chrōma,* color, + *pherein,* to bear). Pigment cell, usually in the dermis, in which usually the pigment can be dispersed or concentrated.

chromomere (krō′mō-mir) (Gr. *chrōma,* color, + *meros,* part). One of the chromatin granules of characteristic size on the chromosome; may be identical with a gene or a cluster of genes.

chromonema (krō-mə-nē′mə) (Gr. *chrōma,* color, + *nēma,* thread). A convoluted thread in prophase of mitosis or the central thread in a chromosome.

chromoplast (krō′mə-plast) (Gr. *chrōma,* color, + *plastos,* molded). A plastid-containing pigment.

chromosome (krō′mə-sōm) (Gr. *chrōma,* color, + *sōma,* body). A complex body, spherical or rod shaped, that arises from the nuclear network during mitosis, splits longitudinally, and carries a part of the organism's genetic information as genes composed of DNA.

chrysalis (kris′ə-lis) (L. from Gr. *chrysos,* gold). The pupal stage of a butterfly.

chyme (kīm) (Gr. *chymos,* juice). Semifluid mass of partly digested food in stomach and small intestine as digestion proceeds.

cilium (sil′i-əm), pl. **cilia** (L. eyelid). A hairlike, vibratile organelle process found on many animal cells. Cilia may be used in moving particles along the cell surface or, in ciliate protozoans, for locomotion.

cinclides (sing′klid-əs), sing. **cinclis** (sing′kləs) (Gr. *kinklis,* latticed gate or partition). Small pores in the external body wall of sea anemones for extrusion of acontia.

circadian (sər-kād′ē-ən) (L. *circa,* around, + *dies,* day). Occurring at a period of approximately 24 hours.

cirrus (sir′əs) (L. curl). A hairlike tuft on an insect appendage; locomotor organelle of fused cilia; male copulatory organ of some invertebrates.

cisternae (sis-ter′nē) (L. *cista,* box). Space between membranes of the endoplasmic reticulum within cells.

cistron (sis′trən) (L. *cista,* box). A series of codons in DNA that code for an entire polypeptide chain.

clade (klād) (Gr. *klados,* branch). A taxon or other group consisting of an ancestral species and all of its descendants, forming a distinct branch on a phylogenetic tree.

cladistics (klad-is′-təks) (Gr. *klados,* branch, sprout). A system of arranging taxa by analysis of evolutionarily derived characteristics so that the arrangement will reflect phylogenetic relationships.

cladogram (klād′ə-gram) (Gr. *klados,* branch, + *gramma,* letter). A branching diagram showing the pattern of sharing of evolutionarily derived characters among species or higher taxa.

clathrin (kla′thrən) (L. *chathri,* latticework). A protein forming a lattice structure lining the invaginated pits during receptor-mediated endocytosis.

cleavage (O.E. *cleofan,* to cut). Process of nuclear and cell division in animal zygote.

climax (klī′maks) (Gr. *klimax,* ladder). Stage of relative stability attained by a community of organisms, often the culminating development of a natural succession. Also, orgasm.

climax community (Gr. *klimax,* ladder, staircase, climax). A self-perpetuating, more-or-less stable community of organisms that continues as long as environmental conditions under which it developed prevail.

clitellum (klī-tel′əm) (L. *clitellae,* packsaddle). Thickened saddlelike portion of certain midbody segments of many oligochaetes and leeches.

cloaca (klō-ā′kə) (L. sewer). Posterior chamber of digestive tract in many vertebrates, receiving feces and urogenital products. In certain invertebrates, a terminal portion of digestive tract that serves also as respiratory, excretory, or reproductive tract.

clone (klōn) (Gr. *klōn,* twig). All descendants derived by asexual reproduction from a single individual.

cnidoblast (nī′də-blast) (Gr. *knidē,* nettle, + *blastos,* germ). See **cnidocyte.**

cnidocil (nī′də-sil) (Gr. *knidē,* nettle, + L. *cilium,* hair). Modified cilium on nematocyst-bearing cnidocytes in cnidarians; triggers nematocyst.

cnidocyte (nī′də-sīt) (Gr. *knidē,* nettle, + *kytos,* hollow vessel). Modified interstitial cell that holds the nematocyst; during development of the nematocyst, the cnidocyte is a cnidoblast.

coacervate (kō′ə-sər′vət) (L. *coacervatus,* to heap up). An aggregate of colloidal droplets held together by electrostatic forces.

coagulation (kō-ag′ū-lā-shən). Process in which a series of enzymes are activated, resulting in clotting of blood.

cochlea (kōk′lēə) (L. snail, from Gr. *kochlos,* a shellfish). A tubular cavity of the inner ear containing the essential organs of hearing; occurs in crocodiles, birds, and mammals; spirally coiled in mammals.

cocoon (kə-kun′) (Fr. *cocon,* shell). Protective covering of a resting or developmental stage, sometimes used to refer to both the covering and its contents; for example, the cocoon of a moth or the protective covering

for the developing embryos in some annelids.

codominance See **intermediate inheritance.**

codon (kō′dän) (L. code, + on). In messenger RNA a sequence of three adjacent nucleotides that codes for one amino acid.

coelenteron (sē-len′tər-on) (Gr. *koilos,* hollow, + *enteron,* intestine). Internal cavity of a cnidarian; gastrovascular cavity; archenteron.

coelom (sē′lōm) (Gr. *koilōma,* cavity). The body cavity in triploblastic animals, lined with mesodermal peritoneum.

coelomocyte (sē′lō′mə-sīt) (Gr. *koilōma,* cavity, + *kytos,* hollow vessel). Another name for amebocyte; primitive or undifferentiated cell of the coelom and the water-vascular system.

coelomoduct (sē-lō′mə-dukt) (Gr. *koilos,* hollow, + L. *ductus,* a leading). A duct that carries gametes or excretory products (or both) from the coelom to the exterior.

coenecium, coenoecium (sə-nēs[h]′ē-əm) (Gr. *koinos,* common, + *oikion,* house). The common secreted investment of an ectoproct colony; may be chitinous, gelatinous, or calcareous.

coenenchyme (sēn′ən-kīm) (Gr. *koinos,* shared in common, + *enchyma,* something poured in). Extensive mesogleal tissue between the polyps of an alcyonarian (phylum Cnidaria) colony.

coenocytic (sē-nə-sit′ik) (Gr. *koinos,* common, + *kytos,* hollow vessel). A tissue in which the nuclei are not separated by cell membranes; syncytial.

coenosarc (sē′nə-särk) (Gr. *koinos,* shared in common, + *sarkos,* flesh). The inner, living part of hydrocauli in hydroids.

coenzyme (kō-en′zīm) (L. prefix, *co,* with, + Gr. *enzymos,* leavened, from *en,* in, + *zymē,* leaven). A required substance in the activation of an enzyme; a prosthetic or nonprotein constituent of an enzyme.

collagen (käl′ə-jən) (Gr. *kolla,* glue, + *genos,* descent). A structural protein, the most abundant protein in the animal kingdom, characterized by high content of the amino acids glycine, alanine, proline, and hydroxyproline.

collenchyme (käl′ən-kīm) (Gr. *kolla,* glue, + *enchyma,* infusion). A gelatinous mesenchyme containing undifferentiated cells; found in cnidarians and ctenophores.

collencyte (käl′lən-sīt) (Gr. *kolla,* glue, + *en,* in, + *kytos,* hollow vessel). A type of cell in sponges that is star shaped and apparently contractile.

colloblast (käl′ə-blast) (Gr. *kolla,* glue, + *blastos,* germ). A glue-secreting cell on the tentacles of ctenophores.

colloid (kä′loid) (Gr. *kolla,* glue, + *eidos,* form). A two-phase system in which particles of one phase are suspended in the second phase.

columella (kä′lə-mel′ə) (L. small column). Central pillar in gastropod shells.

comb plate One of the plates of fused cilia that are arranged in rows for ctenophore locomotion.

commensalism (kə-men′səl-iz′əm) (L. *cum,* together with, + *mensa,* table). A relationship in which one individual lives close to or on another and benefits, and the host is unaffected; often symbiotic.

community (L. *communitas,* community, fellowship). An assemblage of organisms that are associated in a common environment and interact with each other in a self-sustaining and self-regulating relation.

competition Some degree of overlap in ecological niches of two populations in the same community, such that both depend on the same food source, shelter, or other resources, and negatively affect each other's survival.

complement Collective name for a series of enzymes and activators in the blood, some of which may bind to antibody and may lead to rupture of a foreign cell.

complementary DNA (cDNA) DNA prepared by transcribing the base sequence from mRNA into DNA by reverse transcriptase; also called **copy DNA.**

compound A substance whose molecules are composed of atoms of two or more elements.

condensation reaction A chemical reaction in which reactant molecules are combined by the removal of a water molecule (a hydrogen from one and a hydroxyl from the other reactant).

condyle (kän′dīl) (Gr. *kondylos,* bump). A process on a bone used for articulation.

conjugation (kon′ju-gā′shən) (L. *conjugare,* to yoke together). Temporary union of two ciliate protozoa while they are exchanging chromatin material and undergoing nuclear phenomena resulting in binary fission. Also, formation of cytoplasmic bridges between bacteria for transfer of plasmids.

conspecific (L. *com,* together, + *species*). A member of the same species.

contractile vacuole A clear fluid-filled cell vacuole in protozoa and a few lower metazoa; takes up water and releases it to the outside in a cyclical manner, for osmoregulation and some excretion.

control That part of a scientific experiment to which the experimental variable is not applied but which is similar to the experimental group in all other respects.

coprophagy (kə-prä′fə-jē) (Gr. *kopros,* dung, + *phagein,* to eat). Feeding on dung or excrement as a normal behavior among animals; reinjestion of feces.

copulation (Fr. from L. *copulare,* to couple). Sexual union to facilitate the reception of sperm by the female.

copy DNA See **complementary DNA.**

coralline algae Algae that precipitate calcium carbonate in their tissues; important contributors to coral reef mass.

corium (kō′re-um) (L. *corium,* leather). The deep layer of the skin; dermis.

cornea (kor′nē-ə) (L. *corneus,* horny). The outer transparent coat of the eye.

corneum (kor′nē-əm) (L. *corneus,* horny). Epithelial layer of dead, keratinized cells. Stratum corneum.

cornified (kor′nə-fīd) (L. *corneus,* horny). Adjective for conversion of epithelial cells into nonliving, keratinized cells.

corona (kə-rō′nə) (L. crown). Head or upper portion of a structure; ciliated disc on anterior end of rotifers.

corpora allata (kor′pə-rə əl-la′tə) (L. *corpus,* body, + *allatum,* aided). Endocrine glands in insects that produce juvenile hormone.

corpora cardiaca (kor′pə-rə kar-dī′ə-cə) (L. *corpus,* body, + Gr. *kardiakos,* belonging to the heart). Paired organs behind the brain of insects, serve as storage and release organs for brain hormone.

cortex (kor′teks) (L. bark). The outer layer of a structure.

covalent bond. A chemical bond in which electrons are shared between atoms.

coxa, coxopodite (kox′ə, kəx-ä′pə-dīt) (L. *coxa,* hip, + Gr. *pous, podos,* foot). The proximal joint of an insect or arachnid leg; in crustaceans, the proximal joint of the protopod.

creatine phosphate High-energy phosphate compound found in the muscle of vertebrates and some invertebrates, used to regenerate stores of ATP.

cretin (krēt′n) (Fr. *crétin,* [dialect], fr. L. *christianus,* Christian, to indicate idiots so afflicted were also human). A human with severe mental, somatic, and sexual retardation resulting from hypothyroidism during early stages of development.

crista (kris′ta), pl. **cristae** (L. *crista,* crest). A crest or ridge on a body organ or organelle; a platelike projection formed by the inner membrane of mitochondrion.

crossing over Exchange of parts of nonsister chromatids at synapsis in the first meiotic division.

cryptobiotic (Gr. *kryptos,* hidden, + *biōticus,* pertaining to life). Living in concealment; refers to insects and other animals that live in secluded situations, such as underground or in wood; also tardigrades and some nematodes, rotifers, and others that survive harsh environmental conditions by assuming for a time a state of very low metabolism.

ctenidia (te-ni′dē-ə) (Gr. *kteis,* comb). Comblike structures, especially gills of molluscs; also applied to comb plates of Ctenophora.

ctenoid scales (ten′oid) (Gr. *kteis, ktenos,* comb). Thin, overlapping dermal scales of the more advanced fishes; exposed posterior margins have fine, toothlike spines.

cupula (kū′pū-lə) (L. little tub). Small inverted cup-like structure housing another structure; gelatinous matrix covering hair cells in lateral line and equilibrium organs.

cuticle (kū′ti-kəl) (L. *cutis,* skin). A protective, noncellular, organic layer secreted by the

external epithelium (hypodermis) of many invertebrates. In higher animals the term refers to the epidermis or outer skin.

cyanobacteria (sī-an-ō-bak-ter′ē-ə) (Gr. *kyanos,* a dark-blue substance, + *bakterion,* dim. of *baktron,* a staff). Photosynthetic prokaryotes, also called blue-green algae, cyanophytes.

cyanophyte (sī-an′ō-fit) (Gr. *kyanos,* a dark-blue substance, + *phyton,* plant). A cyanobacterium, blue-green alga.

cyclin A protein important in the control of the cell division cycle and mitosis.

cycloid scales (sī′-kloid) (Gr. *kyklos,* circle). Thin, overlapping dermal scales of the more primitive fishes; posterior margins are smooth.

cydippid larva (sī-dip′pid) (Gr. *kydippe,* mythological Athenian maiden). Free-swimming larva of most ctenophores; superficially similar to the adult.

cynodonts (sin′ə-dänts) (Gr. *kynodōn,* canine tooth). A group of mammal-like carnivorous synapsids of the Upper Permian and Triassic.

cyrtocyte (ser′tō-sīt) (Gr. *kyrtē,* a fish basket, cage, + *kytos,* hollow vessel). A protonephridial cell with a single flagellum enclosed in a cylinder of cytoplasmic rods.

cystacanth (sis′tə-kanth) (Gr. *kystis,* bladder, pouch, + *akantha,* thorn). Juvenile stage of an acanthocephalan that is infective to the definitive host.

cysticercoid (sis′tə-ser′koəd) (Gr. *kystis,* bladder, + *kerkos,* tail, + *eidos,* form). A type of juvenile tapeworm composed of a solid-bodied cyst containing an invaginated scolex; contrast with **cysticercus.**

cysticercus (sis′tə-ser′kəs) (Gr. *kystis,* bladder, + *kerkos,* tail). A type of juvenile tapeworm in which an invaginated and introverted scolex is contained in a fluid-filled bladder; contrast with **cysticercoid.**

cystid (sis′tid) (Gr. *kystis,* bladder). In an ectoproct, the dead secreted outer parts plus the adherent underlying living layers.

cytochrome (sī′tə-krōm) (Gr. *kytos,* hollow vessel, + *chrōma,* color). Several iron-containing pigments that serve as electron carriers in aerobic respiration.

cytokine (sī′tə-kīn) (Gr. *kytos,* hollow vessel, + *kinein,* to move). A molecule secreted by an activated or stimulated cell, for example, macrophages, that causes physiological changes in certain other cells.

cytokinesis (sī′tə-kin-ē′sis) (Gr. *kytos,* hollow vessel, + *kinesis,* movement). Division of the cytoplasm of a cell.

cytopharynx (Gr. *kytos,* hollow vessel, + *pharynx,* throat). Short tubular gullet in ciliate protozoa.

cytoplasm (sī′tə-plasm) (Gr. *kytos,* hollow vessel, + *plasma,* mold). The living matter of the cell, excluding the nucleus.

cytoproct (sī′tə-prokt) (Gr. *kytos,* hollow vessel, + *prōktos,* anus). Site on a protozoan where undigestible matter is expelled.

cytopyge (sī′tə-pīj) (Gr. *kytos,* hollow vessel, + *pyge,* rump or buttocks). In some protozoa, localized site for expulsion of wastes.

cytosol (sī′tə-sol) (Gr. *kytos,* hollow vessel, + L. *sol,* from *solutus,* to loosen). Unstructured portion of the cytoplasm in which the organelles are bathed.

cytosome (sī′tə-sōm) (Gr. *kytos,* hollow vessel, + *sōma,* body). The cell body inside the plasma membrane.

cytostome (sī′tə-stōm) (Gr. *kytos,* hollow vessel, + *stoma,* mouth). The cell mouth in many protozoa.

cytotoxic T cells (Gr. *kytos,* hollow vessel, + toxin). A special T cell activated during cell-mediated immune responses that recognizes and destroys virus-infected cells.

D

dactylozooid (dak-til′ə-zō-id) (Gr. *dakos,* bite, sting, + *tylos,* knob, + *zōon,* animal). A polyp of a colonial hydroid specialized for defense or killing food.

Darwinism Theory of evolution emphasizing common descent of all living organisms, gradual change, multiplication of species and natural selection.

data sing. **datum** (Gr. *dateomai,* to divide, cut in pieces). The results in a scientific experiment, or descriptive observations, upon which a conclusion is based.

deciduous (də-sij′ə-wəs) (L. *decidere,* to fall off). Shed or falling off at end of a growing period.

deduction (L. *deductus,* led apart, split, separated). Reasoning from the general to the particular, that is, from given premises to their necessary conclusion.

definitive host The host in which sexual reproduction of a symbiont takes place; if no sexual reproduction, then the host in which the symbiont becomes mature and reproduces; contrast **intermediate host.**

delayed type hypersensitivity Inflammatory reaction based primarily on cell-mediated immunity.

deme (dēm) (Gr. populace). A local population of closely related animals.

demography (də-mäg′rə-fē) (Gr. *demos,* people, + *graphy*). The properties of the rate of growth and the age structure of populations.

dendrite (den′drīt) (Gr. *dendron,* tree). Any of nerve cell processes that conduct impulses toward the cell body.

deoxyribonucleic acid (DNA) The genetic material of all organisms, characteristically organized into linear sequences of genes.

deoxyribose (dē-ok′sē-rī′bōs) (L. *deoxy,* loss of oxygen, + *ribose,* a pentose sugar). A 5-carbon sugar having 1 oxygen atom less than ribose; a component of deoxyribonucleic acid (DNA).

dermal (Gr. *derma,* skin). Pertaining to the skin; cutaneous.

dermis The inner, sensitive mesodermal layer of skin; corium.

desmosome (dez′mə-sōm) (Gr. *desmos,* bond, + *sōma,* body). Buttonlike plaque serving as an intercellular connection.

determinate cleavage The type of cleavage, usually spiral, in which the fate of the blastomeres is determined very early in development; mosaic cleavage.

detritus (də-trī′tus) (L. that which is rubbed or worn away). Any fine particulate debris of organic or inorganic origin.

Deuterostomia (dū′də-rō-stō′mē-ə) (Gr. *deuteros,* second, secondary, + *stoma,* mouth). A group of higher phyla in which cleavage is indeterminate (regulative) and primitively radial. The endomesoderm is enterocoelous, and the mouth is derived away from the blastopore. Includes Echinodermata, Chordata, and a number of minor phyla. Compare with Protostomia.

dextral (dex′trəl) (L. *dexter,* right-handed). Pertaining to the right; in gastropods, shell is dextral if opening is to right of columella when held with spire up and facing observer.

diapause (dī′ə-pawz) (Gr. *diapausis,* pause). A period of arrested development in the life cycle of insects and certain other animals in which physiological activity is very low and the animal is highly resistant to unfavorable external conditions.

diapsids (dī-ap′səds) (Gr. *di,* two, + *apsis,* arch). Amniotes in which the skull bears two pairs of temporal openings; includes reptiles (except turtles) and birds.

diastole (dī-as′tə-lē) (Gr. *diastolē,* dilation). Passive relaxation and expansion of the heart during which the chambers are filled with blood.

diffusion (L. *diffusus,* dispersion). The movement of particles or molecules from area of high concentration of the particles or molecules to area of lower concentration.

digitigrade (dij′ə-də-grād) (L. *digitus,* finger, toe, + *gradus,* step, degree). Walking on the digits with the posterior part of the foot raised; compare plantigrade.

dihybrid (dī-hī′brəd) (Gr. *dis,* twice, + L. *hibrida,* mixed offspring). A hybrid whose parents differ in two distinct characters; an offspring having two different alleles at two different loci, for example, *A/a B/b.*

dimorphism (dī-mor′fizm) (Gr. *di,* two, + *morphē,* form). Existence within a species of two distinct forms according to color, sex, size, organ structure, and so on. Occurrence of two kinds of zooids in a colonial organism.

dioecious (dī-ē′shəs) (Gr. *di,* two, + *oikos,* house). Having male and female organs in separate individuals.

diphycercal (dif′i-ser′kəl) (Gr. *diphyēs,* twofold, + *kerkos,* tail). A tail that tapers to a point, as in lungfishes; vertebral column extends to tip without upturning.

diphyodont (di′fi-ə-dänt) (Gr. *diphyēs,* twofold, + *odous,* tooth). Having deciduous and permanent sets of teeth successively.
diploblastic (di′plə-blas′tək) (Gr. *diploos,* double, + *blastos,* bud). Organism with two germ layers, endoderm and ectoderm.
diploid (dip′loid) (Gr. *diploos,* double, + *eidos,* form). Having the somatic (double, or 2*n*) number of chromosomes or twice the number characteristic of a gamete of a given species.
disaccharides (dī-sak′ə-rīds) (Gr. *dis,* twice, + L. *saccharum,* sugar). A class of sugars (such as lactose, maltose, and sucrose) that yield two monosaccharides on hydrolysis.
distal (dis′təl). Farther from the center of the body than a reference point.
DNA See **deoxyribonucleic acid.**
dominance hierarchy A social ranking, formed through agonistic behavior, in which individuals are associated with each other so that some have greater access to resources than do others.
dominant An allele that is expressed regardless of the nature of the corresponding allele on the homologous chromosome.
dorsal (dor′səl) (L. *dorsum,* back). Toward the back, or upper surface, of an animal.
Down syndrome A congenital syndrome including mental retardation, caused by the cells in a person's body having an extra chromosome 21; also called trisomy 21.
dual-gland adhesive organ Organs in the epidermis of most turbellarians, with three cell types; viscid and releasing gland cells and anchor cells.
duodenum (dū-ə-dēn′əm) (L. *duodeni,* twelve each, fr. its length, about 12 fingers' width). The first and shortest portion of the small intestine lying between the pyloric end of the stomach and the jejunum.
dyad (dī′əd) (Gr. *dyas,* two). One of the groups of two chromosomes formed by the division of a tetrad during the first meiotic division.

E

eccrine (ek′rən) (Gr. *ek,* out of, + *krinein,* to separate). Applies to a type of mammalian sweat gland that produces a watery secretion.
ecdysiotropin (ek-dē-zē-o-tro′pən) (Gr. *ekdysis,* to strip off, escape, + *tropos,* a turn, change). Hormone secreted in brain of insects that stimulates prothoracic gland to secrete molting hormone. Prothoracicotropic hormone; brain hormone.
ecdysis (ek′də-sis) (Gr. *ekdysis,* to strip off, escape). Shedding of outer cuticular layer; molting, as in insects or crustaceans.
ecdysone (ek-dī′sōn) (Gr. *ekdysis,* to strip off). Molting hormone of arthropods, stimulates growth and ecdysis, produced by prothoracic glands in insects and Y organs in crustaceans.
ecocline (ek′ō-klīn) (Gr. *oikos,* home, + *klino,* to slope, recline). The gradient between adjacent biomes; a gradient of environmental conditions.
ecology (Gr. *oikos,* house, + *logos,* discourse). Part of biology that deals with the relationship between organisms and their environment.
ecosystem (ek′ō-sis-təm) (eco[logy] from Gr. *oikos,* house, + system). An ecological unit consisting of both the biotic communities and the nonliving (abiotic) environment, which interact to produce a stable system.
ecotone (ek′ō-tōn) (eco[logy] from Gr. *oikos,* home, + *tonos,* stress). The transition zone between two adjacent communities.
ectoderm (ek′tō-derm) (Gr. *ektos,* outside, + *derma,* skin). Outer layer of cells of an early embryo (gastrula stage); one of the germ layers, also sometimes used to include tissues derived from ectoderm.
ectognathous (ek′tə-nā′thəs) (Gr. *ektos,* outside, without, + *gnathos,* jaw). Derived character of most insects; mandibles and maxillae not in pouches.
ectolecithal (ek′tō-les′ə-thəl) (Gr. *ektos,* outside, + *lekithos,* yolk). Yolk for nutrition of the embryo contributed by cells that are separate from the egg cell and are combined with the zygote by envelopment within the eggshell.
ectoneural (ek′tə-nu-rəl) (Gr. *ektos,* outside, without, + *neuron,* nerve). Oral (chief) nervous system in echinoderms.
ectoplasm (ek′tō-plazm) (Gr. *ektos,* outside, + *plasma,* form). The cortex of a cell or that part of cytoplasm just under the cell surface; contrasts with **endoplasm.**
ectothermic (ek′tō-therm′ic) (Gr. *ektos,* outside, + *thermē,* heat). Having a variable body temperature derived from heat acquired from the environment; contrasts with **endothermic.**
edema (ē-dē′mə) (Gr. *oidēma,* swelling). Escape of fluid from blood into interstitial space, causing swelling.
effector (L. *efficere,* bring to pass). An organ, tissue, or cell that becomes active in response to stimulation.
efferent (ef′ə-rənt) (L. *ex,* out, + *ferre,* to bear). Leading or conveying away from some organ, for example, nerve impulses conducted away from the brain, or blood conveyed away from an organ; contrasts with **afferent.**
egestion (ē-jes′chən) (L. *egestus,* to discharge). Act of casting out indigestible or waste matter from the body by any normal route.
electron A subatomic particle with a negative charge and a mass of 9.1066×10^{-28} gram.
eleocyte (el′ē-ə-sīt) (Gr. *elaion,* oil, + *kytos,* hollow vessel). Fat-containing cells in annelids that originate from the chlorogogen tissue.
elephantiasis (el-ə-fən-tī′ə-səs). Disfiguring condition caused by chronic infection with filarial worms *Wuchereria bancrofti* and *Brugia malayi.*
embryogenesis (em′brē-ō-jen′ə-səs) (Gr. *embryon,* embryo, + *genesis,* origin). The origin and development of the embryo; embryogeny.
emergence (L. *e,* out, + *mergere,* to plunge). The appearance of properties in a biological system (at the molecular, cellular, organismal, or species levels) that cannot be deduced from knowledge of the component parts taken separately or in partial combinations; such properties are termed **emergent properties.**
emigrate (L. *emigrare,* to move out). To move *from* one area to another to take up residence.
emulsion (ə-məl′shən) (L. *emulsus,* milked out). A colloidal system in which both phases are liquids.
endemic (en-dem′ik) (Gr. *en,* in, + *demos,* populace). Peculiar to a certain region or country; native to a restricted area; not introduced.
endergonic (en-dər-gän′ik) (Gr. *endon,* within, + *ergon,* work). Used in reference to a chemical reaction that requires energy; energy absorbing.
endite (en′dīt) (Gr. *endon,* within). Medial process on an arthropod limb.
endochondral (en′dō-kän′drōl) (Gr. *endon,* within, + *chondros,* cartilage). Occurring with the substance of cartilage, especially bone formation.
endocrine (en′də-krən) (Gr. *endon,* within, + *krinein,* to separate). Refers to a gland that is without a duct and that releases its product directly into the blood or lymph.
endocytosis (en′dō-sī-tō-səs) (Gr. *endon,* within, + *kytos,* hollow vessel). The engulfment of matter by phagocytosis, potocytosis, receptor-mediated endocytosis, and by bulk-phase (nonspecific) endocytosis.
endoderm (en′də-dərm) (Gr. *endon,* within, + *derma,* skin). Innermost germ layer of an embryo, forming the primitive gut; also may refer to tissues derived from endoderm.
endognathous (en′də-nā-thəs) (Gr. *endon,* within, + *gnathous,* jaw). Ancestral character in insects, found in orders Diplura, Collembola, and Protura, in which the mandibles and maxillae are located in pouches.
endolecithal (en′də-les′ə-thəl) (Gr. *endon,* within, + *lekithos,* yolk). Yolk for nutrition of the embryo incorporated into the egg cell itself.
endolymph (en′də-limf) (Gr. *endon,* within, + *lympha,* water). Fluid that fills most of the membranous labyrinth of the vertebrate ear.
endometrium (en′də-mē′trē-əm) (Gr. *endon,* within, + *mētra,* womb). The mucous membrane lining the uterus.
endoplasm (en′də-pla-zm) (Gr. *endon,* within, + *plasma,* mold or form). The portion of cytoplasm that immediately surrounds the nucleus.

endoplasmic reticulum A complex of membranes within a cell; may bear ribosomes (rough) or not (smooth).

endopod, endopodite (en′də-päd, en-dop′ə-dīt) (Gr. *endon,* within, + *pous, podos,* foot). Medial branch of a biramous crustacean appendage.

endopterygote (en′dəp-ter′i-gōt) (Gr. *endon,* within, + *pteron,* feather, wing). Insect in which the wing buds develop internally; has holometabolous metamorphosis.

endorphin (en-dor′fin) (contraction of endogenous morphine). Group of opiate-like brain neuropeptides that modulate pain perception and are implicated in many other functions.

endoskeleton (Gr. *endon,* within, + *skeletos,* hard). A skeleton or supporting framework within the living tissues of an organism; contrasts with **exoskeleton.**

endosome (en′də-sōm) (Gr. *endon,* within, + *sōma,* body). Nucleolus in nucleus of some protozoa that retains its identity through mitosis.

endostyle (en′də-stīl) (Gr. *endon,* within, + *stylos,* a pillar). Ciliated groove(s) in the floor of the pharynx of tunicates, cephalochordates, and larval jawless fishes useful for accumulating and moving food particles to the stomach.

endothelium (en-də-thē′lē-əm) (Gr. *endon,* within, + *thēlē,* nipple). Squamous epithelium lining internal body cavities such as heart and blood vessels. Adj., **endothelial.**

endothermic (en′də-therm′ic) (Gr. *endon,* within, + *thermē,* heat). Having a body temperature determined by heat derived from the animal's own oxidative metabolism; contrasts with **ectothermic.**

enkephalin (en-kef′ə-lin) (Gr. *endon,* within, + *kephale,* head). Group of small brain neuropeptides with opiate-like qualities.

enterocoel (en′tər-ō-sēl′) (Gr. *enteron,* gut, + *koilos,* hollow). A type of coelom formed by the outpouching of a mesodermal sac from the endoderm of the primitive gut.

enterocoelic mesoderm formation Embryonic formation of mesoderm by a pouchlike outfolding from the archenteron, which then expands and obliterates the blastocoel, thus forming a large cavity, the coelom, lined with mesoderm.

enterocoelomate (en′ter-ō-sēl′ō-māte) (Gr. *enteron,* gut, + *koilōma,* cavity, + Eng. *ate,* state of). An animal having an enterocoel, such as an echinoderm or a vertebrate.

enteron (en′tə-rän) (Gr. intestine). The digestive cavity.

entomology (en′tə-mol′ə-jē) (Gr. *entoma,* an insect, + *logos,* discourse). Study of insects.

entozoic (en-tə-zō′ic) (Gr. *entos,* within, + *zōon,* animal). Living within another animal; internally parasitic (chiefly parasitic worms).

entropy (en′trə-pē) (Gr. *en,* in, on, + *tropos,* turn, change in manner). A quantity that is the measure of energy in a system not available for doing work.

enzyme (en′zīm) (Gr. *enzymos,* leavened, from *en,* in, + *zyme,* leaven). A substance, produced by living cells, that is capable of speeding up specific chemical transformations, such as hydrolysis, oxidation, or reduction, but is unaltered itself in the process; a biological catalyst.

eocytes (ē′ə-sīts) (Gr. *ēōs,* the dawn, + *kytos,* hollow vessel). A group of prokaryotes currently classified among the Archaebacteria but possibly a sister group of eukaryotes.

ephyra (ef′ə-rə) (Gr. *Ephyra,* Greek city). Refers to castlelike appearance. Medusa bud from a scyphozoan polyp.

epidermis (ep′ə-dər′məs) (Gr. *epi,* on, upon, + *derma,* skin). The outer, nonvascular layer of skin of ectodermal origin; in invertebrates, a single layer of ectodermal epithelium.

epididymis (ep′ə-did′ə-məs) (Gr. *epi,* on, upon, + *didymos,* testicle). Part of the sperm duct that is coiled and lying near the testis.

epigenesis (ep′ə-jen′ə-sis) (Gr. *epi,* on, upon, + *genesis,* birth). The embryological (and generally accepted) view that an embryo is a new creation that develops and differentiates step by step from an initial stage; the progressive production of new parts that were nonexistent as such in the original zygote.

epigenetics (ep′ə-je-net′iks) (Gr. *epi,* on, upon, + *genesis,* birth). Study of the relationship between genotype and phenotype as mediated by developmental processes.

epipod, epipodite (ep′ē-päd, e-pip′ə-dīt) (Gr. *epi,* on, upon, + *pous, podos,* foot). A lateral process on the protopod of a crustacean appendage, often modified as a gill.

epistasis (e-pis′tə-səs) (Gr. *epi,* on, upon, + *stasis,* standing). Prevention of expression of an allele at one locus by an allele at another locus.

epistome (ep′i-stōm) (Gr. *epi,* on, upon, + *stoma,* mouth). Flap over the mouth in some lophophorates bearing the protocoel.

epithelium (ep′ə-thē′lē-əm) (Gr. *epi,* on, upon, + *thēlē,* nipple). A cellular tissue covering a free surface or lining a tube or cavity.

epitoke (ep′ə-tōk) (Gr. *epitokos,* fruitful). Posterior part of a marine polychaete when swollen with developing gonads during the breeding season; contrast with **atoke.**

epitope That portion of an antigen to which an antibody or T-cell receptor binds. Also called **antigenic determinant.**

erythroblastosis fetalis (ə-rith′rə-blas-tō′səs fə-tal′əs) (Gr. *erythros,* red, + *blastos,* germ, + *osis,* a disease; L. *fetalis,* relating to a fetus). A disease of newborn infants caused when Rh-negative mothers develop antibodies against the Rh-positive blood of the fetus. See **blood type.**

erythrocyte (ə-rith′rə-sīt) (Gr. *erythros,* red, + *kytos,* hollow vessel). Red blood cell; has hemoglobin to carry oxygen from lungs or gills to tissues; during formation in mammals, erythrocytes lose their nuclei, those of other vertebrates retain the nuclei.

esthete (es-thēt′) (Gr. *esthēs,* a garment). Light sensory receptor on a shell of a chiton (phylum Mollusca).

estrus (es′trəs) (L. *oestrus,* gadfly, frenzy). The period of heat, or rut, especially of the female during ovulation of the egg. Associated with maximum sexual receptivity.

estuary (es′chə-we′rē) (L. *aestuarium,* estuary). An arm of the sea where the tide meets the current of a freshwater drainage.

ethology (e-thäl′-ə-jē) (Gr. *ethos,* character, + *logos,* discourse). The study of animal behavior in natural environments.

euchromatin (ū′krō-mə-tən) (Gr. *eu,* good, well, + *chrōma,* color). Part of the chromatin that takes up stain less than heterochromatin, contains active genes.

eukaryotic, eucaryotic (ū′ka-rē-ot′ik) (Gr. *eu,* good, true, + *karyon,* nut, kernel). Organisms whose cells characteristically contain a membrane-bound nucleus or nuclei; contrasts with **prokaryotic.**

euploidy (ū′ploid′ē) (Gr. *eu,* good, well, + *ploid,* multiple of). Change in chromosome number from one generation to the next in which there is an addition or deletion of a complete set of chromosomes in the progeny; the most common type is polyploidy.

euryhaline (ū′-rə-hā′līn) (Gr. *eurys,* broad, + *hals,* salt). Able to tolerate wide ranges of saltwater concentrations.

euryphagous (yə-rif′ə-gəs) (Gr. *eurys,* broad, + *phagein,* to eat). Eating a large variety of foods.

eurytopic (ū-rə-täp′ik) (Gr. *eurys,* broad, + *topos,* place). Refers to an organism with a wide environmental range.

eutely (u′te-lē) (Gr. *euteia,* thrift). Condition of a body composed of a constant number of cells or nuclei in all adult members of a species, as in rotifers, acanthocephalans, and nematodes.

evagination (ē-vaj′ə-nā′shən) (L. *e,* out, + *vagina,* sheath). An outpocketing from a hollow structure.

evolution (L. *evolvere,* to unfold). Organic evolution encompasses all changes in the characteristics and diversity of life on earth throughout its history.

evolutionary duration The length of time that a species or higher taxon exists in geological time.

evolutionary species concept A single lineage of ancestral-descendant populations that maintains its identity from other such lineages and has its own evolutionary tendencies and historical fate; differs from the biological species concept by explicitly including a time dimension and including asexual lineages.

evolutionary taxonomy A system of classification, formalized by George Gaylord Simpson, that groups species into Linnean higher taxa representing a hierarchy of distinct adaptive zones; such taxa may be monophyletic or paraphyletic but not polyphyletic.

excision repair Means by which cells are able to repair certain kinds of damage (dimerized pyrimidines) in their DNA.

exergonic (ek′sər-gān′ik) (Gr. *exō,* outside of, + *ergon,* work). An energy-yielding reaction.

exite (ex′īt) (Gr. *exō,* outside). Process from lateral side of an arthropod limb.

exocrine (ek′sə-krən) (Gr. *exō,* outside, + *krinein,* to separate). A type of gland that releases its secretion through a duct; contrasts with **endocrine.**

exocytosis (eks′ə-sī-tō′səs) (Gr. *exo,* outside, + *kytos,* hollow vessel). Transport of a substance from inside a cell to the outside.

exon (ex′ən) (Gr. *exō,* outside). Part of the mRNA as transcribed from the DNA that contains a portion of the information necessary for final gene product.

exopod, exopodite (ex′ə-päd, ex-äp′ə-dīt) (Gr. *exō,* outside, + *pous, podos,* foot). Lateral branch of a biramous crustacean appendage.

exopterygote (ek′səp-ter′i-gōt) (Gr. *exō,* without, + *pteron,* feather, wing). Insect in which the wing buds develop externally during nymphal instars; has hemimetabolous metamorphosis.

exoskeleton (ek′sō-skel′ə-tən) (Gr. *exō,* outside, + *skeletos,* hard). A supporting structure secreted by ectoderm or epidermis; external, not enveloped by living tissue, as opposed to **endoskeleton.**

experiment (L. *experiri,* to try). A trial made to support or disprove a hypothesis.

exteroceptor (ek′stər-ō-sep′tər) (L. *exter,* outward, + *capere,* to take). A sense organ excited by stimuli from the external world.

F

facilitated diffusion Mediated transport in which a permease makes possible diffusion of a molecule across a cell membrane in the direction of a concentration gradient; contrast with **active transport.**

FAD Abbreviation for flavine adenine dinucleotide, an electron acceptor in the respiratory chain.

fascicle (fas′ə-kəl) (L. *fasciculus,* small bundle). A small bundle, usually referring to a collection of muscle fibers or nerve axons.

fatty acid Any of a series of saturated organic acids having the general formula $C_nH_{2n}O_2$, occurs in natural fats of animals and plants.

fermentation (L. *fermentum,* ferment). Enzymatic transformation, without oxygen, or organic substrates, especially carbohydrates, yielding products such as alcohols, acids, and carbon dioxide.

fiber (L. *fibra,* thread). A fiberlike cell or strand of protoplasmic material produced or secreted by a cell and lying outside the cell.

fibril (L. *fibra,* thread). A strand of protoplasm produced by a cell and lying within the cell.

fibrillar (fī′brə-lər) (L. *fibrilla,* small fiber). Composed of or pertaining to fibrils or fibers.

fibrin Protein that forms a meshwork, trapping erythrocytes, to become blood clot. Precursor is fibrinogen.

fibrosis (fī-brō′səs). Deposition of fibrous connective tissue in a localized site, during process of tissue repair or to wall off a source of antigen.

filipodium (fī′li-pō′de-əm) (L. *filum,* thread, + Gr. *pous, podos,* a foot). A type of pseudopodium that is very slender and may branch but does not rejoin to form a mesh.

filter feeding Any feeding process by which particulate food is filtered from water in which it is suspended.

fission (L. *fissio,* a splitting). Asexual reproduction by a division of the body into two or more parts.

fitness Degree of adjustment and suitability for a particular environment. Genetic fitness is relative contribution to one genetically distinct organism to the next generation; organisms with high genetic fitness are naturally selected and become prevalent in a population.

flagellum (flə-jel′em) pl. **flagella** (L. a whip). Whiplike organelle of locomotion.

flame cell Specialized hollow excretory or osmoregulatory structure of one or several small cells containing a tuft of flagella (the "flame") and situated at the end of a minute tubule; connected tubules ultimately open to the outside. See **solenocyte, protonephridium.**

fluke (O.E. *flōc,* flatfish). A member of class Trematoda or class Monogenea. Also, certain of the flatfishes (order Pleuronectiformes).

FMN Abbreviation for flavin mononucleotide, the prosthetic group of a protein (flavoprotein) and a carrier in the electron transport chain in respiration.

food vacuole A digestive organelle in the cell.

foraminiferan (for′əm-i-nif′-ər-ən) (L. *foramin,* hole, performation, + *fero,* to bear). A member of the class Granuloreticulosea (phylum Sarcomastigophora) bearing a test with many openings.

fossil (fos′əl). Any remains or impression of an organism from a past geological age that has been preserved by natural processes, usually by mineralization in the earth's crust.

fossorial (fä-sōr′ē-əl) (L. *fossor,* digger). Characterized by digging or burrowing.

fouling Contamination of feeding or respiratory areas of an organism by excrement, sediment, or other matter. Also, accumulation of sessile marine organisms on the hull of a boat or ship so as to impede its progress through the water.

founder event Establishment of a new population by a small number of individuals (sometimes a single female carrying fertile eggs) that disperse from their parental population to a new location geographically isolated from the parental population.

fovea (fō′vē-ə) (L. small pit). A small pit or depression; especially the fovea centralis, a small rodless pit in the retina of some vertebrates, a point of acute vision.

free energy The energy available for doing work in a chemical system.

frontal plane A plane parallel to the main axis of the body and at right angles to the sagittal plane.

fusiform (fū′zə-form) (L. *fusus,* spindle, + *forma,* shape). Spindle shaped; tapering toward each end.

G

gamete (ga′mēt, gə-mēt′) (Gr. *gamos,* marriage). A mature haploid sex cell; usually, male and female gametes can be distinguished. An egg or a sperm.

gametic meiosis Meiosis that occurs during formation of the gametes, as in humans and other metazoa.

gametocyte (gə-mēt′ə-sīt) (Gr. *gametēs,* spouse, + *kytos,* hollow vessel). The mother cell of a gamete, that is, immature gamete.

ganglion (gang′lē-ən) pl. **ganglia** (Gr. little tumor). An aggregation of nerve tissue containing nerve cells.

ganoid scales (ga′noid) (Gr. *ganos,* brightness). Thick, bony, rhombic scales of some primitive bony fishes; not overlapping.

gap junction An area of tiny canals communicating the cytoplasm between two cells.

gastrodermis (gas′tro-dər′mis) (Gr. *gastēr,* stomach, + *derma,* skin). Lining of the digestive cavity of cnidarians.

gastrolith (gas′trə-lith) (Gr. *gastēr,* stomach, + *lithos,* stone). Calcareous body in the wall of the cardiac stomach of crayfish and other Malacostraca, preceding the molt.

gastrovascular cavity (Gr. *gastēr,* stomach, + L. *vasculum,* small vessel). Body cavity in certain lower invertebrates that functions in both digestion and circulation and has a single opening serving as both mouth and anus.

gastrozooid (gas′trə-zō-id) (Gr. *gastēr,* stomach, + *zōon,* animal). The feeding polyp of a hydroid, a hydranth.

gastrula (gas′trə-lə) (Gr. *gastēr,* stomach, + L. *ula,* dim.). Embryonic stage, usually cap or sac shaped, with walls of two layers of cells surrounding a cavity (archenteron) with one opening (blastopore).

gastrulation (gas′trə-lā′shən) (Gr. *gastēr,* stomach). Process by which an early metazoan embryo becomes a gastrula, acquiring first two and then three layers of cells.

gel (jel) (from gelatin, from L. *gelare,* to freeze). That state of a colloidal system in which the solid particles form the continuous phase and the fluid medium the discontinuous phase.

gemmule (je′mūl) (L. *gemma,* bud, + *ula,* dim.). Asexual, cystlike reproductive unit in freshwater sponges; formed in summer or autumn and capable of overwintering.

gene (Gr. *genos,* descent). A nucleic acid sequence (usually DNA) that encodes a functional polypeptide or RNA sequence.

gene pool A collection of all of the alleles of all of the genes in a population.

genetic drift Random change in allelic frequencies in a population occurring by chance. In small populations, genetic variation at a locus may be lost by chance fixation of a single allelic variant.

genome (jē′nōm) (Gr. *genos,* offspring, + *ōma,* abstract group). All the DNA in a haploid set of chromosomes (nuclear genome), organelle (mitochondrial genome, chloroplast genome) or virus (viral genome, which in some viruses consists of RNA rather than DNA).

genomics (jē-nō′miks). Mapping and sequencing of genomes (= structural genomics). Functional genomics is development and application of genome or systemwide experimental approaches to assess gene function. Functional genomics uses information derived from structural genomics.

genotype (jēn′ō-tīp) (Gr. *genos,* offspring, + *typos,* form). The genetic constitution, expressed and latent, of an organism; the total set of genes present in the cells of an organism; contrasts with **phenotype.**

genus (jē-nus), pl. **genera** (L. race). A group of related species with taxonomic rank between family and species.

germ layer In the animal embryo, one of three basic layers (ectoderm, endoderm, mesoderm) from which the various organs and tissues arise in the multicellular animal.

germ plasm Cell lineages giving rise to the germ cells of a multicellular organism, as distinct from the somatoplasm.

germovitellarium (jer′mə-vit-ə-lar′ē-əm) (L. *germen,* a bud, offshoot, + *vitellus,* yolk). Closely associated ovary (germarium) and yolk-producing structure (vitellarium) in rotifers.

gestation (jes-tā′shən) (L. *gestare,* to bear). The period in which offspring are carried in the uterus.

globulins (glo′bū-lənz) (L. *globus,* a globe, ball, + *-ulus,* ending denoting tendency). A large group of compact proteins with high molecular weight; includes immunoglobulins (antibodies).

glochidium (glō-kid′e-əm) (Gr. *glochis,* point, + *idion,* dim.). Bivalved larval stage of freshwater mussels.

glomerulus (glä-mer′u-ləs) (L. *glomus,* ball). A tuft of capillaries projecting into a renal corpuscle in a kidney. Also, a small spongy mass of tissue in the proboscis of hemichordates, presumed to have an excretory function. Also, a concentration of nerve fibers situated in the olfactory bulb.

gluconeogenesis (glū-cō-nē-ō-gən′ə-səs) (Gr. *glykys,* sweet, + *neos,* new, + *genesis,* origin). Synthesis of glucose from protein or lipid precursors.

glycogen (glī′kə-jən) (Gr. *glykys,* sweet, + *genēs,* produced). A polysaccharide constituting the principal form in which carbohydrate is stored in animals; animal starch.

glycolysis (glī-kol′ə-səs) (Gr. *glykys,* sweet, + *lysis,* a loosening). Enzymatic breakdown of glucose (especially) or glycogen into phosphate derivatives with release of energy.

gnathobase (nāth′ə-bās′) (Gr. *gnathos,* jaw, + base). A median basic process on certain appendages in some arthropods, usually for biting or crushing food.

gnathostomes (nath′ə-stōms) (Gr. *gnathos,* jaw, + *stoma,* mouth). Vertebrates with jaws.

Golgi complex (gōl′jē) (after Golgi, Italian histologist). An organelle in cells that serves as a collecting and packaging center for secretory products.

gonad (gō′nad) (N.L. *gonas,* primary sex organ). An organ that produces gametes (ovary in the female and testis in the male).

gonangium (gō-nan′jē-əm) (N.L. *gonas,* primary sex organ, + *angeion,* dim. of vessel). Reproductive zooid of hydroid colony (Cnidaria).

gonoduct (Gr. *gonos,* seed, progeny, + duct). Duct leading from a gonad to the exterior.

gonopore (gän′ə-pōr) (Gr. *gonos,* seed, progeny, + *poros,* an opening). A genital pore found in many invertebrates.

grade (L. *gradus,* step). A level of organismal complexity or adaptive zone characteristic of a group of evolutionarily related organisms.

gradualism (graj′ə-wal-iz′əm). A component of Darwin's evolutionary theory postulating that evolution occurs by the temporal accumulation of small, incremental changes, usually across very long periods of geological time; it opposes claims that evolution can occur by large, discontinuous or macromutational changes.

granulocytes (gran′ū-lə-sīts) (L. *granulus,* small grain, + Gr. *kytos,* hollow vessel). White blood cells (neutrophils, eosinophils, and basophils) bearing "granules" (vacuoles) in their cytoplasm that stain deeply.

green gland Excretory gland of certain Crustacea; the antennal gland.

gregarious (L. *grex,* herd). Living in groups or flocks.

guanine (gwä′nēn) (Sp. from Quechua, *huanu,* dung). A white crystalline purine base, $C_5H_5N_5O$, occurring in various animal tissues and in guano and other animal excrements.

guild (gild) (M.E. *gilde,* payment, tribute). In ecology, a group of species that exploit the same class of environment in a similar way.

gynandromorph (ji-nan′drə-mawrf) (Gr. *gyn,* female, + *andr,* male, + *morphē,* form). An abnormal individual exhibiting characteristics of both sexes in different parts of the body; for example the left side of a bilateral organism may show characteristics of one sex and the right side those of the other sex.

gynocophoric canal (gī′nə-kə-fōr′ik) (Gr. *gynē,* woman, + *pherein,* to carry). Groove in male schistosomes (certain trematodes) that carries the female.

H

habitat (L. *habitare,* to dwell). The place where an organism normally lives or where individuals of a population live.

habituation. A kind of learning in which continued exposure to the same stimulus produces diminishing responses.

halter (hal′tər), pl. **halteres** (hal-ti′rēz) (Gr. leap). In Diptera, small club-shaped structure on each side of the metathorax representing the hindwings; believed to be sense organs for balancing; also called balancer.

haplodiploidy (Gr. *haploos,* single, + *diploos,* double, + *eidos,* form). Reproduction in which haploid males are produced parthenogenetically, and diploid females are from fertilized eggs.

haploid (Gr. *haploos,* single). The reduced, or *n,* number of chromosomes, typical of gametes, as opposed to the diploid, or 2*n,* number found in somatic cells. In certain groups, mature organisms may have a haploid number of chromosomes.

Hardy-Weinberg equilibrium Mathematical demonstration that the Mendelian hereditary process does not change the populational frequencies of alleles or genotypes across generations, and that change in allelic or genotypic frequencies requires factors such as natural selection, genetic drift in finite populations, recurring mutation, migration of individuals among populations, and nonrandom mating.

hectocotylus (hek-tə-kät′ə-ləs) (Gr. *hekaton,* hundred, + *kotylē,* cup). Specialized, and sometimes autonomous, arm that serves as a male copulatory organ in cephalopods.

hemal system (hē′məl) (Gr. *haima,* blood). System of small vessels in echinoderms; function unknown.

hemerythrin (hē′mə-rith′rin) (Gr. *haima,* blood, + *erythros,* red). A red, iron-containing respiratory pigment found in the blood of some polychaetes, sipunculids, priapulids, and brachiopods.

hemimetabolous (he′mi-mə-ta′bə-ləs) (Gr. *hēmi,* half, + *metabolē,* change). Refers to gradual metamorphosis during development of insects, without a pupal stage.

hemocoel (hēm′ə-sēl) (Gr. *haima,* blood, + *koiloma,* cavity). Major body space in arthropods replacing the coelom, contains the blood (hemolymph).

hemoglobin (Gr. *haima,* blood, + L. *globulus,* globule). An iron-containing respiratory pigment occurring in vertebrate red blood cells and in blood plasma of many invertebrates; a compound of an iron porphyrin heme and globin proteins.

hemolymph (hē′mə-limf) (Gr. *haima,* blood, + L. *lympha,* water). Fluid in the coelom or hemocoel of some invertebrates that represents the blood and lymph of vertebrates.

hemozoin (hē-mə-zo′ən) (Gr. *haima,* blood, + *zōon,* an animal). Insoluble digestion product of malaria parasites produced from hemoglobin.

hepatic (hə-pat′ik) (Gr. *hēpatikos,* of the liver). Pertaining to the liver.

herbivore ([h]ərb′ə-vōr′) (L. *herba,* green crop, + *vorare,* to devour). Any organism subsisting on plants. Adj., **herbivorous.**

heredity (L. *heres,* heir). The faithful transmission of biological traits from parents to their offspring.

hermaphrodite (hə[r]-maf′rə-dīt) (Gr. *hermaphroditos,* containing both sexes; from Greek mythology, Hermaphroditos, son of Hermes and Aphrodite). An organism with both male and female functional reproductive organs. **Hermaphroditism** may refer to an aberration in unisexual animals; **monoecy** implies that this is the normal condition for the species.

hermatypic (hər-mə-ti′pik) (Gr. *herma,* reef, + *typos,* pattern). Relating to reef-forming corals.

heterocercal (het′ər-o-sər′kəl) (Gr. *heteros,* different, + *kerkos,* tail). In some fishes, a tail with the upper lobe larger than the lower, and the end of the vertebral column somewhat upturned in the upper lobe, as in sharks.

heterochromatin (het′ə-rō-krōm′ə-tən) (Gr. *heteros,* different, + *chrōma,* color). Chromatin that stains intensely and appears to represent inactive genetic areas.

heterochrony (het′ə-rō-krōn-y) (Gr. *heteros,* different, + *chronos,* time). Evolutionary change in the relative time of appearance or rate of development of characteristics from ancestor to descendant.

heterodont (het′ə-ro-dänt) (Gr. *heteros,* different, + *odous,* tooth). Having teeth differentiated into incisors, canines, and molars for different purposes.

heterotroph (het′ə-rō-träf) (Gr. *heteros,* different, + *trophos,* feeder). An organism that obtains both organic and inorganic raw materials from the environment in order to live; includes most animals and those plants that do not carry on photosynthesis.

heterozygote (het′ə-rō-zī′gōt) (Gr. *heteros,* different, + *zygōtos,* yoked). An organism in which homologous chromosomes contain different allelic forms (often dominant and recessive) of a locus; derived from a zygote formed by union of gametes of dissimilar allelic constitution.

hexamerous (hek-sam′ər-əs) (Gr. *hex,* six, + *meros,* part). Six parts, specifically, symmetry based on six or multiples thereof.

hibernation (L. *hibernus,* wintry). Condition, especially of mammals, of passing the winter in a torpid state in which the body temperature drops nearly to freezing and the metabolism drops close to zero.

hierarchical system A scheme arranging organisms into a series of taxa of increasing inclusiveness, as illustrated by Linnean classification.

histogenesis (his-tō-jen′ə-sis) (Gr. *histos,* tissue, + *genesis,* descent). Formation and development of tissue.

histone (hi′stōn) (Gr. *histos,* tissue). Any of several simple proteins found in cell nuclei and complexed at one time or another with DNA. Histones yield a high proportion of basic amino acids on hydrolysis; characteristic of eukaryotes.

holoblastic cleavage (Gr. *holo,* whole, + *blastos,* germ). Complete and approximately equal division of cells in early embryo. Found in mammals, amphioxus, and many aquatic invertebrates that have eggs with a small amount of yolk.

holometabolous (hō′lō-mə-ta′bə-ləs) (Gr. *holo,* complete, + *metabolē,* change). Complete metamorphosis during development.

holophytic nutrition (hōl′ō-fit′ik) (Gr. *holo,* whole, + *phyt,* plant). Occurs in green plants and certain protozoa and involves synthesis of carbohydrates from carbon dioxide and water in the presence of light, chlorophyll, and certain enzymes.

holozoic nutrition (hōl′ō-zō′ik) (Gr. *holo,* whole, + *zoikos,* of animals). Type of nutrition involving ingestion of liquid or solid organic food particles.

home range The area over which an animal ranges in its activities. Unlike territories, home ranges are not defended.

homeobox (hō′mē-ō-box) (Gr. *homoios,* like, resembling, + L. *buxus,* boxtree [used in the sense of enclosed, contained]). A highly conserved 180-base pair sequence found in regulatory sequences of protein-coding genes that regulate development.

homeostasis (hō′mē-ō-stā′sis) (Gr. *homeo,* alike, + *stasis,* state or standing). Maintenance of an internal steady state by means of self-regulation.

homeothermic (hō′mē-ō-thər′mik) (Gr. *homeo,* alike, + *thermē,* heat). Having a nearly uniform body temperature, regulated independent of the environmental temperature; "warm blooded."

homeotic genes (hō-mē-ät′ik) (Gr. *homoios,* like, resembling). Genes, identified through mutations, that give developmental identity to specific body segments.

hominid (häm′ə-nid) (L. *homo, hominis,* man). A member of the family Hominidae, now represented by one living species, *Homo sapiens.*

hominoid (häm′ə-noid). Relating to the Hominoidea, a superfamily of primates to which the great apes and humans are assigned.

homocercal (hō′mə-ser′kəl) (Gr. *homos,* same, common, + *kerkos,* tail). A tail with the upper and lower lobes symmetrical and the vertebral column ending near the middle of the base, as in most telost fishes.

homodont (hō′mō-dänt) (Gr. *homos,* same, + *odous,* tooth). Having all teeth similar in form.

homograft See **allograft.**

homology (hō-mäl′ə-jē) (Gr. *homologos,* agreeing). Similarity of parts or organs of different organisms caused by evolutionary derivation from a corresponding part or organ in a remote ancestor, and usually having a similar embryonic origin. May also refer to a matching pair of chromosomes. Serial homology is the correspondence in the same individual of repeated structures having the same origin and development, such as the appendages of arthropods. Adj., **homologous.**

homoplasy (hō′mō′plā′sē). Phenotypic similarity among characteristics of different species or populations (including molecular, morphological, behavioral or other features) that does not accurately represent patterns of common evolutionary descent (= nonhomologous similarity); it is produced by evolutionary parallelism, convergence and/or reversal, and is revealed by incongruence among different characters on a cladogram or phylogenetic tree.

homozygote (hō-mə-zī′gōt) (Gr. *homos,* same, + *zygotos,* yoked). An organism having identical alleles at one or more genetic loci. Adj., **homozygous.**

humoral (hū′mər-əl) (L. *humor,* a fluid). Pertaining to an endocrine secretion.

humoral immune response Immune response involving production of antibodies, specifically the T_H2 arm of the immune response. Contrast **cell-mediated immune response.**

hyaline (hī′ə-lən) (Gr. *hyalos,* glass). Adj., glassy, translucent. Noun, a clear, glassy, structureless material occurring, for example, in cartilage, vitreous body, mucin, and glycogen.

hybridoma (hī-brid-ō′mah) (contraction of hybrid + myeloma). Fused product of a normal and a myeloma (cancer) cell, which has some of the characteristics of the normal cell.

hydatid cyst (hī-da′təd) (Gr. *hydatis,* watery vesicle). A type of cyst formed by juveniles of certain tapeworms (*Echinococcus*) in their vertebrate hosts.

hydranth (hī′dranth) (Gr. *hydōr,* water, + *anthos,* flower). Nutritive zooid of hydroid colony.

hydrocaulus (hī′drə-kä′ləs) (Gr. *hydōr,* water, + *kaulos,* stem of a plant). Stalks or "stems"

of a hydroid colony, the parts between the hydrorhiza and the hydranths.

hydrocoel (hī′-drə-sēl) (Gr. *hydōr,* water, + *koilos,* hollow). Second or middle coelomic compartment in echinoderms; left hydrocoel gives rise to water vascular system.

hydrocorals Members of phylum Cnidaria, class Hydrozoa, with massive calcareous skeletons.

hydrogen bond A relatively weak chemical bond resulting from unequal charge distribution within molecules, in which a hydrogen atom covalently bonded to another atom is attracted to the electronegative portion of another molecule.

hydroid The polyp form of a cnidarian as distinguished from the medusa form. Any cnidarian of the class Hydrozoa, order Hydroida.

hydrolysis (Gr. *hydōr,* water, + *lysis,* a loosening). The decomposition of a chemical compound by the addition of water; the splitting of a molecule into its groupings so that the split products acquire hydrogen and hydroxyl groups.

hydrorhiza (hī′drə-rī′zə) (Gr. *hydōr,* water, + *rhiza,* a root). Rootlike stolon that attaches a hydroid to its substrate.

hydrosphere (Gr. *hydōr,* water, + *sphaira,* ball, sphere). Aqueous envelope of the earth.

hydrostatic pressure The pressure exerted by a fluid (gas or liquid), defined as force per unit area. For example, the hydrostatic pressure of one atmosphere (1 atm) is 14.7 lb/in^2.

hydrostatic skeleton A mass of fluid or plastic parenchyma enclosed within a muscular wall to provide the support necessary for antagonistic muscle action; for example, parenchyma in acoelomates and perivisceral fluids in pseudocoelomates serve as hydrostatic skeletons.

hydrothermal vent A submarine hot spring; seawater seeping through the sea bottom is heated by magma and expelled back into the sea through the hydrothermal vent.

hydroxyl (hydrogen + oxygen, + yl). Containing an OH^- group, a negatively charged ion formed by alkalies in water.

hyomandibular (hī-ō-mən-dib′yə-lər) (Gr. *hyoeides* [shaped like the Gr. letter upsilon Y, + *eidos,* form], + L. *mandere,* to chew). Bone derived from the hyoid gill arch, forming part of articulation of the lower jaw of fishes, and forming the stapes of the ear of amniotic vertebrates.

hyperosmotic (Gr. *hyper,* over, + *ōsmos,* impulse). Refers to a solution whose osmotic pressure is greater than that of another solution to which it is compared; contains a greater concentration of dissolved particles and gains water through a selectively permeable membrane from a solution containing fewer particles; contrasts with **hypoosmotic.**

hyperparasitism (hī′pər-par′ə-sid-iz-əm) (Gr. *hyper,* over, + *para,* beside, + *sitos,* food). Parasitism of a parasite by another parasite.

hypertrophy (hī-pər′trə-fē) (Gr. *hyper,* over, + *trophē,* nourishment). Abnormal increase in size of a part or organ.

hypodermis (hī′pə-dər′mis) (Gr. *hypo,* under, + L. *dermis,* skin). The cellular layer lying beneath and secreting the cuticle of annelids, arthropods, and certain other invertebrates.

hypoosmotic (Gr. *hypo,* under, + *ōsmos,* impulse). Refers to a solution whose osmotic pressure is less than that of another solution with which it is compared or taken as a standard, contains a lesser concentration of dissolved particles and loses water during osmosis; contrasts with **hyperosmotic.**

hypophysis (hī-pof′ə-sis) (Gr. *hypo,* under, + *physis,* growth). Pituitary body.

hypostome (hī′pə-stōm) (Gr. *hypo,* under, + *stoma,* mouth). Name applied to structure in various invertebrates (such as mites and ticks), located at posterior or ventral area of mouth.

hypothalamus (hī-pō-thal′ə-mis) (Gr. *hypo,* under, + *thalamos,* inner chamber). A ventral part of the forebrain beneath the thalamus; one of the centers of the autonomic nervous system.

hypothesis (Gr. *hypothesis,* foundation, supposition). A statement or proposition that can be tested by experiment.

hypothetico-deductive (Gr. *hypotithenai,* to suppose, + L. *deducere,* to lead). Scientific process of making a conjecture and then seeking empirical tests that potentially lead to its rejection.

I

imago (ə-mā′gō). The adult and sexually mature insect.

immediate hypersensitivity Inflammatory reaction based primarily on humoral immunity.

immunity Ability by tissues in an organism to recognize and defend against nonself invaders. **Innate immunity** is a mechanism of defense that does not depend on prior exposure to the invader; **acquired immunity** is specific to a nonself material, requires time for development, and occurs more quickly and vigorously on secondary response.

immunoglobulin (im′yə-nə-glä′byə-lən) (L. *immunis,* free, + *globus,* globe). Any of a group of plasma proteins, produced by plasma cells, that participates in the immune response by combining with the antigen that stimulated its production. Antibody.

imprinting (im′print-ing) (L. *imprimere,* to impress, imprint). Rapid and usually stable learning pattern appearing early in the life of a member of a social species and involving recognition of its own species; may involve attraction to the first moving object seen.

inbreeding The tendency among members of a population to mate preferentially with close relatives.

incomplete dominance See **intermediate inheritance.**

incus (in′kəs) (L. *incus,* anvil). The middle of a chain of three bones of the mammalian middle ear.

indeterminate cleavage A type of embryonic development in which the fate of the blastomeres is not determined very early as to tissues or organs, for example, in echinoderms and vertebrates; regulative cleavage.

indigenous (ən-dij′ə-nəs) (L. *indigena,* native). Pertains to organisms that are native to a particular region; not introduced.

induction (L. *inducere, inductum,* to lead). Reasoning from the particular to the general, that is, deriving a general statement (hypothesis) based on individual observations. In embryology, the alteration of cell fates as the result of interaction with neighboring cells.

inductor (in-duk′ter) (L. *inducere,* to introduce, lead in). In embryology, a tissue or organ that causes the differentiation of another tissue or organ.

inflammation (in′fləm-mā′shən) (L. *inflammare,* from *flamma,* flame). The complicated physiological process in mobilization of body defenses against foreign substances and infectious agents and repair of damage from such agents.

infraciliature (in-frə-sil′e-ə-tər) (L. *infra,* below, + *cilia,* eyelashes). The organelles just below the cilia in ciliate protozoa.

infundibulum (in′fun-dib′u-ləm) (L. funnel). Stalk of the neurohypophysis linking the pituitary to the diencephalon.

innate (i-nāt′) (L. *innatus,* inborn). A characteristic based partly or wholly on genetic or epigenetic constitution.

instar (inz′tär) (L. form). Stage in the life of an insect or other arthropod between molts.

instinct (L. *instinctus,* impelled). Stereotyped, predictable, genetically programmed behavior. Learning may or may not be involved.

integument (ən-teg′ū-mənt) (L. *integumentum,* covering). An external covering or enveloping layer.

intercellular (in-tər-sel′yə-lər) (L. *inter,* among, + *cellula,* chamber). Occurring between body cells.

interferons Several cytokines encoded by different genes, important in mediation of natural immunity and inflammation.

interleukin-1 A cytokine produced by macrophages that stimulates T helper lymphocytes.

interleukin-2 A lymphokine produced by T helper lymphocytes that leads to proliferation of T helper cells and other T lymphocytes.

interleukins A series of cytokines produced primarily by various leukocytes, such as

macrophages and T cells, whose target cells are various leukocytes and other cells. Given the name "interleukins" when it was believed that they were produced only by leukocytes and their target cells were limited to leukocytes.

intermediary meiosis Meiosis that occurs neither during gamete formation nor immediately after zygote formation, resulting in both haploid and diploid generations, such as in foraminiferan protozoa.

intermediate host A host in which some development of a symbiont occurs, but in which maturation and sexual reproduction do not take place.

intermediate inheritance Neither of alternate alleles of a gene are completely dominant, and heterozygote shows a condition intermediate between or different from homozygotes for each allele.

interstitial (in-tər-sti′shəl) (L. *inter,* among, + *sistere,* to stand). Situated in the interstices or spaces between structures such as cells, organs, or grains of sand.

intracellular (in-trə-sel′yə-lər) (L. *intra,* inside, + *cellula,* chamber). Occurring within a body cell or within body cells.

intrinsic growth rate Exponential growth rate of a population, that is, the difference between the density-independent components of the birth and death rates of a natural population with stable age distribution.

intron (in′trän) (L. *intra,* within). Portion of mRNA as transcribed from DNA that will not form part of mature mRNA, and therefore does not encode an amino-acid sequence in the protein product.

introvert (L. *intro,* inward, + *vertere,* to turn). The anterior narrow portion that can be withdrawn (introverted) into the trunk of a sipunculid worm.

invagination (in-vaj′ə-nā′shən) (L. *in,* in, + *vagina,* sheath). An infolding of a layer of tissue to form a sac-like structure.

inversion (L. *invertere,* to turn upside down). A turning inward or inside out, as in embryogenesis of sponges; also, reversal in order of genes or reversal of a chromosome segment.

ion An atom or group of atoms with a net positive or negative electrical charge because of the loss or gain of electrons.

ionic bond A chemical bond formed by transfer of one or more electrons from one atom to another; characteristic of salts.

iridophore (ī-rid′ə-fōr) (Gr. *iris,* rainbow, or iris of eye). Iridescent or silvery chromatophores containing crystals or plates of guanine or other purine.

irritability (L. *irritare,* to provoke). A general property of all organisms involving the ability to respond to stimuli or changes in the environment.

isogametes (īs′o-gam′ēts) (Gr. *isos,* equal, + *gametēs,* spouse). Gametes of a species in which gametes of both sexes are alike in size and appearance.

isolecithal (ī′sə-les′ə-thəl) (Gr. *isos,* equal, + *lekithos,* yolk, + *al*). Pertaining to a zygote (or ovum) with yolk evenly distributed. Homolecithal.

isosmotic A liquid having the same osmotic pressure as another, reference liquid.

isotonic (Gr. *isos,* equal, + *tonikos,* tension). Pertaining to solutions having the same or equal osmotic pressure; isosmotic.

isotope (Gr. *isos,* equal, + *topos,* place). One of several different forms (species) of a chemical element, differing from each other in atomic mass but not in atomic number.

J

juvenile hormone Hormone produced by the corpora allata of insects; among its effects are maintenance of larval or nymphal characteristics during development.

juxtaglomerular apparatus (jək′stə-glä-mer′yə-lər) (L. *juxta,* close to, + *glomus,* ball). Complex of sensory cells located in the afferent arteriole adjacent to the glomerulus and a loop of the distal tubule, which produces the enzyme renin.

K

kentrogon (ken′trə-gən) (Gr. *kentron,* a point, spine, + *gonos,* progeny, generation). A larva of the cirripede order Rhizocephala (subphylum Crustacea) that functions to inject the parasite cells into the host hemocoel.

keratin (ker′ə-tən) (Gr. *kera,* horn, + *in,* suffix of proteins). A scleroprotein found in epidermal tissues and modified into hard structures such as horns, hair, and nails.

keystone species A species (typically a predator) whose removal leads to reduced species diversity within the community.

kinesis (kə-nē′səs) (Gr. *kinēsis,* movement). Movements by an organism in random directions in response to stimulus.

kinetochore (kī-nēt′ə-kōr) (Gr. *kinein,* to move, + *choris,* asunder, apart). A disc of proteins located on the centromere, specialized to interact with the spindle fibers during mitosis.

kinetodesma (kə-nē′tə-dez′mə). pl. **kinetodesmata** (Gr. *kinein,* to move, + *desma,* bond). Fibril arising from the kinetosome of a cilium in a ciliate protozoan, and passing along the kinetosomes of cilia in that same row.

kinetosome (kən-ēt′ə-sōm) (Gr. *kinētos,* moving, + *sōma,* body). The self-duplicating granule at the base of the flagellum or cilium; similar to centriole, also called basal body or blepharoplast.

kinety (kə-nē′tē) (Gr. *kinein,* to move). All the kinetosomes and kinetodesmata of a row of cilia.

kinin (kī′nin) (Gr. *kinein,* to move, + *in,* suffix of hormones). A type of local hormone that is released near its site of origin; also called parahormone or tissue hormone.

K-selection (from the K term in the logistic equation). Natural selection under conditions that favor survival when populations are controlled primarily by density-dependent factors.

Kupffer cells Phagocytic cells in the liver, part of the reticuloendothelial system.

kwashiorkor (kwash-ē-or′kər) (from Ghana). Malnutrition caused by diet high in carbohydrate and extremely low in protein.

L

labium (lā′bē-əm) (L. a lip). The lower lip of the insect formed by fusion of the second pair of maxillae.

labrum (lā′brəm) (L. a lip). The upper lip of insects and crustaceans situated above or in front of the mandibles; also refers to the outer lip of a gastropod shell.

labyrinth (L. *labyrinthus,* labyrinth). Vertebrate internal ear, composed of a series of fluid-filled sacs and tubules (membranous labyrinth) suspended within bone cavities (osseous labyrinth).

labyrinthodont (lab′ə-rin′thə-dänt) (Gr. *labyrinthos,* labyrinth, + *odous, odontos,* tooth). A group of Paleozoic amphibians containing the temnospondyls and the anthracosaurs.

lachrymal (lak′rə-məl) (L. *lacrimia,* tear). Secreting or relating to tears.

lacteal (lak′te-əl) (L. *lacteus,* of milk). Noun, one of the lymph vessels in the villus of the intestine. Adj., relating to milk.

lacuna (lə-kū′nə), pl. **lacunae** (L. pit, cavity). A sinus; a space between cells; a cavity in cartilage or bone.

lagena (lə-jē′nə) (L. large flask). Portion of the primitive ear in which sound is translated into nerve impulses; evolutionary beginning of cochlea.

Lamarckism Hypothesis, as expounded by Jean Baptiste de Lamarck, of evolution by the acquisition during an organism's lifetime of characteristics that are transmitted to offspring.

lamella (lə-mel′ə) (L. dim. of *lamina,* plate). One of the two plates forming a gill in a bivalve mollusc. One of the thin layers of bone laid concentrically around an osteon (Haversian canal). Any thin, platelike structure.

lappets Lobes around the margin of scyphozoan medusae (phylum Cnidaria).

larva (lar′və), pl. **larvae** (L. a ghost). An immature stage that is quite different from the adult.

larynx (lar′inks) (Gr., the larynx, gullet). Modified upper portion of respiratory tract of air-breathing vertebrates, bounded by the glottis above and the trachea below; voice box; adj., **laryngeal** (lə-rin′j(ē)əl), relating to the larynx.

lateral (L. *latus,* the side, flank). Of or pertaining to the side of an animal; a *bilateral* animal has two sides.

laterite (lad′ə-rīt) (L. *later,* brick). Group of hard, red soils from topical areas that show intense weathering and leaching of bases and silica, leaving aluminum hydroxides and iron oxides; adj. **lateritic.**

lecithotrophy (le′sə-thə-trō′fē) (Gr. *lekithos,* yolk of egg, + *trophos,* one who feeds). Nutrition of an embryo directly from the yolk of an ovum.

lek (lek) (Sw. play, game). An area where animals assemble for communal courtship display and mating.

lemniscus (lem-nis′kəs) (L. ribbon). One of a pair of internal projections of the epidermis from the neck region of Acanthocephala, which functions in fluid control in the protrusion and invagination of the proboscis.

lentic (len′tik) (L. *lentus,* slow). Of or relating to standing water such as swamp, pond, or lake.

lepidosaurs (lep′ə-dō-sors) (L. *lepidos,* scale, + *sauros,* lizard). A lineage of diapsid reptiles that appeared in the Permian and that includes the modern snakes, lizards, amphisbaenids, and tuataras, and the extinct ichthyosaurs.

lepospondyls (lep′ə-spänd′ls) (Gr. *lepos,* scale, + *spondylos,* vertebra). A group of Paleozoic amphibians distinguished by the possession of spool-shaped vertebral centra.

leptocephalus (lep′tə-sef′ə-ləs) pl. **leptocephali** (Gr. *leptos,* thin, + *kephalē,* head). Transparent, ribbonlike migratory larva of the European or American eel.

leukemism (lū′kə-mi-zəm) (Gr. *leukos,* white, + *ismos,* condition of). Presence of white pelage or plumage in animals with normally pigmented eyes and skin.

leukocyte (lū′kə-sīt) (Gr. *leukos,* white, + *kytos,* hollow vessel). Any of several kinds of white blood cells (for example, granulocytes, lymphocytes, monocytes), so called because they bear no hemoglobin, as do red blood cells.

library In molecular biology, a set of clones containing recombinant DNA. Obtained from and representing the genome of the organism.

ligament (lig′ə-mənt) (L. *ligamentum,* bandage). A tough, dense band of connective tissue connecting one bone to another.

ligand (lī′gənd) (L. *ligo,* to bind). A molecule that specifically binds to a receptor; for example, a hormone (ligand) binds specifically to its receptor on the cell surface.

limax form (lī′məx) (L. *limax,* slug). Form of pseudopodial movement in which entire organism moves without extending a discrete pseudopodium.

lipase (lī′pās) (Gr. *lipos,* fat, + *ase,* enzyme suffix). An enzyme that accelerates the hydrolysis or synthesis of fats.

lipid, lipoid (lī′pid) (Gr. *lipos,* fat). Certain fatlike substances, often containing other groups such as phosphoric acid; lipids combine with proteins and carbohydrates to form principal structural components of cells.

lithosphere (lith′ə-sfir) (Gr. *lithos,* rock, + *sphaira,* ball). The rocky component of the earth's surface layers.

littoral (lit′ə-rəl) (L. *litoralis,* seashore). Adj., pertaining to the shore. Noun, that portion of the sea floor between the extent of high and low tides, intertidal; in lakes, the shallow part from the shore to the lakeward limit of aquatic plants.

lobopodium (lō′bə-pō′de-əm) (Gr. *lobos,* lobe, + *pous, podos,* foot). Blunt, lobelike pseudopodium.

locus (lō′kəs), pl. **loci** (lō′sī) (L. place). Position of a gene in a chromosome.

logistic equation A mathematical expression describing an idealized sigmoid curve of population growth.

lophocyte (lō′fə-sīt) (Gr. *lophos,* crest, + *kytos,* hollow vessel). Type of sponge amebocyte that secretes bundles of fibrils.

lophophore (lōf′ə-fōr) (Gr. *lophos,* crest, + *phoros,* bearing). Tentacle-bearing ridge or arm within which is an extension of the coelomic cavity in lophophorate animals (ectoprocts, brachiopods, and phoronids).

lorica (lo′rə-kə) (L. corselet). Protective external case found in some protozoa, rotifers, and others.

lotic (lō′tik) (L. *lotus,* action of washing or bathing). Of or pertaining to running water, such as a brook or river.

lumbar (lum′bär) (L. *lumbus,* loin). Relating to or near the loins or lower back.

lumen (lū′mən) (L. light). The cavity of a tube or organ.

lymph (limf) (L. *lympha,* water). The interstitial (intercellular) fluid in the body, also the fluid in the lymphatic system.

lymphocyte (lim′fō-sīt) (L. *lympha,* water, goddess of water, + Gr. *kytos,* hollow vessel). Cell in blood and lymph that has central role in immune responses. See **T cell** and **B cell.**

lymphokine (limf′ə-kīn) (L. *lympha,* water, + Gr. *kinein,* to move). A molecule secreted by an activated or stimulated lymphocyte that causes physiological changes in certain other cells.

lysosome (lī′sə-sōm) (Gr. *lysis,* loosing, + *sōma,* body). Intracellular organelle consisting of a membrane enclosing several digestive enzymes that are released when the lysosome ruptures.

M

macroevolution (L. *makros,* long, large, + *evolvere,* to unfold). Evolutionary change on a grand scale, encompassing the origin of novel designs, evolutionary trends, adaptive radiation, and mass extinction.

macrogamete (mak′rə-gam′ēt) (Gr. *makros,* long, large, + *gamos,* marriage). The larger of the two gamete types in a heterogametic organism, considered the female gamete.

macromere (mak′rə-mer′) (Gr. *makros,* long, large, + *meros,* part). The largest size class of blastomeres in a cleaving embryo when the blastomeres differ in size from one another.

macromolecule A very large molecule, such as a protein, polysaccharide, or nucleic acid.

macronucleus (ma′krō-nū′klē-əs) (Gr. *makros,* long, large, + *nucleus,* kernel). The larger of the two kinds of nuclei in ciliate protozoa; controls all cell functions except reproduction.

macrophage (mak′rə-fāj) (Gr. *makros,* long, large, + *phagō,* to eat). A phagocytic cell type in vertebrates that performs crucial functions in the immune response and inflammation, such as presenting antigenic epitopes to T cells and producing several cytokines.

madreporite (ma′drə-pōr′īt) (Fr. *madrépore,* reef-building coral, + *ite,* suffix for some body parts). Sievelike structure that is the intake for the water-vascular system of echinoderms.

major histocompatibility complex (MHC) Complex of genes coding for proteins inserted in the cell membrane; the proteins are the basis of self-nonself recognition by the immune system.

malacostracan (mal′ə-käs′trə-kən) (Gr. *malako,* soft, + *ostracon,* shell). Any member of the crustacean subclass Malacostraca, which includes both aquatic and terrestrial forms of crabs, lobsters, shrimps, pillbugs, sand fleas, and others.

malleus (mal′ē-əs) (L. hammer). The ossicle attached to the tympanum in middle ears of mammals.

malpighian tubules (mal-pig′ē-ən) (Marcello Malpighi, Italian anatomist, 1628–1694). Blind tubules opening into the hindgut of nearly all insects and some myriapods and arachnids, and functioning primarily as excretory organs.

mantle Soft extension of the body wall in certain invertebrates, for example, brachiopods and molluscs, which usually secretes a shell; thin body wall of tunicates.

manubrium (man-ū′bri-əm) (L. handle). The portion projecting from the oral side of a jellyfish medusa, bearing the mouth; oral cone; presternum or anterior part of sternum; handle-like part of malleus of ear.

marasmus (mə-raz′məs) (Gr. *marasmos,* to waste away). Malnutrition, especially of infants, caused by a diet deficient in both calories and protein.

marsupial (mär-sū′pē-əl) (Gr. *marsypion,* little pouch). One of the pouched mammals of the subclass Metatheria.

mast cells Inflammatory cells in a variety of locations. Upon activation by an antigen they release pharmacologically active compounds leading to redness and swelling.

mastax (mas′təx) (Gr. jaws). Pharyngeal mill of rotifers.

matrix (mā′triks) (L. *mater,* mother). The intercellular substance of a tissue, or that part of a tissue into which an organ or process is set.

maturation (L. *maturus,* ripe). The process of ripening; the final stages in the preparation of gametes for fertilization.

maxilla (mak-sil′ə) (L. dim. of *mala,* jaw). One of the upper jawbones in vertebrates; one of the head appendages in arthropods.

maxilliped (mak-sil′ə-ped) (L. *maxilla,* jaw, + *pes,* foot). One of the pairs of head appendages located just posterior to the maxilla in crustaceans, a thoracic appendage that has become incorporated into the feeding mouthparts.

medial (mē′dē-əl). Situated, or occurring, in the middle.

mediated transport Transport of a substance across a cell membrane mediated by a carrier molecule in the membrane.

medulla (mə-dul′ə) (L. marrow). The inner portion of an organ in contrast to the cortex or outer portion. Also, hindbrain.

medusa (mə-dū-sə) (Gr. mythology, female monster with snake-entwined hair). A jellyfish, or the free-swimming stage in the life cycle of cnidarians.

Mehlis' gland (me′ləs). Glands of uncertain function surrounding the ootype of trematodes and cestodes.

meiofauna (mī′ō-faw-nə) (Gr. *meion,* smaller, + L. *faunus,* god of the woods). Small invertebrates found in the interstices between sand grains.

meiosis (mī-ō′səs) (Gr. from *mieoun,* to make small). The nuclear changes by means of which the chromosomes are reduced from the diploid to the haploid number; in animals, usually occurs in the last two divisions in the formation of the mature egg or sperm.

melanin (mel′ə-nin) (Gr. *melas,* black). Black or dark-brown pigment found in plant or animal structures.

melanophore (mel′ə-nə-fōr, mə-lan′ə-fōr) (Gr. *melania,* blackness, + *pherein,* to bear). Black or brown chromatophore containing melanin.

memory cells Population of long-lived B lymphocytes remaining after initial immune response that provides for the secondary response.

meninges (mə-nin′jez), sing. **meninx** (Gr. *mēninx,* membrane). Any of three membranes (arachnoid, dura mater, pia mater) that envelop the vertebrate brain and spinal cord. Also, solid connective tissue sheath enclosing the central nervous system of some vertebrates.

menopause (men′ō-pawz) (Gr. *men,* month, + *pauein,* to cease). In the human female, that time of life when ovulation ceases; cessation of the menstrual cycle.

menstruation (men′stroo-ā′shən) (L. *menstrua,* the menses, from *mensis,* month). The discharge of blood and uterine tissue from the vagina at the end of a menstrual cycle.

meroblastic (mer-ə-blas′tik) (Gr. *meros,* part, + *blastos,* germ). Partial cleavage occurring in zygotes having a large amount of yolk at the vegetal pole; cleavage restricted to a small area on the surface of the egg.

merozoite (me′rə-zō′īt) (Gr. *meros,* part, + *zōon,* animal). A very small trophozoite at the stage just after cytokinesis has been completed in multiple fission of a protozoan.

mesenchyme (me′zən-kīm) (Gr. *mesos,* middle, + *enchyma,* infusion). Embryonic connective tissue; irregular or amebocytic cells often embedded in gelatinous matrix.

mesentery (mes′ən-ter′ē) (L. *mesenterium,* mesentery). Peritoneal fold serving to hold the viscera in position.

mesocoel (mez′ō-sēl) (Gr. *mesos,* middle, + *koilos,* hollow). Middle body coelomic compartment in some deuterostomes, anterior in lophophorates, corresponds to hydrocoel in echinoderms.

mesoderm (me′zə-dərm) (Gr. *mesos,* middle, + *derma,* skin). The third germ layer, formed in the gastrula between the ectoderm and endoderm; gives rise to connective tissues, muscle, urogenital and vascular systems, and the peritoneum.

mesoglea (mez′ō-glē′ə) (Gr. *mesos,* middle, + *glia,* glue). The layer of jellylike or cement material between the epidermis and gastrodermis in cnidarians and ctenophores; also may refer to jellylike matrix between epithelial layers in sponges.

mesohyl (me′sə-hil) (Gr. *mesos,* middle, + *hylē,* a wood). Gelatinous matrix surrounding sponge cells; mesoglea, mesenchyme.

mesolecithal (me′zō-ləs′ə-thəl) (Gr. *mesos,* middle, + *lekithos,* yolk). Pertaining to a zygote (or ovum) having a moderate amount of yolk concentrated in the vegetal pole.

mesonephros (me-zō-nef′rōs) (Gr. *mesos,* middle, + *nephros,* kidney). The middle of three pairs of embryonic renal organs in vertebrates. Functional kidney of fishes and amphibians; its collecting duct is a Wolffian duct. Adj., **mesonephric.**

mesosome (mez′ə-sōm) (Gr. *mesos,* middle, + *sōma,* body). The portion of the body in lophophorates and some deuterostomes that contains the mesocoel.

messenger RNA (mRNA) A form of ribonucleic acid that carries genetic information from the gene to the ribosome, where it determines the order of amino acids as a polypeptide is formed.

metabolism (Gr. *metabolē,* change). A group of processes that includes digestion, production of energy (respiration), and synthesis of molecules and structures by organisms; the sum of the constructive (anabolic) and destructive (catabolic) processes.

metacentric (me′tə-sen′trək) (Gr. *meta,* between, among, after, + *kentron,* center). Chromosome with centromere at or near the middle.

metacercaria (me′tə-sər-ka′rē-ə) (Gr. *meta,* between, among, after, + *kerkos,* tail, + L. *aria,* connected with). Fluke juvenile (cercaria) that has lost its tail and has become encysted.

metacoel (met′ə-sēl) (Gr. *meta,* between, among, after, + *koilos,* hollow). Posterior coelomic compartment in some deuterostomes and lophophorates; corresponds to somatocoel in echinoderms.

metamere (met′ə-mēr) (Gr. *meta,* after, + *meros,* part). A repeated body unit along the longitudinal axis of an animal; a somite, or segment.

metamerism (mə-ta′mə-ri′zəm) (Gr. *meta,* between, among, after, + *meros,* part). Condition of being made up of serially repeated parts (metameres); serial segmentation.

metamorphosis (Gr. *meta,* between, among, after, + *morphē,* form, + *osis,* state of). Sharp change in form during postembryonic development, for example, tadpole to frog or larval insect to adult.

metanephridium (me′tə-nə-fri′di-əm) (Gr. *meta,* between, among, after, + *nephros,* kidney). A type of tubular nephridium with the inner open end draining the coelom and the outer open end discharging to the exterior.

metanephros (me′tə-ne′fräs) (Gr. *meta,* between, among, after, + *nephros,* kidney). Embryonic renal organs of vertebrates arising behind the mesonephros; the functional kidney of reptiles, birds, and mammals. It is drained from a ureter.

metasome (met′ə-som) (Gr. *meta,* after, behind, + *sōma,* body). The portion of the body in lophophorates and some deuterostomes that contains the metacoel.

metazoa (met-ə-zō′ə) *Gr.* meta, after, + *zōon,* animal). Multicellular animals.

MHC See **major histocompatibility complex.**

microevolution (mī-krō-ev-ə-lü′shən). (L. *mikros,* small, + *evolvere,* to unfold). A change in the gene pool of a population across generations.

microfilament (mī′krō-fil′ə-mənt) (Gr. *mikros,* small, + L. *filum,* a thread). A thin, linear structure in cells; of actin in muscle cells and others.

microfilariae (mīk′rə-fil-ar′ē-ē) (Gr. *mikros,* small, + L. *filum,* a thread). Partially developed juveniles borne alive by filarial worms (phylum Nematoda).

microgamete (mīk′rə-gam′et) (Gr. *mikros,* small, + *gamos,* marriage). The smaller of the two gamete types in a heterogametic organism, considered the male gamete.

microglial cells Phagocytic cells in the central nervous system, part of the reticuloendothelial system.

micromere (mīk′rə-mer′) (Gr. *mikros,* small, + *meros,* part). The smallest size class of blastomeres in a cleaving embryo when the blastomeres differ in size from one another.

micron (μ) (mī′krän) (Gr. neuter of *mikros,* small). One one-thousandth of a millimeter; about 1/25,000 of an inch. Now largely replaced by micrometer (μm).

microneme (mī′krə-nēm) (Gr. *mikros,* small, + *nēma,* thread). One of the types of structures composing the apical complex in the phylum Apicomplexa, slender and elongate, leading to the anterior and thought to function in host cell penetration.

micronucleus A small nucleus found in ciliate protozoa; controls the reproductive functions of these organisms.

micropyle (mīk′rə-pīl) (Gr. *mikros,* small, + *pileos,* a cap). The small opening through which the cells emerge from a gemmule (phylum Porifera).

microthrix See **microvillus.**

microtubule (Gr. *mikros,* small, + L. *tubule,* pipe). A long, tubular cytoskeletal element with an outside diameter of 20 to 27 μm. Microtubules influence cell shape and play important roles during cell division.

microvillus (Gr. *mikros,* small, + L. *villus,* shaggy hair). Narrow, cylindrical cytoplasmic projection from epithelial cells; microvilli form the brush border of several types of epithelial cells. Also, microvilli with unusual structure cover the surface of cestode tegument (also called **microthrix** [pl. **microtriches**]).

mictic (mik′tik) (Gr. *miktos,* mixed or blended). Pertaining to haploid egg of rotifers or the females that lay such eggs.

mineralocorticoids (min(ə)rəl-ō-kord′ə-koids) (M. E. *minerale,* ore, + L. *cortex,* bark, + *oid,* suffix denoting likeness of form). Hormones of the adrenal cortex, especially aldosterone, that regulate salt balance.

miracidium (mīr′ə-sid′ē-əm) (Gr. *meirakidion,* youthful person). A minute ciliated larval stage in the life of flukes.

mitochondrion (mīd′ə-kän′drē-ən) (Gr. *mitos,* a thread, + *chondrion,* dim. of *chondros,* corn, grain). An organelle in the cell in which aerobic metabolism takes place.

mitosis (mī-tō′səs) (Gr. *mitos,* thread, + *osis,* state of). Nuclear division in which there is an equal qualitative and quantitative division of the chromosomal material between the two resulting nuclei; ordinary cell division.

molecule A configuration of atomic nuclei and electrons bound together by chemical bonds.

monocyte (mon′ə-sīt) (Gr. *monos,* single, + *kytos,* hollow vessel). A type of leukocyte that becomes a phagocytic cell (macrophage) after moving into tissues.

monoecious (mə-nē′shəs) (Gr. *monos,* single, + *oikos,* house). Having both male and female gonads in the same organism; hermaphroditic.

monogamy (mə-näg′ə-mē) adj. **monogamous** (Gr. *monos,* single, + *gamos,* marriage). The condition of having a single mate at any one time.

monohybrid (Gr. *monos,* single, + L. *hybrida,* mongrel). A hybrid offspring of parents different in one specified character.

monomer (mä′nə-mər) (Gr. *monos,* single, + *meros,* part). A molecule of simple structure, but capable of linking with others to form polymers.

monophyly (män′ə-fī-lē) (Gr. *monos,* single, + *phyle,* tribe). The condition that a taxon or other group of organisms contains the most recent common ancestor of the group and all of its descendants; contrasts with **polyphyly** and **paraphyly.**

monosaccharide (män′nə-sa′kə-rīd) (Gr. *monos,* one, + *sakcharon,* sugar, from Sanskrit *sarkarā,* gravel, sugar). A simple sugar that cannot be decomposed into smaller sugar molecules; the most common are pentoses (such as ribose) and hexoses (such as glucose).

monozoic (mo′nə-zō′ik) (Gr. *monos,* single, + *zōon,* animal). Tapeworms with a single proglottid, do not undergo strobilation to form chain of proglottids.

morphogenesis (mor′fə-je′nə-səs) (Gr. *morphē,* form, + *genesis,* origin). Development of the architectural features of organisms; formation and differentiation of tissues and organs.

morphology (Gr. *morphē,* form, + L. *logia,* study, from Gr. *logos,* work). The science of structure. Includes cytology, the study of cell structure; histology, the study of tissue structure; and anatomy, the study of gross structure.

morula (mär′u-lə) (L. *morum,* mulberry, + *ula,* dim.). Solid ball of cells in early stage of embryonic development.

mosaic cleavage Embryonic development characterized by independent differentiation of each part of the embryo; determinate cleavage.

mucin (mū′sən) (L. *mucus,* nasal mucus). Any of a group of glycoproteins secreted by certain cells, especially those of salivary glands.

mucus (mū′kəs) (L. *mucus,* nasal mucus). Viscid, slippery secretion rich in mucins produced by secretory cells such as those in mucous membranes. Adj., **mucous.**

Müller's larva Free-swimming ciliated larva that resembles a modified ctenophore, characteristic of certain marine polyclad turbellarians.

multiple fission A mode of asexual reproduction in some protistans in which the nuclei divide more than once before cytokinesis occurs.

mutation (mū-tā′shən) (L. *mutare,* to change). A stable and abrupt change of a gene; the heritable modification of a characteristic.

mutualism (mū′chə-wə-li′zəm) (L. *mutuus,* lent, borrowed, reciprocal). A type of interaction in which two different species derive benefit from their association and in which the association is necessary to both; often symbiotic.

myelin (mī′ə-lən) (Gr. *myelos,* marrow). A fatty material forming the medullary sheath of nerve fibers.

myocyte (mī′ə-sīt) (Gr. *mys,* muscle, + *kytos,* hollow vessel). Contractile cell (pinacocyte) in sponges.

myofibril (Gr. *mys,* muscle, + L. dim. of *fibra,* fiber). A contractile filament within muscle or muscle fiber.

myogenic (mī′o-jen′ik) (Gr. *mys,* muscle, + N.L., *genic,* giving rise to). Originating in muscle, such as heartbeat arising in vertebrate cardiac muscle because of inherent rhythmical properties of muscle rather than because of neural stimuli.

myomere (mī′ə-mer) (Gr. *mys,* muscle, + *meros,* part). A muscle segment of successive segmental trunk musculature.

myosin (mī′ə-sin) (Gr. *mys,* muscle, + *in,* suffix, belonging to). A large protein of contractile tissue that forms the thick myofilaments of striated muscle. During contraction it combines with actin to form actomyosin.

myotome (mī′ə-tōm) (Gr. *mys,* muscle, + *tomos,* cutting). That part of a somite destined to form muscles; the muscle group innervated by a single spinal nerve.

N

nacre (nā′kər) (F. mother-of-pearl). Innermost lustrous layer of mollusc shell, secreted by mantle epithelium. Adj., **nacreous.**

NAD Abbreviation of nicotinamide adenine dinucleotide, an electron acceptor or donor in many metabolic reactions.

nares (na′rēz), sing. **naris** (L. nostrils). Openings into the nasal cavity, both internally and externally, in the head of a vertebrate.

natural killer cells Lymphocyte-like cells that can kill virus-infected cells and tumor cells in the absence of antibody.

natural selection A nonrandom reproduction of varying organisms in a population that results in the survival of those best adapted to their environment and elimination of those less well adapted; leads to evolutionary change if the variation is heritable.

nauplius (naw′plē-əs) (L. a kind of shellfish). A free-swimming microscopic larval stage of certain crustaceans, with three pairs of appendages (antennules, antennae, and mandibles) and median eye. Characteristic of ostracods, copepods, barnacles, and some others.

nekton (nek′tən) (Gr. neuter of *nēktos,* swimming). Term for actively swimming organisms, essentially independent of wave and current action. Compare with **plankton.**

nematocyst (ne-mad′ə-sist′) (Gr. *nēma,* thread, + *kystis,* bladder). Stinging organelle of cnidarians.

neo-Darwinism (nē′ō′ där′wə-niz′əm). A modified version of Darwin's evolutionary theory that eliminates elements of the Lamarckian inheritance of acquired characteristics and pangenesis that were present in Darwin's formulation; this theory originated with August Weismann in the late nineteenth century and, after incorporating Mendelian genetic principles, has become the currently favored version of Darwinian evolutionary theory.

neopterygian (nē-äp′tə-rij′ē-ən) (Gr. *neos,* new, + *pteryx,* fin). Any of a large group of bony fishes that includes most modern species.

neotenine See **juvenile hormone.**

neoteny (nē′ə-tē′nē, nē-ot′ə-nē) (Gr. *neos,* new, + *teinein,* to extend). An evolutionary process by which organismal development is retarded relative to sexual maturation; produces a descendant that reaches sexual maturity while retaining a morphology characteristic of the preadult or larval stage of an ancestor.

nephridiopore (nə-frid′ē-ə-pōr) (Gr. *nephros,* kidneys, + *porus,* pore). An external excretory opening in invertebrates.

nephridium (nə-frid′ē-əm) (Gr. *nephridios,* of the kidney). One of the segmentally arranged, paired excretory tubules of many invertebrates, notably the annelids. In a broad sense, any tubule specialized for excretion and/or osmoregulation; with an external opening and with or without an internal opening.

nephron (ne′frän) (Gr. *nephros,* kidney). Functional unit of kidney structure of vertebrates, consisting of a Bowman's capsule, an enclosed glomerulus, and the attached uriniferous tubule.

nephrostome (nef′rə-stōm) (Gr. *nephros,* kidney, + *stoma,* mouth). Ciliated, funnel-shaped opening of a nephridium.

neritic (nə-rid′ik) (Gr. *nērites,* a mussel). Portion of the sea overlying the continental shelf, specifically from the subtidal zone to a depth of 200 m.

nested hierarchy A pattern in which species are ordered into a series of increasingly more inclusive clades according to the taxonomic distribution of synapomorphies.

neurogenic (nū-rä-jen′ik) (Gr. *neuron,* nerve, + N.L. *genic,* give rise to). Originating in nervous tissue, as does the rhythmical beat of some arthropod hearts.

neuroglia (nū-räg′le-ə) (Gr. *neuron,* nerve, + *glia,* glue). Tissue supporting and filling the spaces between the nerve cells of the central nervous system.

neurolemma (nū-rə-lem′ə) (Gr. *neuron,* nerve, + *lemma,* skin). Delicate nucleated outer sheath of a nerve cell; sheath of Schwann.

neuromast (Gr. *neuron,* sinew, nerve, + *mastos,* knoll). Cluster of sense cells on or near the surface of a fish or amphibian that is sensitive to vibratory stimuli and water.

neuron (Gr. nerve). A nerve cell.

neuropodium (nū′rə-pō′de-əm) (Gr. *neuron,* nerve, + *pous, podos,* foot). Lobe of parapodium nearer the ventral side in polychaete annelids.

neurosecretory cell (nu′rō-sə-krēd′ə-rē). Any cell (neuron) of the nervous system that produces a hormone.

neutron A subatomic particle lacking an electrical charge and having a mass 1839 times that of an electron and found in the nucleus of atoms.

niche The role of an organism in an ecological community; its unique way of life and its relationship to other biotic and abiotic factors.

nictitating membrane (nik′tə-tā-ting) (L. *nicto,* to wink). Third eyelid, a transparent membrane of birds and many reptiles and mammals, that can be pulled across the eye.

nitrogen fixation (Gr. *nitron,* soda, + *gen,* producing). Reduction of molecular nitrogen to ammonia by some bacteria and cyanobacteria, often followed by **nitrification,** the oxidation of ammonia to nitrites and nitrates by other bacteria.

nondisjunction Failure of a pair of homologous chromosomes to separate during meiosis, leading to one gamete with $n + 1$ chromosomes (see **trisomy**) and another gamete with $n - 1$ chromosomes.

notochord (nōd′ə-kord′) (Gr. *nōtos,* back, + *chorda,* cord). An elongated cellular cord, enclosed in a sheath, which forms the primitive axial skeleton of chordate embryos and adult cephalochordates.

notopodium (nō′tə-pō′de-əm) (Gr. *nōtos,* back, + *pous, podos,* foot). Lobe of parapodium nearer the dorsal side in polychaete annelids.

nucleic acid (nu′klē′ik) (L. *nucleus,* kernel). One of a class of molecules composed of joined nucleotides; chief types are deoxyribonucleic acid (DNA), found in cell nuclei (chromosomes) and mitochondria, and ribonucleic acid (RNA), found both in cell nuclei (chromosomes and nucleoli) and in cytoplasmic ribosomes.

nucleoid (nu′klē-oid) (L. *nucleus,* kernel, + *oid,* like). The region in a prokaryotic cell where the chromosome is found.

nucleolus (nu-klē′ə-ləs) (dim. of L. *nucleus,* kernel). A deeply staining body within the nucleus of a cell and containing RNA; nucleoli are specialized portions of certain chromosomes that carry multiple copies of the information to synthesize ribosomal RNA.

nucleoplasm (nu′klē-ə-plazm′) (L. *nucleus,* kernel, + Gr. *plasma,* mold). Protoplasm of nucleus, as distinguished from cytoplasm.

nucleoprotein A molecule composed of nucleic acid and protein; occurs in the nucleus and cytoplasm of all cells.

nucleosome (nu′klē-ə-som) (L. *nucleus,* kernel, + *sōma,* body). A repeating subunit of chromatin in which one and three-quarter turns of the double-helical DNA are wound around eight molecules of histones.

nucleotide (nu′klē-ə-tīd). A molecule consisting of phosphate, 5-carbon sugar (ribose or deoxyribose), and a purine or a pyrimidine; the purines are adenine and guanine, and the pyrimidines are cytosine, thymine, and uracil.

nucleus (nū′klē-əs) (L. *nucleus,* a little nut, the kernel). The organelle in eukaryotes that contains the chromatin and which is bounded by a double membrane (nuclear envelope).

nuptial flight (nup′shəl). The mating flight of insects, especially that of the queen with male or males.

nurse cells Single cells or layers of cells surrounding or adjacent to other cells or structures for which the nurse cells provide nutrient or other molecules (for example, for insect oocytes or *Trichinella* spp. juveniles).

nymph (L. *nympha,* nymph, bride). An immature stage (following hatching) of a hemimetabolous insect that lacks a pupal stage.

O

ocellus (ō-sel′əs) (L. dim. of *oculus,* eye). A simple eye or eyespot in many types of invertebrates.

octomerous (ok-tom′ər-əs) (Gr. *oct,* eight, + *meros,* part). Eight parts, specifically, symmetry based on eight.

odontophore (ō-don′tə-fōr′) (Gr. *odous,* tooth, + *pherein,* to carry). Tooth-bearing organ in molluscs, including the radula, radular sac, muscles, and cartilages.

olfactory (äl-fakt′(ə)-rē) (L. *olor,* smell, + *factus,* to bring about). Pertaining to the sense of smell.

omasum (ō-mā′səm) (L. paunch). The third compartment of the stomach of a ruminant mammal.

ommatidium (ä′mə-tid′ē-əm) (Gr. *omma,* eye, + *idium,* small). One of the optical units of the compound eye of arthropods.

omnivore (äm′nə-vōr) (L. *omnis,* all, + *vorare,* to devour). An animal that uses a variety of animal and plant material in its diet.

oncogene (än′kə-jen) (Gr. *onkos,* protuberance, tumor, + *genos,* descent). Any of a number of genes that are associated with neoplastic growth (cancer). The gene in its benign state, either inactivated or carrying on its normal role, is a **proto-oncogene.**

oncomiracidium (än′kō-mīr′ə-sid′ē-əm) (Gr. *onkos,* barb, hook, + *meirakidion,* youthful

person). A ciliated larva of a monogenetic trematode.

oncosphere (än′kəs-fər) (Gr. *onkinos,* a hook, + *sphaira,* ball). Rounded larva common to all cestodes, bears hooks.

ontogeny (än-tä′jə-nē) (Gr. *ontos,* being, + *geneia,* act of being born, from *genēs,* born). The course of development of an individual from egg to senescence.

oocyst (ō′ə-sist) (Gr. *ōion,* egg, + *kystis,* bladder). Cyst formed around zygote of malaria and related organisms.

oocyte (ō′ə-sīt) (Gr. *ōion,* egg, + *kytos,* hollow). Stage in formation of ovum, just preceding first meiotic division (primary oocyte) or just following first meiotic division (secondary oocyte).

ooecium (ō-ēs′ē-əm) (Gr. *ōion,* egg, + *oikos,* house, + L. *ium,* from). Brood pouch; compartment for developing embryos in ectoprocts.

oogenesis (ō-ə-jen′ə-səs) (Gr. *ōion,* egg, + *genesis,* descent). Formation, development, and maturation of a female gamete or ovum.

oogonium (ō′ə-gōn′ē-əm) (Gr. *ōion,* egg, + *gonos,* offspring). A cell that, by continued division, gives rise to oocytes; an ovum in a primary follicle immediately before the beginning of maturation.

ookinete (ō-ə-kī′nēt) (Gr. *ōion,* egg, + *kinein,* to move). The motile zygote of malarial parasites.

ootid (ō-ə-tid′) (Gr. *ōion,* egg, + *idion,* dim.). Stage of formation of ovum after second meiotic division following expulsion of second polar body.

ootype (ō′ə-tīp) (Gr. *ōion,* egg, + *typos,* mold). Part of oviduct in flatworms that receives ducts from vitelline glands and Mehlis' gland.

operculum (ō-per′kū-ləm) (L. cover). The gill cover in bony fishes; horny plate in some snails.

operon (äp′ə-rän). A genetic unit consisting of a cluster of genes under the control of other genes, found in prokaryotes.

ophthalmic (äf-thal′mik) (Gr. *ophthalamos,* an eye). Pertaining to the eye.

opisthaptor (ä′pəs-thap′tər) (Gr. *opisthen,* behind, + *haptein,* to fasten). Posterior attachment organ of a monogenetic trematode.

opisthosoma (ō-pis′thə-sō′mə) (Gr. *opisthe,* behind, + *sōma,* body). Posterior body region in arachnids and pogonophorans.

opsonization (op′sən-i-zā′shən) (Gr. *opsonein,* to buy victuals, to cater). The facilitation of phagocytosis of foreign particles by phagocytes in the blood or tissues, mediated by antibody bound to the particles.

organelle (Gr. *organon,* tool, organ, + L. *ella,* dim.). Specialized part of a cell; literally, a small organ that performs functions analogous to organs of multicellular animals.

organizer (or′gan-ī-zer) (Gr. *organos,* fashioning). Area of an embryo that directs subsequent development of other parts.

orthogenesis (ōr′thō-jen′ə-səs). A unidirectional trend in the evolutionary history of a lineage as revealed by the fossil record; also, a now discredited, anti-Darwinian evolutionary theory, popular around 1900, postulating that genetic momentum forced lineages to evolve in a predestined linear direction that was independent of external factors and often led to decline and extinction.

osculum (os′kū-ləm) (L. *osculum,* a little mouth). Excurrent opening in a sponge.

osmole Molecular weight of a solute, in grams, divided by the number of ions or particles into which it dissociates in solution. Adj., **osmolar.**

osmoregulation Maintenance of proper internal salt and water concentrations in a cell or in the body of a living organism, active regulation of internal osmotic pressure.

osmosis (oz-mō′sis) (Gr. *ōsmos,* act of pushing, impulse). The flow of solvent (usually water) through a semipermeable membrane.

osmotic potential Osmotic pressure.

osmotroph (oz′mə-trōf) (Gr. *ōsmos,* a thrusting, impulse, + *trophē,* to eat). A heterotrophic organism that absorbs dissolved nutrients.

osphradium (äs-frā′dē-əm) (Gr. *osphradion,* small bouquet, dim. of *osphra,* smell). A sense organ in aquatic snails and bivalves that tests incoming water.

ossicles (L. *ossiculum,* small bone). Small separate pieces of echinoderm endoskeleton. Also, tiny bones of the middle ear of vertebrates.

osteoblast (os′tē-ō-blast) (Gr. *osteon,* bone, + *blastos,* bud). A bone-forming cell.

osteoclast (os′tē-ō-clast) (Gr. *osteon,* bone, + *klan,* to break). A large, multinucleate cell that functions in bone dissolution.

osteocyte (os′tē-ə-sīt) (Gr. *osteon,* bone, + *kytos,* hollow). A bone cell that is characteristic of adult bone, has developed from an osteoblast, and is isolated in a lacuna of the bone substance.

osteoderm (äs′tē-ə-dərm) (Gr. *osteon,* bone, + *derma,* skin). A bony, dermal plate located under and supporting an epidermal scale.

osteon (os′tē-on) (Gr. bone). Unit of bone structure; Haversian system.

osteostracans (os-tē-os′trə-kənz) (Gr. *osteon,* bone, + *ostrakon,* shell). A group of Paleozoic (Upper Silurian to Upper Devonian) agnathans belonging to the order Cephalaspidiformes.

ostium (L. door). Opening.

otolith (ōd′əl-ith′) (Gr. *ous, otos,* ear, + *lithos,* stone). Calcareous concretions in the membranous labyrinth of the inner ear of lower vertebrates, or in the auditory organ of certain invertebrates.

outgroup In phylogenetic systematic studies, a species or group of species closely related to but not included within a taxon whose phylogeny is being studied, and used to polarize variation of characters and to root the phylogenetic tree.

oviger (ō′vi-jər) (L. *ovum,* egg, + *gerere,* to bear). Leg that carries eggs in pycnogonids.

oviparity (ō′və-pa′rəd-ē) (L. *ovum,* egg, + *parere,* to bring forth). Reproduction in which eggs are released by the female; development of offspring occurs outside the maternal body. Adj., **oviparous** (ō-vip′ə-rəs).

ovipositor (ō′və-päz′əd-ər) (L. *ovum,* egg, + *positor,* builder, placer, + *or,* suffix denoting agent or doer). In many female insects a structure at the posterior end of the abdomen for laying eggs.

ovoviviparity (ō′vo-vī-və-par′ə-dē) (L. *ovum,* egg, + *vivere,* to live, + *parere,* to bring forth). Reproduction in which eggs develop within the maternal body without additional nourishment from the parent and hatch within the parent, or immediately after laying. Adj., **ovoviviparous** (ō′vo-vī-vip′ə-rəs).

ovum (L. *ovum,* egg). Mature female germ cell (egg).

oxidation (äk′sə-dā-shən) (Fr. *oxider,* to oxidize, from Gr. *oxys,* sharp, + *ation*). The loss of an electron by an atom or molecule; sometimes addition of oxygen chemically to a substance. Opposite of reduction, in which an electron is accepted by an atom or molecule.

oxidative phosphorylation (äk′sə-dād′iv fäs′fər-i-lā′shən). The conversion of inorganic phosphate to energy-rich phosphate of ATP, involving electron transport through a respiratory chain to molecular oxygen.

P

p53 protein A tumor suppressor protein with critical functions in normal cells. A mutation in the gene that encodes it, *p53,* can result in loss of control over cell division and thus cancer.

paedogenesis (pē-dō-jen′ə-sis) (Gr. *pais,* child, + *genēs,* born). Reproduction by immature or larval animals caused by acceleration of maturation. Progenesis.

paedomorphosis (pē-dō-mor′fə-səs) (Gr. *pais,* child, + *morphē,* form). Retention of ancestral juvenile features in later stages of the ontogeny of descendants.

pair bond An affiliation between an adult male and an adult female for reproduction. Characteristic of monogamous species.

pallium (pal′e-əm) (L. mantle). Mantle of a mollusc or brachiopod.

pangenesis (pan-jen′ə-sis) (Gr. *pan,* all, + *genesis,* descent). Darwin's hypothesis that hereditary characteristics are carried by individual body cells that produce particles that collect in the germ cells.

papilla (pə-pil′ə) (L. nipple). A small nipplelike projection. A vascular process that nourishes the root of a hair, feather, or developing tooth.

papula (pa′pū-lə) (L. pimple). Respiratory processes on skin of sea stars; also, pustules on skin.

parabiosis (pa′rə-bī-ō′sis) (Gr. *para,* beside, + *biosis,* mode of life). The fusion of two individuals, resulting in mutual physiological intimacy.

paramylon bodies (par′ə-mī-lən) (Gr. *para,* beside, + *mylos,* mill, grinder). Organelles containing the starch-like substance paramylon; in some algae and flagellates.

paraphyly (par′ə-fī-lē) (Gr. *para,* beside, + *phyle,* tribe). The condition that a taxon or other group of organisms contains the most recent common ancestor of all members of the group but excludes some descendants of that ancestor; contrasts with **monophyly** and **polyphyly.**

parapodium (pa′rə-pō′dē-əm) (Gr. *para,* beside, + *pous, podos,* foot). One of the paired lateral processes on each side of most segments in polychaete annelids; variously modified for locomotion, respiration, or feeding.

parasitism (par′ə-sīd′izəm) (Gr. *parasitos,* from *para,* beside, + *sitos,* food). The condition of an organism living in or on another organism (host) at whose expense the parasite is maintained; destructive symbiosis.

parasympathetic (par′ə-sim-pə-thed′ik) (Gr. *para,* beside, + *sympathes,* sympathetic, from *syn,* with, + *pathos,* feeling). One of the subdivisions of the autonomic nervous system, whose fibers originate in the brain and in anterior and posterior parts of the spinal cord.

parenchyma (pə-ren′kə-mə) (Gr. anything poured in beside). In lower animals, a spongy mass of vacuolated mesenchyme cells filling spaces between viscera, muscles, or epithelia; in some, cell bodies of muscle cells. Also, the specialized tissue of an organ as distinguished from the supporting connective tissue.

parenchymula (pa′rən-kī′mū-lə) (Gr. *para,* beside, + *enchyma,* infusion). Flagellated, solid-bodied larva of some sponges.

parietal (pä-rī-ə-təl) (L. *paries,* wall). Something next to, or forming part of, a wall of a structure.

parthenogenesis (pär′thə-nō-gen′ə-sis) (Gr. *parthenos,* virgin, + L. from Gr. *genesis,* origin). Unisexual reproduction involving the production of young by females not fertilized by males; common in rotifers, cladocerans, aphids, bees, ants, and wasps. A parthenogenetic egg may be diploid or haploid.

pathogenic (path′ə-jen′ik) (Gr. *pathos,* disease, + N.L. *genic,* giving rise to). Producing or capable of producing disease.

PCR See **polymerase chain reaction.**

peck order A hierarchy of social privilege in a flock of birds.

pecten (L. comb). Any of several types of comblike structures on various organisms, for example, a pigmented, vascular, and comblike process that projects into the vitreous humor from the retina at a point of entrance of the optic nerve in the eyes of all birds and many reptiles.

pectines (pek′tīnz) (L. comb, pl. of **pecten**). Sensory appendage on abdomens of scorpions.

pectoral (pek′tə-rəl) (L. *pectoralis,* from *pectus,* the breast). Of or pertaining to the breast or chest; to the pectoral girdle; or to a pair of horny shields of the plastron of certain turtles.

pedal laceration Asexual reproduction found in sea anemones, a form of fission.

pedalium (pə-dal′ē-əm) (L. *pedalis,* of or belonging to the foot). Flattened blade at the base of the tentacles in cubozoan medusae (Cnidaria).

pedicel (ped′ə-sel) (L. *pediculus,* little foot). A small or short stalk or stem. In insects, the second segment of an antenna or the waist of an ant.

pedicellaria (ped′ə-sə-lar′ē-ə) (L. *pediculus,* little foot, + *aria,* like or connected with). One of many minute pincerlike organs on the surface of certain echinoderms.

pedipalps (ped′ə-palps′) (L. *pes, pedis,* foot, + *palpus,* stroking, caress). Second pair of appendages of arachnids.

pedogenesis See **paedogenesis.**

peduncle (pē′dun-kəl) (L. *pedunculus,* dim. of *pes,* foot). A stalk. Also, a band of white matter joining different parts of the brain.

pelage (pel′ij) (Fr. fur). Hairy covering of mammals.

pelagic (pə-laj′ik) (Gr. *pelagos,* the open sea). Pertaining to the open ocean.

pellicle (pel′ə-kəl) (L. *pellicula,* dim. of *pellis,* skin). Thin, translucent, secreted envelope covering many protozoa.

pelvic (pel′vik) (L. *pelvis,* a basin). Situated at or near the pelvis, as applied to girdle, cavity, fins, and limbs.

pelycosaur (pel′ə-kō-sor) (Gr. *pelyx,* basin, + *sauros,* lizard). Any of a group of carnivorous Permian synapsids distinguished by powerful jaws, stabbing teeth, and a large skin-covered sail on the back.

pentadactyl (pen-tə-dak′təl) (Gr. *pente,* five, + *daktylos,* finger). With five digits, or five fingerlike parts, to the hand or foot.

pentamerous symmetry (pen-tam′ər-əs) (Gr. *pente,* five, + *meros,* part). A radial symmetry based on five or multiples thereof.

peptidase (pep′tə-dās) (Gr. *peptein,* to digest, + *ase,* enzyme suffix). An enzyme that breaks down simple peptides, releasing amino acids.

peptide bond A bond that binds amino acids together into a polypeptide chain, formed by removing an OH from the carboxyl group of one amino acid and an H from the amino group of another to form an amide group—CO—NH—.

perennibranchiate (pə-ren′ə-brank′ē-āt) (L. *perennis,* throughout the year, + Gr. *branchia,* gills). Having permanent gills, relating especially to certain paedomorphic salamanders.

pericardium (pə-ri-kär′dē-əm) (Gr. *peri,* around, + *kardia,* heart). Area around heart; membrane around heart.

periostracum (pe-rē-äs′trə-kəm) (Gr. *peri,* around, + *ostrakon,* shell). Outer horny layer of a mollusc shell.

peripheral (pə-ri′fər-əl) (Gr. *peripherein,* to move around). Structure or location distant from center, near outer boundaries.

periproct (per′ə-präkt) (Gr. *peri,* around, + *prōktos,* anus). Region of aboral plates around the anus of echinoids.

perisarc (per′ə-särk) (Gr. *peri,* around, + *sarx,* flesh). Sheath covering the stalk and branches of a hydroid.

perissodactyl (pə-ris′ə-dak′təl) (Gr. *perissos,* odd, + *daktylos,* finger, toe). Pertaining to an order of ungulate mammals with an odd number of digits.

peristalsis (per′ə-stal′səs) (Gr. *peristaltikos,* compressing around). The series of alternate relaxations and contractions that serve to force food through the alimentary canal.

peristomium (per′ə-stō′mē-əm) (Gr. *peri,* around, + *stoma,* mouth). Foremost true segment of an annelid; it bears the mouth.

peritoneum (per′ə-tə-nē′əm) (Gr. *peritonaios,* stretched around). The membrane that lines the coelom and covers the coelomic viscera.

permease A transporter molecule; a molecule in the cell membrane that makes it possible for another molecule (to which the membrane is not otherwise permeable) to be transported across the membrane, that is, mediated transport.

petaloids (pe′tə-loids) (Gr. *petalon,* leaf, + *eidos,* form). Describes flowerlike arrangement of respiratory podia in irregular sea urchins.

pH (*p*otential of *h*ydrogen). A symbol referring to the relative concentration of hydrogen ions in a solution; pH values are from 0 to 14, and the lower the value, the more acid or hydrogen ions in the solution. Equal to the negative logarithm of the hydrogen ion concentration.

phagocyte (fag′ə-sīt) (Gr. *phagein,* to eat, + *kytos,* hollow vessel). Any cell that engulfs and devours microorganisms or other particles.

phagocytosis (fag′ə-sī-tō-səs) (Gr. *phagein,* to eat, + *kytos,* hollow vessel). The engulfment of a particle by a phagocyte or a protozoan.

phagosome (fa′gə-sōm) (Gr. *phagein,* to eat, + *sōma,* body). Membrane-bound vesicle in cytoplasm containing food material engulfed by phagocytosis.

phagotroph (fag′ə-trōf) (Gr. *phagein,* to eat, + *trophē,* food). A heterotrophic organism that ingests solid particles for food.

pharynx (far′inks), pl. **pharynges** (Gr. *pharynx,* gullet). The part of the digestive tract between the mouth cavity and the esophagus that, in vertebrates, is common to both digestive and respiratory tracts. In cephalochordates the gill slits open from it.

phasmid (faz′mid) (Gr. *phasma,* apparition, phantom, + *id*). One of a pair of glands or sensory structures found in the posterior end of certain nematodes.

phenetic (fə-ne′tik) (Gr. *phaneros,* visible, evident). Refers to the use of a criterion of overall similarity to classify organisms into taxa; contrasts with classifications based explicitly on a reconstruction of phylogeny.

phenotype (fē′nə-tīp) (Gr. *phainein,* to show). The visible or expressed characteristics of an organism, controlled by the genotype, but not all genes in the genotype are expressed.

phenotypic gradualism The hypothesis that new traits, even those that are strikingly different from ancestral ones, evolve by a long series of small, incremental steps.

pheromone (fer′ə-mōn) (Gr. *pherein,* to carry, + *hormōn,* exciting, stirring up). Chemical substance released by one organism that influences the behavior or physiological processes of another organism.

phosphagen (fäs′fə-jən) (phosphate + gen). A term for creatine phosphate and arginine phosphate, which store and may be sources of high-energy phosphate bonds.

phosphatide (fäs′fə-tīd′) (phosphate + ide). A lipid with phosphorus, such as lecithin. A complex phosphoric ester lipid, such as lecithin, found in all cells. Phospholipid.

phosphorylation (fäs′fə-rə-lā′shən). The addition of a phosphate group, that is, —PO_3, to a compound.

photoautotroph (fōt-ō-aw′-tō-trōf) (Gr. *photōs,* light, + *autos,* self, + *trophos,* feeder). An organism requiring light as a source of energy for making organic nutrients from inorganic raw materials.

photosynthesis (fōt-ō-sin′thə-sis) (Gr. *phōs,* light, + *synthesis,* action or putting together). The synthesis of carbohydrates from carbon dioxide and water in chlorophyll-containing cells exposed to light.

phototaxis (fōt′ō-tak′sis) (Gr. *phōs,* light, + *taxis,* arranging, order). A taxis in which light is the orienting stimulus. An involuntary tendency for an organism to turn toward (positive) or away from (negative) light.

phototrophs (fōt′-ō-trōfs) (Gr. *phōs, phōtos,* light, + *trophē,* nourishment). Organisms capable of using CO_2 in the presence of light as a source of metabolic energy.

phyletic gradualism A model of evolution in which morphological evolutionary change is continuous and incremental and occurs mainly within unbranched species or lineages over long periods of geological time; contrasts with **punctuated equilibrium.**

phyllopodium (fī′lə-pō′dē-əm) (Gr. *phyllon,* leaf, + *pous, podos,* foot). Leaflike swimming appendage of branchiopod crustaceans.

phylogenetic species concept An irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent.

phylogenetic systematics See **cladistics.**

phylogeny (fī-loj′ə-nē) (Gr. *phylon,* tribe, race, + *geneia,* origin). The origin and diversification of any taxon, or the evolutionary history of its origin and diversification, usually presented in the form of a dendrogram.

phylum (fī′ləm), pl. **phyla** (N.L. from Gr. *phylon,* race, tribe). A chief category, between kingdom and class, of taxonomic classifications into which are grouped organisms of common descent that share a fundamental pattern of organization.

physiology (L. *physiologia,* natural science). A branch of biology dealing with the organic processes and phenomena of an organism or any of its parts or of a particular bodily process.

phytoflagellates (fī-tə-fla′jə-lāts). Members of the class Phytomastigophorea, plantlike flagellates.

phytophagous (fī-täf′ə-gəs) (Gr. *phyton,* plant, + *phagein,* to eat). Organisms that feed on plants.

pilidium (pī-lid′ē-əm) (Gr. *pilidion,* dim. of *pilos,* felt cap). Free-swimming, hat-shaped larva of nemertine worms.

pinacocyte (pin′ə-kō-sīt′) (Gr. *pinax,* tablet, + *kytos,* hollow vessel). Flattened cells composing dermal epithelium in sponges.

pinacoderm (pə-nak′ə-dərm) (Gr. *pinax,* plank, tablet, + *derma,* skin). The layer of pinacocytes in sponges.

pinna (pin′ə) (L. feather, sharp point). The external ear. Also a feather, wing, or fin or similar part.

pinocytosis (pin′o-sī-tō′sis, pīn′o-sī-to′sis) (Gr. *pinein,* to drink, + *kytos,* hollow vessel, + *osis,* condition). Taking up of fluid by endocytosis; cell drinking.

placenta (plə-sen′tə) (L. flat cake). The vascular structure, embryonic and maternal, through which the embryo and fetus are nourished while in the uterus.

placentotrophy (plə-sent′ə-trō′fē) (L. *placenta,* flat cake, + *trophos,* one who feeds). Nutrition of an embryo from a placenta.

placode (pla′kōd) (Gr. *plakos,* flat round plate). Localized, plate-like thickening of vertebrate head ectoderm from which a specialized structure develops; such structures include eye lens, special sense organs, and certain neurons.

placoderms (plak′ə-dərm) (Gr. *plax,* plate, + *derma,* skin). A group of heavily armored jawed fishes of the Lower Devonian to Lower Carboniferous.

placoid scale (pla′koid) (Gr. *plax, plakos,* tablet, plate). Type of scale found in cartilaginous fishes, with basal plate of dentin embedded in the skin and a backward-pointing spine tipped with enamel.

plankton (plank′tən) (Gr. neuter of *planktos,* wandering). The passively floating animal and plant life of a body of water; compares with **nekton.**

plantigrade (plan′tə-grād′) (L. *planta,* sole, + *gradus,* step, degree). Pertaining to animals that walk on the whole surface of the foot (for example, humans and bears); compares with **digitigrade.**

planula (plan′yə-lə) (N.L. dim. from L. *planus,* flat). Free-swimming, ciliated larval type of cnidarians; usually flattened and ovoid, with an outer layer of ectodermal cells and an inner mass of endodermal cells.

planuloid ancestor (plan′yə-loid) (L. *planus,* flat, + Gr. *eidos,* form). Hypothetical form representing ancestor of Cnidaria and Platyhelminthes.

plasma cell (plaz′mə) (Gr. *plasma,* a form, mold). A descendant cell of a B cell, functions to secrete antibodies.

plasma membrane (plaz′mə) (Gr. *plasma,* a form, mold). A living, external, limiting, protoplasmic structure that functions to regulate exchange of nutrients across the cell surface.

plasmalemma (plaz′mə-lem-ə) (Gr. *plasma,* a form, mold, + *lemma,* rind, sheath). The cell membrane.

plasmid (plaz′məd) (Gr. *plasma,* a form, mold). A small circle of DNA that may be carried by a bacterium in addition to its genomic DNA.

plasmodium (plaz-mō′dē-əm) (Gr. *plasma,* a form, mold, + *eidos,* form). Multinucleate ameboid mass, syncytial.

plastid (plas′təd) (Gr. *plast,* formed, molded, + L. *id,* feminine stem for particle of specified kind). A membranous organelle in plant cells functioning in photosynthesis and/or nutrient storage, for example, chloroplast.

plastron (plast′trən) (Fr. *plastron,* breast plate). Ventral body shield of turtles; structure in corresponding position in certain arthropods; thin film of gas retained by epicuticle hairs of aquatic insects.

platelet (plāt′lət) (Gr. dim. of *plattus,* flat). A tiny, incomplete cell in the blood that releases substances initiating blood clotting.

pleiotropic (plī-ə-trō′pic) (Gr. *pleiōn,* more, + *tropos,* to turn). Pertaining to a gene producing more than one effect; affecting multiple phenotypic characteristics.

pleopod (plē′ə-päd) (Gr. *plein,* to sail, + *pous, podos,* foot). One of the swimming appendages on the abdomen of a crustacean.

plesiomorphic (plē′sē-ə-mōr′fik). An ancestral condition of a variable character.

pleura (plu′rə) (Gr. side, rib). The membrane that lines each half of the thorax and covers the lungs.

plexus (plek′səs) (L. network, braid). A network, especially of nerves or blood vessels.

pluteus (plū′dē-əs), pl. **plutei** (L. *pluteus,* movable shed, reading desk). Echinoid or ophiuroid larva with elongated processes like the supports of a desk; originally called "painter's easel larva."

pneumostome (nū′mə-stōm) (Gr. *pneuma,* breathing, + *stoma,* mouth). The opening of the mantle cavity (lung) of pulmonate gastropods to the outside.

podium (pō′de-əm) (Gr. *pous, podos,* foot). A footlike structure, for example, the tube foot of echinoderms.

poikilothermic (poi-ki′lə-thər′mik) (Gr. *poikilos,* variable, + thermal). Pertaining to animals whose body temperature is variable and fluctuates with that of the environment; cold blooded; compares with **ectothermic.**

polarity (Gr. *polos,* axis). In systematics, the ordering of alternative states of a taxonomic character from evolutionarily ancestral to derived conditions. In developmental biology, the tendency for the axis of an ovum to orient corresponding to the axis of the mother. Also, condition of having opposite poles; differential distribution of gradation along an axis.

polarization (L. *polaris,* polar, + Gr. *iz,* make). The arrangement of positive electrical charges on one side of a surface membrane and negative electrical charges on the other side (in nerves and muscles).

Polian vesicles (pō′le-ən) (from G. S. Poli, Italian naturalist). Vesicles opening into ring canal in most asteroids and holothuroids.

polyandry (pol′ē-an′drē) (Gr. *polys,* many, + *anēr,* man). Condition of having more than one male mate at one time.

polygamy (pə-lig′ə-mē) (Gr. *polys,* many, + *gamos,* marriage). Condition of having more than one mate at a time.

polygenic inheritance Inheritance of traits influenced by multiple alleles; traits show continuous variation between extremes; offspring are usually intermediate between the two parents; also known as **blending** and **quantitative inheritance.**

polygyny (pə-lij′ə-nē) (Gr. *polys,* many, + *gynē,* woman). Condition of having more than one female mate at one time.

polymer (pä′lə-mər) (Gr. *polys,* many, + *meros,* part). A chemical compound composed of repeated structural units called monomers.

polymerase chain reaction (PCR) A technique for preparing large quantities of DNA from tiny samples, making it easy to clone a specific gene as long as part of the sequence of the gene is known.

polymerization (pə-lim′ər-ə-zā′shən). The process of forming a polymer or polymeric compound.

polymorphism (pä′lē-mor′fī-zəm) (Gr. *polys,* many, + *morphē,* form). The presence in a species of more than one structural type of individual.

polynucleotide (poly + nucleotide): A nucleotide of many mononucleotides combined.

polyp (pä′lip) (Gr. *polypous,* many-footed). Individual of the phylum Cnidaria, generally adapted for attachment to the substratum at the aboral end, often form colonies.

polypeptide (pä-lē-pep′tīd) (Gr. *polys,* many, + *peptein,* to digest). A molecule consisting of many joined amino acids, not as complex as a protein.

polyphyly (päl′ē-fī′lē) (Gr. *polys,* many, + *phylon,* tribe). The condition that a taxon or other group of organisms does not contain the most recent common ancestor of all members of the group, implying that it has multiple evolutionary origins; such groups are not valid as formal taxa and are recognized as such only through error. Contrasts with **monophyly** and **paraphyly.**

polyphyodont (pä′lē-fī′ə-dänt) (Gr. *polyphyes,* manifold, + *odous,* tooth). Having several sets of teeth in succession.

polypide (pä′li-pīd) (L. *polypus,* polyp). An individual or zooid in a colony, specifically in ectoprocts, which has a lophophore, digestive tract, muscles, and nerve centers.

polyploid (pä′lə-ploid′) (Gr. *polys,* many, + *ploidy,* number of chromosomes). An organism possessing more than two full homologous sets of chromosomes.

polysaccharide (pä′lē-sak′ə-rid, -rīd). (Gr. *polys,* many, + *sakcharon,* sugar, from Sanskrit *sarkarā,* gravel, sugar). A carbohydrate composed of many monosaccharide units, for example, glycogen, starch, and cellulose.

polysome (polyribosome) (Gr. *polys,* many, + *sōma,* body). Two or more ribosomes connected by a molecule of messenger RNA.

polytene chromosomes (pä′li-tēn) (Gr. *polys,* many, + *tainia,* band). Chromosomes in the somatic cells of some insects in which the chromatin replicates repeatedly without undergoing mitosis.

polyzoic (pä′lē-zō′ik) (Gr. *polys,* many, + *zōon,* animal). A tapeworm forming a strobila of several to many proglottids; also, a colony of many zooids.

pongid (pän′jəd) (L. *Pongo,* type genus of orangutan). Of or relating to the primate family Pongidae, comprising the anthropoid apes (gorillas, chimpanzees, gibbons, orangutans).

population (L. *populus,* people). A group of organisms of the same species inhabiting a specific geographical locality.

populational gradualism The observation that new genetic variants become established in a population by increasing their frequencies across generations incrementally, initially from one or a few individuals and eventually characterizing a majority of the population.

porocyte (pō′rə-sīt) (Gr. *porus;* passage, pore, + *kytos,* hollow vessel). Type of cell found in asconoid sponges through which water enters the spongocoel.

portal system (L. *porta,* gate). System of large veins beginning and ending with a bed of capillaries; for example, hepatic portal and renal portal system in vertebrates.

posterior (L. latter). Situated at or toward the rear of the body; situated toward the back; in human anatomy the upright posture makes posterior and dorsal identical.

potocytosis (pä′tə-sī-tō′səs) (Gr. *potos,* a drinking, + *kytos,* hollow vessel). Endocytosis of certain small molecules and ions bound to specific receptors limited to small areas on the cell surface. The areas of the receptors are invaginated and pinch off to form tiny vesicles. See **caveolae.**

preadaptation The possession of a trait that coincidentally predisposes an organism for survival in an environment different from those encountered in its evolutionary history.

prebiotic synthesis The chemical synthesis that occurred before the emergence of life.

precocial (prē-kō′shəl) (L. *praecoquere,* to ripen beforehand). Referring (especially) to birds whose young are covered with down and are able to run about when newly hatched.

predaceous, predacious (prē-dā′shəs) (L. *praedator,* a plunderer, *praeda,* prey). Living by killing and consuming other animals; predatory.

predator (pred′ə-tər) (L. *praedator,* a plunderer, *praeda,* prey). An organism that preys on other organisms for its food.

prehensile (prē-hen′səl) (L. *prehendere,* to seize). Adapted for grasping.

premunition A resistance to reinfection by an animal (host) when some infective organisms remain in the host's body.

primary bilateral symmetry Usually applied to a radially symmetrical organism descended from a bilateral ancestor and developing from a bilaterally symmetrical larva.

primary radial symmetry Usually applied to a radially symmetrical organism that did not have a bilateral ancestor or larva, in contrast to a secondarily radial organism.

primate (prī-māt) (L. *primus,* first). Any mammal of the order Primates, which includes the tarsiers, lemurs, marmosets, monkeys, apes, and humans.

primitive (L. *primus,* first). Primordial; ancient; little evolved; said of characteristics closely approximating those possessed by early ancestral types.

proboscis (prō-bäs′əs) (Gr. *pro,* before, + *boskein,* feed). A snout or trunk. Also, tubular sucking or feeding organ with the mouth at the end as in planarians, leeches,

and insects. Also, the sensory and defensive organ at the anterior end of certain invertebrates.

producers (L. *producere,* to bring forth). Organisms, such as plants, able to produce their own food from inorganic substances.

production In ecology, the energy accumulated by an organism that becomes incorporated into new biomass.

progesterone (prō-jes′tə-rōn′) (L. *pro,* before, + *gestare,* to carry). Hormone secreted by the corpus luteum and the placenta; prepares the uterus for the fertilized egg and maintains the capacity of the uterus to hold the embryo and fetus.

proglottid (prō-gläd′əd) (Gr. *proglōttis,* tongue tip, from *pro,* before, + *glōtta,* tongue, + *id,* suffix). Portion of a tapeworm containing a set of reproductive organs; usually corresponds to a segment.

prohormone (prō′hor-mōn) (Gr. *pro,* before, + *hormaein,* to excite). A precursor of a hormone, especially a peptide hormone.

prokaryotic, procaryotic (pro-kar′ē-ät′ik) (Gr. *pro,* before, + *karyon,* kernel, nut). Not having a membrane-bound nucleus or nuclei. Prokaryotic cells characterize the bacteria and cyanobacteria.

promoter A region of DNA to which the RNA polymerase must have access for transcription of a structural gene to begin.

pronephros (prō-nef′rəs) (Gr. *pro,* before, + *nephros,* kidney). Most anterior of three pairs of embryonic renal organs of vertebrates, functional only in adult hagfishes and larval fishes and amphibians, and vestigial in mammalian embryos. Adj, **pronephric.**

proprioceptor (prō′prē-ə-sep′tər) (L. *proprius,* own, particular, + receptor). Sensory receptor located deep within the tissues, especially muscles, tendons, and joints, that is responsive to changes in muscle stretch, body position, and movement.

prosimian (prō-sim′ē-ən) (Gr. *pro,* before, + L. *simia,* ape). Any member of a group of arboreal primates including lemurs, tarsiers, and lorises, but excluding monkeys, apes, and humans.

prosoma (prō-sōm′ə) (Gr. *pro,* before, + *sōma,* body). Anterior part of an invertebrate in which primitive segmentation is not visible; fused head and thorax of arthropod; cephalothorax.

prosopyle (präs′ə-pīl) (Gr. *prosō,* forward, + *pyle,* gate). Connections between the incurrent and radial canals in some sponges.

prostaglandins (präs′tə-glan′dənz). A family of fatty-acid hormones, originally discovered in semen, known to have powerful effects on smooth muscle, nerves, circulation, and reproductive organs.

prostomium (prō-stōm′ē-əm) (Gr. *protos,* first, + *stoma,* mouth, + *-idion,* dim. ending). Anterior closure of a metameric animal, anterior to the mouth.

protandrous (prō-tan′drəs) (Gr. *prōtos,* first, + *anēr,* male). Condition of hermaphroditic animals and plants in which male organs and their products appear before the corresponding female organs and products, thus preventing self-fertilization.

protease (prō′tē-ās) (Gr. *protein,* + *ase,* enzyme). An enzyme that digests proteins; includes proteinases and peptidases.

protein (prō′tēn, prō′tē-ən) (Gr. *protein,* from *proteios,* primary). A macromolecule of carbon, hydrogen, oxygen, and nitrogen and sometimes sulfur and phosphorus; composed of chains of amino acids joined by peptide bonds; present in all cells.

prothoracic glands Glands in the prothorax of insects that secrete the hormone ecdysone.

prothoracicotropic hormone See **ecdysiotropin.**

prothrombin (prō-thräm′bən) (Gr. *pro,* before, + *thrombos,* clot). A constituent of blood plasma that is changed to thrombin by a catalytic sequence that includes thromboplastin, calcium, and plasma globulins; involved in blood clotting.

protist (prō′tist) (Gr. *protos,* first). A member of the kingdom Protista, generally considered to include the protozoa and eukaryotic algae.

protocoel (prō′tə-sēl) (Gr. *protos,* first, + *koilos,* hollow). The anterior coelomic compartment in some deuterostomes, corresponds to the axocoel in echinoderms.

protocooperation A mutually beneficial interaction between organisms in which the interaction is not physiologically necessary to the survival of either.

proton A subatomic particle with a positive electrical charge and having a mass of 1836 times that of an electron; found in the nucleus of atoms.

protonephridium (prō′tə-nə-frid′ē-əm) (Gr. *protos,* first, + *nephros,* kidney). Primitive osmoregulatory or excretory organ consisting of a tubule terminating internally with flame bulb or solenocyte; the unit of a flame bulb system.

proto-oncogene See **oncogene.**

protoplasm (prō′tə-plazm) (Gr. *protos,* first, + *plasma,* form). Organized living substance; cytoplasm and nucleoplasm of the cell.

protopod, protopodite (prō′tə-päd, prō-top′ə-dīt) (Gr. *protos,* first, + *pous, podos,* foot). Basal portion of crustacean appendage, containing coxa and basis.

Protostomia (prō′tə-stō′mē-ə) (Gr. *protos,* first, + *stoma,* mouth). A group of phyla in which cleavage is determinate, the coelom (in coelomate forms) is formed by proliferation of mesodermal bands (schizocoelic formation), the mesoderm is formed from a particular blastomere (called 4d), and the mouth is derived from or near the blastopore. Includes the Annelida, Arthropoda, Mollusca, and a number of minor phyla. Compares with **Deuterostomia.**

proventriculus (prō′ven-trik′ū-ləs) (L. *pro,* before, + *ventriculum,* ventricle). In birds the glandular stomach between the crop and gizzard. In insects, a muscular dilation of foregut armed internally with chitinous teeth.

proximal (L. *proximus,* nearest). Situated toward or near the point of attachment; opposite of distal, distant.

proximate cause (L. *proximus,* nearest, + *causa*). The factors that underlie the functioning of a biological system at a particular place and time, including those responsible for metabolic, physiological, and behavioral functions at the molecular, cellular, organismal, and population levels.

pseudocoel (sū′do-sēl) (Gr. *pseudēs,* false, + *koilōma,* cavity). A body cavity not lined with peritoneum and not a part of the blood or digestive systems, embryonically derived from the blastocoel.

pseudopodium (sū′də-pō′dē-əm) (Gr. *pseudēs,* false, + *podion,* small foot, + *eidos,* form). A temporary cytoplasmic protrusion extended out from a protozoan or ameboid cell, and serving for locomotion or for taking up food.

puff Strands of DNA spread apart at certain locations on giant chromosomes of some flies where that DNA is being transcribed.

pulmonary (pul′mən-ner-ē) (L. *pulmo,* lung, + *aria,* suffix denoting connected to). Relating to or associated with lungs.

punctuated equilibrium A model of evolution in which morphological evolutionary change is discontinuous, being associated primarily with discrete, geologically instantaneous events of speciation leading to phylogenetic branching; morphological evolutionary stasis characterizes species between episodes of speciation; contrasts with **phyletic gradualism.**

pupa (pū′pə) (L. girl, doll, puppet). Inactive quiescent stage of the holometabolous insects. It follows the larval stages and precedes the adult stage.

purine (pū′rēn) (L. *purus,* pure, + *urina,* urine). Organic base with carbon and nitrogen atoms in two interlocking rings. The parent substance of adenine, guanine, and other naturally occurring bases.

pygidium (pī-jid′e-əm) (Gr. *pygē,* rump, buttocks, + *-idion,* dim. ending). Posterior closure of a metameric animal, bearing the anus.

pyrimidine (pī-rim′ə-dēn) (alter. of pyridine, from Gr. *pyr,* fire, + *id,* adj. suffix, + *ine*). An organic base composed of a single ring of carbon and nitrogen atoms; parent substance of several bases found in nucleic acids.

Q

quantitative inheritance See **polygenic inheritance.**

queen In entomology, the single fully developed female in a colony of social

insects such as bees, ants, and termites, distinguished from workers, nonreproductive females, and soldiers.

R

radial canals Canals along the ambulacra radiating from the ring canal of echinoderms; also choanocyte-lined canals in syconoid sponges.

radial cleavage Embryonic development in which early cleavage planes are symmetrical to the polar axis, each blastomere of one tier lying directly above the corresponding blastomere of the next layer; indeterminate cleavage.

radial symmetry A morphological condition in which the parts of an animal are arranged concentrically around an oral-aboral axis, and more than one imaginary plane through this axis yields halves that are mirror images of each other.

radiolarian (rā′dē-ə-la′rē-ən) (L. *radius,* ray, spoke of a wheel, + *Lar,* tutelary god of house and field). Members of the classes Acantharea, Phaeodarea, and Polycystinea (phylum Sarcomastigophora) with actinopodia and beautiful tests.

radioles (rā′dē-ōlz) (L. *radius,* ray, spoke of a wheel). Featherlike processes from the head of many tubicolous polychaete worms (phylum Annelida), used primarily for feeding.

radula (re′jə-lə) (L. scraper). Rasping tongue found in most molluscs.

Ras protein A protein that initiates a cascade of reactions leading to cell division when a growth factor is bound to the cell surface. The gene encoding Ras becomes an oncogene when a mutation produces a form of Ras protein that initiates the cascade even in the absence of the growth factor.

ratite (ra′tīt) (L. *ratis,* raft). Referring to birds having an unkeeled sternum; compares with **carinate.**

recapitulation Summing up or repeating; hypothesis that an individual repeats its phylogenetic history in its development.

receptor-mediated endocytosis Endocytosis of large molecules, which are bound to surface receptors in clathrin-coated pits.

recessive An allele that must be homozygous for the allele to be expressed.

recombinant DNA DNA from two different species, such as a virus and a mammal, combined into a single molecule.

redia (rē′dē-ə), pl. **rediae** (rē′dē-ē) (from Redi, Italian biologist). A larval stage in the life cycle of flukes; it is produced by a sporocyst larva, and in turn gives rise to many cercariae.

reduction In chemistry, the gain of an electron by an atom or molecule of a substance; also the addition of hydrogen to, or the removal of oxygen from, a substance.

regulative development Progressive determination and restriction of initially totipotent embryonic material.

releaser (L. *relaxare,* to unloose). Simple stimulus that elicits an innate behavior pattern.

renin (rē′nin) (L. *ren,* kidney). An enzyme produced by the kidney juxtaglomerular apparatus that initiates changes leading to increased blood pressure and increased sodium reabsorption.

rennin (re′nən) (M.E. *renne,* to run). A milk-clotting endopeptidase secreted by the stomach of some young mammals, including bovine calves and human infants.

replication (L. *replicatio,* a folding back). In genetics, the duplication of one or more DNA molecules from the preexisting molecule.

reproductive barrier (L. *re* + *producere,* to lead forward; M.F. *barriere,* bar). The factors that prevent one sexually propagating population from interbreeding and exchanging genes with another population.

repugnatorial glands (L. *repugnare,* to resist). Glands secreting a noxious substance for defense or offense, for example, as in the millipedes.

respiration (L. *respiratio,* breathing). Gaseous interchange between an organism and its surrounding medium. In the cell, the release of energy by the oxidation of food molecules.

restriction endonuclease An enzyme that cleaves a DNA molecule at a particular base sequence.

rete mirabile (rē′tē mə-rab′ə-lē) (L. wonderful net). A network of small blood vessels so arranged that the incoming blood runs countercurrent to the outgoing blood and thus makes possible efficient exchange between the two bloodstreams. Such a mechanism serves to maintain the high concentration of gases in the fish swim bladder.

reticular (rə-tīk′ū-lər) (L. *reticulum,* small net). Resembling a net in appearance or structure.

reticuloendothelial system (rə-tic′ū-lō-en-dō-thēl′i-əl) (L. *reticulum,* dim. of net, + Gr. *endon,* within, + *thele,* nipple). The fixed phagocytic cells in the tissues, especially the liver, lymph nodes, spleen, and others; also called RE system.

reticulopodia (rə-tik′ū-lə-pō′dē-ə) (L. *retiulum,* dim. of *rete,* net, + *podos, pous,* foot). Pseudopodia that branch and rejoin extensively.

retina (ret′nə, ret′ən-ə) (L. *rete,* net). The posterior sensory membrane of the eye that receives images.

rhabdite (rab′dit) (Gr. *rhabdos,* rod). Rodlike structures in the cells of the epidermis or underlying parenchyma in certain turbellarians. They are discharged in mucous secretions.

rheoreceptor (rē′ə-rē-cep′tər) (Gr. *rheos,* a flowing, + receptor). A sensory organ of aquatic animals that responds to water current.

rhinarium (rī-na′rē-əm) (Gr. *rhis,* nose). Hairless area surrounding the nose of a mammal.

rhinophore (rī′nə-fōr) (Gr. *rhis,* nose, + *pherein,* to carry). Chemoreceptive tentacles in some molluscs (opisthobranch gastropods).

rhopalium (rō-pā′lē-əm) (N.L. from Gr. *rhopalon,* a club). One of the marginal, club-shaped sense organs of certain jellyfishes; tentaculocyst.

rhoptries (rōp′trēz) (Gr. *rhopalon,* club, + *tryō,* to rub, wear out). Club-shaped bodies in Apicomplexa composing one of the structures of the apical complex; open at anterior and apparently functioning in penetration of host cell.

rhynchocoel (ring′kō-sēl) (Gr. *rhynchos,* snout, + *koilos,* hollow). In nemerteans, the dorsal tubular cavity that contains the inverted proboscis. It has no opening to the outside.

ribosome (rī′bə-sōm). Subcellular structure composed of protein and ribonucleic acid. May be free in the cytoplasm or attached to the membranes of the endoplasmic reticulum; functions in protein synthesis.

ritualization In ethology, the evolutionary modification, usually intensification, of a behavior pattern to serve communication.

RNA Ribonucleic acid, of which there are several different kinds, such as messenger RNA, ribosomal RNA, and transfer RNA (mRNA, rRNA, tRNA).

RNA world Hypothetical stage in the evolution of life on earth in which both catalysis and replication were performed by RNA, not protein enzymes and DNA.

rostellum (räs′tel′ləm) (L. small beak). Projecting structure on scolex of tapeworm, often with hooks.

rostrum (räs′trəm) (L. ship's beak). A snoutlike projection on the head.

rumen (rū′mən) (L. cud). The large first compartment of the stomach of ruminant mammals.

ruminant (rūm′ə-nənt) (L. *ruminare,* to chew the cud). Cud-chewing artiodactyl mammals with a complex four-chambered stomach.

S

saccule (sa′kūl) (L. *sacculus,* small bag). Small chamber of the membranous labyrinth of the inner ear.

sacrum Adj. **sacral** (sā′krəm, sā′krəl) (L. *sacer,* sacred). Bone formed by fused vertebrae to which pelvic girdle is attached; pertaining to the sacrum.

sagittal (saj′ə-dəl) (L. *sagitta,* arrow). Pertaining to the median anteroposterior plane that divides a bilaterally symmetrical organism into right and left halves.

salt (L. *sal,* salt). The reaction product of an acid and a base; dissociates in water solution to negative and positive ions, but not H^+ or OH^-.

saprophagous (sə-präf′ə-gəs) (Gr. *sapros,* rotten, + *phagos,* from *phagein,* to eat). Feeding on decaying matter; saprobic; saprozoic.

saprophyte (sap′rə-fīt) (Gr. *sapros,* rotten, + *phyton,* plant). A plant living on dead or decaying organic matter.

saprozoic nutrition (sap-rə-zō′ik) (Gr. *sapros,* rotten, + *zōon,* animal). Animal nutrition by absorption of dissolved salts and simple organic nutrients from surrounding medium; also refers to feeding on decaying matter.

sarcolemma (sär′kə-lem′ə) (Gr. *sarx,* flesh, + *lemma,* rind). The thin, noncellular sheath that encloses a striated muscle fiber.

sarcomere (sär′kə-mir) (Gr. *sarx,* flesh, + *meros,* part). Transverse segment of striated muscle believed to be the fundamental contractile unit.

sarcoplasm (sär′kə-plaz′əm) (Gr. *sarx,* flesh, + *plasma,* mold). The clear, semifluid cytoplasm between the fibrils of muscle fibers.

sauropterygians (so-räp′tə-rij′ē-ənz) (Gr. *sauros,* lizard, + *pteryginos,* winged). Mesozoic marine reptiles.

schizocoel (skiz′ō-sēl) (Gr. *schizo,* from *schizein,* to split, + *koilōma,* cavity). A coelom formed by the splitting of embryonic mesoderm. Noun, **schizocoelomate,** an animal with a schizocoel, such as an arthropod or mollusc. Adj., **schizocoelous.**

schizocoelous mesoderm formation (skiz′ō-sēl-ləs). Embryonic formation of the mesoderm as cords of cells between ectoderm and endoderm; splitting of these cords results in the coelomic space.

schizogony (skə-zä′gə-nē) (Gr. *schizein,* to split, + *gonos,* seed). Multiple asexual fission.

sclerite (skler′it) (Gr. *sklēros,* hard). A hard chitinous or calcareous plate or spicule; one of the plates making up the exoskeleton of arthropods, especially insects.

scleroblast (skler′ə-blast) (Gr. *sklēros,* hard, + *blastos,* germ). An amebocyte specialized to secrete a spicule, found in sponges.

sclerocyte (skler′ə-sīt) (Gr. *sklēros,* hard, + *kytos,* hollow vessel). An amebocyte in sponges that secretes spicules.

sclerotic (skler-äd′ik) (Gr. *sklēros,* hard). Pertaining to the tough outer coat of the eyeball.

sclerotization (sklər′ə-tə-zā′shən). Process of hardening of the cuticle of arthropods by the formation of stabilizing cross linkages between peptide chains of adjacent protein molecules.

scolex (skō′leks) (Gr. *skōlēx,* worm, grub). The holdfast, or so-called head, of a tapeworm; bears suckers and, in some, hooks, and posterior to it new proglottids are differentiated.

scrotum (skrō′təm) (L. bag). The pouch that contains the testes in most mammals.

scyphistoma (sī-fis′tə-mə) (Gr. *skyphos,* cup, + *stoma,* mouth). A stage in the development of scyphozoan jellyfish just after the larva becomes attached, the polyp form of a scyphozoan.

sebaceous (sə-bāsh′əs) (L. *sebaceus,* made of tallow). A type of mammalian epidermal gland that produces a fatty substance.

sedentary (sed′ən-ter-ē). Stationary, sitting, inactive; staying in one place.

selectively permeable Permeable to small particles, such as water and certain inorganic ions, but not to larger molecules.

seminiferous (sem-ə-nif′rəs) (L. *semen,* semen, + *ferre,* to bear). Pertains to the tubules that produce or carry semen in the testes.

semipermeable (L. *semi,* half, + *permeabilis,* capable of being passed through). Permeable to small particles, such as water and certain inorganic ions, but not to larger molecules.

sensillum, pl. **sensilla** (sin-si′ləm) (L. *sensus,* sense). A small sense organ, especially in the arthropods.

septum, pl. **septa** (L. fence). A wall between two cavities.

serial homology See **homology.**

serosa (sə-rō′sə) (N.L. from L. *serum,* serum). The outer embryonic membrane of birds and reptiles; chorion. Also, the peritoneal lining of the body cavity.

serotonin (sir′ə-tōn′ən) (L. *serum,* serum). A phenolic amine, found in the serum of clotted blood and in many other tissues, that possesses several poorly understood metabolic, vascular, and neural functions; 5-hydroxytryptamine.

serous (sir′əs) (L. *serum,* serum). Watery, resembling serum; applied to glands, tissue, cells, fluid.

serum (sir′əm) (L. whey, serum). The liquid that separates from the blood after coagulation; blood plasma from which fibrinogen has been removed. Also, the clear portion of a biological fluid separated from its particulate elements.

sessile (ses′əl) (L. *sessilis,* low, dwarf). Attached at the base; fixed to one spot, not able to move about.

seta (sīd′ə), pl. **setae** (sē′tē) (L. bristle). A needlelike chitinous structure of the integument of annelids, arthropods, and others.

sex chromosomes Chromosomes that determine gender of an animal. They may bear a few or many other genes.

sibling species Reproductively isolated species that are so similar morphologically that they are difficult or impossible to distinguish using morphological characters.

sickle cell anemia A condition that causes the red blood cells to collapse (sickle) under oxygen stress. The condition becomes manifest when an individual is homozygous for the gene for hemoglobin-S (HbS).

siliceous (sə-li′shəs) (L. *silex,* flint). Containing silica.

simian (sim′ē-ən) (L. *simia,* ape). Pertaining to monkeys or apes.

sinistral (si′nə-strəl, sə-ni′stral) (L. *sinister,* left). Pertaining to the left; in gastropods, shell is sinistral if opening is to left of columella when held with spire up and facing observer.

sinus (sī′nəs) (L. curve). A cavity or space in tissues or in bone.

siphonoglyph (sī′fän′ə-glif′) (Gr. *siphōn,* reed, tube, siphon, + *glyphē,* carving). Ciliated furrow in the gullet of sea anemones.

siphuncle (sī′fun-kəl) (L. *siphunculus,* small tube). Cord of tissue running through the shell of a nautiloid, connecting all chambers with body of animal.

sister group The relationship between a pair of species or higher taxa that are each other's closest phylogenetic relatives.

sociobiology Ethological study of social behavior in humans or other animals.

solenia (sō-len′ē-ə) (Gr. *sōlēn,* pipe). Channels through the coenenchyme connecting the polyps in an alcyonarian colony (phylum Cnidaria).

solenocyte (sō-len′ə-sīt) (Gr. *sōlēn,* pipe, + *kytos,* hollow vessel). Special type of flame bulb in which the bulb bears a flagellum instead of a tuft of flagella. See **flame cell, protonephridium.**

soma (sō′mə) (Gr. body). The whole of an organism except the germ cells (germ plasm).

somatic (sō-mat′ik) (Gr. *sōma,* body). Refers to the body, for example, somatic cells in contrast to germ cells.

somatocoel (sə-mat′ə-sēl) (Gr. *sōma,* the body, + *koilos,* hollow). Posterior coelomic compartment of echinoderms; left somatocoel gives rise to oral coelom, and right somatocoel becomes aboral coelom.

somatoplasm (sō′mə-də-pla′zm) (Gr. *sōma,* body, + *plasma,* anything formed). The living matter that makes up the mass of the body as distinguished from germ plasm, which makes up the reproductive cells. The protoplasm of body cells.

somite (sō′mīt) (Gr. *soma,* body). One of the blocklike masses of mesoderm arranged segmentally (metamerically) in a longitudinal series beside the neural tube of the embryo; metamere.

sorting Differential survival and reproduction among varying individuals; often confused with natural selection which is one possible cause of sorting.

speciation (spē′sē-ā′shən) (L. *species,* kind). The evolutionary process or event by which new species arise.

species (spē′shez, spē′sēz) sing. and pl. (L. particular kind). A group of interbreeding individuals of common ancestry that are

reproductively isolated from all other such groups; a taxonomic unit ranking below a genus and designated by a binomen consisting of its genus and the species name.

spermatheca (spər′mə-thē′kə) (Gr. *sperma,* seed, + *thēkē,* case). A sac in the female reproductive organs for the reception and storage of sperm.

spermatid (spər′mə-təd) (Gr. *sperma,* seed, + *eidos,* form). A growth stage of a male reproductive cell arising by division of a secondary spermatocyte; gives rise to a spermatozoon.

spermatocyte (spər-mad′ə-sīt) (Gr. *sperma,* seed, + *kytos,* hollow vessel). A growth stage of a male reproductive cell; gives rise to a spermatid.

spermatogenesis (spər-mad′ə-jen′-ə-səs) (Gr. *sperma,* seed, + *genesis,* origin). Formation and maturation of spermatozoa.

spermatogonium (spər′mad-ə-gō′nē-əm) (Gr. *sperma,* seed, + *gonē,* offspring). Precursor of mature male reproductive cell; gives rise directly to a spermatocyte.

spermatophore (spər-mad′ə-fōr′) (Gr. *sperma, spermatos,* seed, + *pherein,* to bear). Capsule or packet enclosing sperm, produced by males of several invertebrate groups and a few vertebrates.

sphincter (sfingk′tər) (Gr. *sphinkter,* band, sphincter, from *sphingein,* to bind tight). A ring-shaped muscle capable of closing a tubular opening by constriction.

spicule (spi′kyul) (L. dim. *spica,* point). One of the minute calcareous or siliceous skeletal bodies found in sponges, radiolarians, soft corals, and sea cucumbers.

spiracle (spi′rə-kəl) (L. *spiraculum,* from *spirare,* to breathe). External opening of a trachea in arthropods. One of a pair of openings on the head of elasmobranchs for passage of water. Exhalent aperture of tadpole gill chamber.

spiral cleavage A type of embryonic cleavage in which cleavage planes are diagonal to the polar axis and unequal cells are produced by the alternate clockwise and counterclockwise cleavage around the axis of polarity; determinate cleavage.

spongin (spun′jin) (L. *spongia,* sponge). Fibrous, collagenous material making up the skeletal network of horny sponges.

spongioblast (spun′je-o-blast) (Gr. *spongos,* sponge, + *blastos,* bud). Cell in a sponge that secretes spongin, a protein.

spongocoel (spun′jō-sēl) (Gr. *spongos,* sponge, + *koilos,* hollow). Central cavity in sponges.

spongocyte (spun′jō-sīt) (Gr. *spongos,* sponge, + *kytos,* hollow vessel). A cell in sponges that secretes spongin.

sporocyst (spō′rə-sist) (Gr. *sporos,* seed, + *kystis,* pouch). A larval stage in the life cycle of flukes; it originates from a miracidium.

sporogony (spor-äg′ə-nē) (Gr. *sporos,* seed, + *gonos,* birth). Multiple fission to produce sporozoites after zygote formation.

sporozoite (spō′rə-zō′īt) (Gr. *sporos,* seed, + *zōon,* animal, + *ite,* suffix for body part). A stage in the life history of many sporozoan protozoa; released from oocysts.

squalene (skwā′lēn) (L. *squalus,* a kind of fish). A liquid acyclic triterpene hydrocarbon found especially in the liver oil of sharks.

squamous epithelium (skwā′məs) (L. *squama,* scale, + *osus,* full of). Simple epithelium of flat, nucleated cells.

stapes (stā′pēz) (L. stirrup). Stirrup-shaped innermost bone of the middle ear.

statoblast (stad′ə-blast) (Gr. *statos,* standing, fixed, + *blastos,* germ). Biconvex capsule containing germinative cells and produced by most freshwater ectoprocts by asexual budding. Under favorable conditions it germinates to give rise to new zooid.

statocyst (Gr. *statos,* standing, + *kystis,* bladder). Sense organ of equilibrium; a fluid-filled cellular cyst containing one or more granules (statoliths) used to sense direction of gravity.

statolith (Gr. *statos,* standing, + *lithos,* stone). Small calcareous body resting on tufts of cilia in the statocyst.

stenohaline (sten-ə-hā′līn, -lən) (Gr. *stenos,* narrow, + *hals,* salt). Pertaining to aquatic organisms that have restricted tolerance to changes in environmental saltwater concentration.

stenophagous (stə-näf′ə-gəs) (Gr. *stenos,* narrow, + *phagein,* to eat). Eating few kinds of foods.

stenotopic (sten-ə-tä′pik) (Gr. *stenos,* narrow, + *topos,* place). Refers to an organism with a narrow range of adaptability to environmental change; having a restricted environmental distribution.

stereogastrula (ste′rē-ə-gas′trə-lə) (Gr. *stereos,* solid, + *gastēr,* stomach, + L. *ula,* dim.). A solid type of gastrula, such as the planula of cnidarians.

stereom (ster′ē-ōm) (Gr. *stereos,* solid, hard, firm). Meshwork structure of endoskeletal ossicles of echinoderms.

stereotyped behavior A pattern of behavior repeated with little variation in performance.

sternum (ster′nəm) (L. breastbone). Ventral plate of an arthropod body segment; breastbone of vertebrates.

sterol (ste′rōl), steroid (ste′roid) (Gr. *stereos,* solid, + L. *ol,* from *oleum,* oil). One of a class of organic compounds containing a molecular skeleton of four fused carbon rings; it includes cholesterol, sex hormones, adrenocortical hormones, and vitamin D.

stigma (Gr. *stigma,* mark, tatoo mark). Eyespot in certain protozoa. Spiracle of certain terrestrial arthropods.

stolon (stō′lən) (L. *stolō, stolonis,* a shoot, or sucker of a plant). A rootlike extension of the body wall giving rise to buds that may develop into new zooids, thus forming a compound animal in which the zooids remain united by the stolon. Found in some colonial anthozoans, hydrozoans, ectoprocts, and ascidians.

stoma (stō′mə) (Gr. mouth). A mouthlike opening.

stomochord (stō′mə-kord) (Gr. *stoma,* mouth, + *chordē,* cord). Anterior evagination of the dorsal wall of the buccal cavity into the proboscis of hemichordates; the buccal diverticulum.

strobila (strō′bə-lə) (Gr. *strobilē,* lint plug like a pine cone [*strobilos*]). A stage in the development of the scyphozoan jellyfish. Also, the chain of proglottids of a tapeworm.

strobilation (strō′bə-lā′shən) (Gr. *strobilos,* a pine cone). Repeated, linear budding of individuals, as in scyphozoans (phylum Cnidaria), or sets of reproductive organs, as in tapeworms (phylum Platyhelminthes).

stroma (strō′mə) (Gr. *strōma,* bedding). Supporting connective tissue framework of an animal organ; filmy framework of red blood corpuscles and certain cells.

structural gene A gene carrying the information to construct a protein.

subnivean (səb-ni′vē-ən) (L. *sub,* under, below, + *nivis,* snow). Applied to environments beneath snow, in which snow insulates against a colder atmospheric temperature.

substrate The substance upon which an enzyme acts; also, a base or foundation (substratum); and the substance or base on which an organism grows.

sycon (sī′kon) (Gr. *sykon,* fig). A type of canal system in certain sponges. Sometimes called syconoid.

symbiosis (sim′bī-ōs′əs, sim′bē-ōs′əs) (Gr. *syn,* with, + *bios,* life). The living together of two different species in an intimate relationship. Symbiont always benefits; host may benefit, may be unaffected, or may be harmed (mutualism, commensalism, and parasitism).

sympatric (sim′pa′-trik) (Gr. *syn,* with, + *patra,* native land). Having the same or overlapping regions of geographical distribution. Noun, **sympatry.**

symplesiomorphy (sim-plē′sē-ə-mōr′fē). Sharing among species of ancestral characteristics, not indicative that the species comprise a monophyletic group.

synapomorphy (sin-ap′o-mor′fē) (Gr. *syn,* together with, + *apo,* of, + *morphe,* form). Shared, evolutionarily derived character states that are used to recover patterns of common descent among two or more species.

synapse (si′naps, si-naps′) (Gr. *synapsis,* contact, union). The place at which a nerve impulse passes between neuron processes, typically from an axon of one nerve cell to a dendrite of another nerve cell.

synapsids (si-nap′sədz) (Gr. *synapsis,* contact, union). An amniote lineage comprising the mammals and the ancestral mammal-like

reptiles, having a skull with a single pair of temporal openings.

synapsis (si-nap′səs) (Gr. *synapsis,* contact, union). The time when the pairs of homologous chromosomes lie alongside each other in the first meiotic division.

synaptonemal complex (sin-ap′tə-nē′məl) (Gr. *synapsis,* a joining together, + *nēma,* thread). The structure that holds homologous chromosomes together during synapsis in prophase of meiosis I.

syncytium (sən-sish′e-əm) adj. **syncytial** (Gr. *syn,* with, + *kytos,* hollow). A multinucleated cell.

syndrome (sin′drōm) (Gr. *syn,* with, + *dramein,* to run). A group of symptoms characteristic of a particular disease or abnormality.

syngamy (sin′gə-mē) (Gr. *syn,* with, + *gamos,* marriage). Fertilization of one gamete with another individual gamete to form a zygote, found in most animals with sexual reproduction.

synkaryon (sin-ker′e-on) (Gr. *syn,* with, + *karyon,* nucleus). Zygote nucleus resulting from fusion of pronuclei.

syrinx (sir′inks) (Gr. shepherd's pipe). The vocal organ of birds located at the base of the trachea.

systematics (sis-tə-mat′iks). Science of classification and reconstruction of phylogeny.

systole (sis′tə-lē) (Gr. *systolē,* drawing together). Contraction of heart.

T

T cell A type of lymphocyte important in cellular immune response and in regulation of most immune responses.

T-cell receptors Receptors borne on surfaces of T cells. The variable region of a T-cell receptor binds with a specific antigen.

tactile (tak′til) (L. *tactilis,* able to be touched, from *tangere,* to touch). Pertaining to touch.

tagma, pl. **tagmata** (Gr. *tagma,* arrangement, order, row). A compound body section of an arthropod resulting from embryonic fusion of two or more segments; for example, head, thorax, abdomen.

tagmatization, tagmosis Organization of the arthropod body into tagmata.

taiga (tī′gä) (Russ.). Habitat zone characterized by large tracts of coniferous forests, long, cold winters, and short summers; most typical in Canada and Siberia.

tantulus (tan′tə-ləs) (Gr. *tantulus,* so small). Larva of a tantulocaridan (subphylum Crustacea).

taxis (tak′sis), pl. **taxes** (Gr. *taxis,* arrangement). An orientation movement by a (usually) simple organism in response to an environmental stimulus.

taxon (tak′son), pl. **taxa** (Gr. *taxis,* arrangement). Any taxonomic group or entity.

taxonomy (tak-sän′ə-mi) (Gr. *taxis,* arrangement, + *nomos,* law). Study of the principles of scientific classification; systematic ordering and naming of organisms.

tectum (tek′təm) (L. roof). A rooflike structure, for example, dorsal part of capitulum in ticks and mites.

tegmen (teg′mən) (L. *tegmen,* a cover). External epithelium of crinoids (phylum Echinodermata).

tegument (teg′ū-ment) (L. *tegumentum,* from *tegere,* to cover). An integument: specifically external covering in cestodes and trematodes, formerly believed to be a cuticle.

telencephalon (tel′en-sef′ə-lon) (Gr. *telos,* end, + *encephalon,* brain). The most anterior vesicle of the brain; the anteriormost subdivision of the prosencephalon that becomes the cerebrum and associated structures.

teleology (tel′ē-äl′ə-jē) (Gr. *telos,* end, + L. *logia,* study of, from Gr. *logos,* word). The philosophical view that natural events are goal directed and are preordained, as opposed to the scientific view of mechanical determinism.

telocentric (tē′lō-sen′trək) (Gr. *telos,* end, + *kentron,* center). Chromosome with centromere at the end.

telolecithal (te-lō-les′ə-thəl) (Gr. *telos,* end, + *lekithos,* yolk, + *al*). Having the yolk concentrated at one end of an egg.

telson (tel′sən) (Gr. *telson,* extremity). Posterior projection of the last body segment in many crustaceans.

temnospondyls (tem-nō-spän′dəls) (Gr. *temnō,* to cut, + *spondylos,* vertebra). A large lineage of amphibians that extended from the Carboniferous to the Triassic.

template (tem′plət). A pattern or mold guiding the formation of a duplicate; often used with reference to gene duplication.

tendon (ten′dən) (L. *tendo,* tendon). Fibrous band connecting muscle to bone or other movable structure.

tentaculocyst (ten-tak′u-lō-sist) (L. *tentaculum,* feeler, + *kystis,* pouch). One of the sense organs along the margin of medusae; a rhopalium.

tergum (ter′gəm) (L. back). Dorsal part of an arthropod body segment.

territory (L. *territorium,* from *terra,* earth). A restricted area preempted by an animal or pair of animals, usually for breeding purposes, and guarded from other individuals of the same species.

test (L. *testa,* shell). A shell or hardened outer covering.

tetrad (te′trad) (Gr. *tetras,* four). Group of two pairs of chromatids at synapsis and resulting from the replication of paired homologous chromosomes; the bivalent.

tetrapods (te′trə-pädz) (Gr. *tetras,* four, + *pous, podos,* foot). Four-footed vertebrates; the group includes amphibians, reptiles, birds, and mammals.

thecodonts (thēk′ə-dänts) (Gr. *thēkē,* box, + *odontos,* tooth). A large assemblage of Triassic archosaurian diapsids of the order Thecodontia and characterized by having teeth set in sockets.

therapsids (thə-rap′sidz) (Gr. *theraps,* an attendant). Extinct Mesozoic mammal-like reptiles from which true mammals evolved.

thermocline (thər′mō-klīn) (Gr. *thermē,* heat, + *klinein,* to swerve). Layer of water separating upper warmer and lighter water from lower colder and heavier water in a lake or sea; a stratum of abrupt change in water temperature.

thoracic (thō-ra′sək) (L. *thōrax,* chest). Pertaining to the thorax or chest.

thrombin Enzyme catalyzing fibrinogen transformation into fibrin. Percursor is **prothrombin.**

Tiedemann's bodies (tēd′ə-mənz) (from F. Tiedemann, German anatomist). Four or five pairs of pouchlike bodies attached to the ring canal of sea stars, apparently functioning in production of coelomocytes.

tight junction Region of actual fusion of cell membranes between two adjacent cells.

tissue (ti′shu) (M.E. *tissu,* tissue). An aggregation of cells, usually of the same kind, organized to perform a common function.

titer (tī′tər) (Fr. *titrer,* to titrate). Concentration of a substance in a solution as determined by titration.

tornaria (tor-na′rē-ə) (L. *tornare,* to turn). A free-swimming larva of enteropneusts that rotates as it swims; resembles somewhat the bipinnaria larva of echinoderms.

torsion (L. *torquere,* to twist). A twisting phenomenon in gastropod development that alters the position of the visceral and pallial organs by 180 degrees.

toxicyst (tox′i-sist) (Gr. *toxikon,* poison, + *kystis,* bladder). Structures possessed by predatory ciliate protozoa, which on stimulation expel a poison to subdue the prey.

trabecular net (trə-bek′ū-lər) (L. *trabecula,* a small beam). Network of living tissue formed by pseudopodia of amebocytes in Hexactinellida (phylum Porifera).

trachea (trā′kē-ə) (M.L. windpipe). The windpipe. Also, any of the air tubes of insects.

transcription Formation of messenger RNA from the coded DNA.

transduction Condition in which bacterial DNA (and the genetic characteristics it bears) is transferred from one bacterium to another by the agent of viral infection.

transfer RNA (tRNA) A form of RNA of about 70 or 80 nucleotides, which are adapter molecules in the synthesis of proteins. A specific amino acid molecule is carried by transfer RNA to a ribosome-messenger RNA complex for incorporation into a polypeptide.

transformation Condition in which DNA in the environment of bacteria somehow penetrates them and is incorporated into their genetic complement, so that their progeny inherit the genetic characters so acquired.

translation (L. a transferring). The process in which the genetic information present in messenger RNA is used to direct the order of specific amino acids during protein synthesis.

transporter See **permease.**

transverse plane (L. *transversus,* across). A plane or section that lies or passes across a body or structure.

trichinosis (trik-ən-o′səs). Disease caused by infection with the nematode *Trichinella spiralis.*

trichocyst (trik′ə-sist) (Gr. *thrix,* hair, + *kystis,* bladder). Sac-like protrusible organelle in the ectoplasm of ciliates, which discharges as a threadlike weapon of defense.

triglyceride (trī-glis′ə-rīd) (Gr. *tria,* three, + *glykys,* sweet, + *ide,* suffix denoting compound). A triester of glycerol with one, two, or three acids.

trimerous (trī′mə-rəs) (Gr. *treis,* three, + *meros,* a part). Body in three main divisions, as in lophophorates and some deuterostomes.

tripartite (trī-par′tīt). See **trimerous.**

triploblastic (trip′lō-blas′tik) (Gr. *triploos,* triple, + *blastos,* germ). Pertaining to metazoa in which the embryo has three primary germ layers—ectoderm, mesoderm, and endoderm.

trisomy 21 See **Down syndrome.**

trochophore (trōk′ə-fōr) (Gr. *trochos,* wheel, + *pherein,* to bear). A free-swimming ciliated marine larva characteristic of most molluscs and certain ectoprocts, brachiopods, and marine worms; an ovoid or pyriform body with preoral circlet of cilia and sometimes a secondary circlet behind the mouth.

trophallaxis (trōf′ə-lak′səs) (Gr. *trophē,* food, + *allaxis,* barter, exchange). Exchange of food between young and adults, especially certain social insects.

trophi (trō′fī) (Gr. *trophos,* one who feeds). Jaw-like structures in the mastax of rotifers.

trophic (trō′fək) (Gr. *trophē,* food). Pertaining to feeding and nutrition.

trophoblast (trōf′ə-blast) (Gr. *trephein,* to nourish, + *blastos,* germ). Outer ectodermal nutritive layer of blastodermic vesicle; in mammals it is part of the chorion and attaches to the uterine wall.

trophosome (trof′ə-sōm) (Gr. *trophē,* food, + *sōma,* body). Organ in poganophorans bearing mutualistic bacteria, derived from midgut.

trophozoite (trōf′ə-zō′īt) (Gr. *trophē,* food, + *zōon,* animal). Adult stage in the life cycle of a protozoan in which it is actively absorbing nourishment.

tropic (trä′pic) (Gr. *tropē,* to turn toward). Related to the tropics (tropical); in endocrinology, a hormone that influences the action of another hormone or endocrine gland (usually pronounced trō′pic).

tropomyosin (trōp′ə-mī′ə-sən) (Gr. *tropos,* turn, + *mys,* muscle). Low-molecular weight protein surrounding the actin filaments of striated muscle.

troponin (trə-pōn′in). Complex of globular proteins positioned at intervals along the actin filament of skeletal muscle; thought to serve as a calcium-dependent switch in muscle contraction.

tube feet (podia) Numerous small, muscular, fluid-filled tubes projecting from body of echinoderms; part of water-vascular system; used in locomotion, clinging, food handling, and respiration.

tubercle (tū′bər-kəl) (L. *tuberculum,* small hump). Small protuberance, knob, or swelling.

tubulin (tū′bū-lən) (L. *tubulus,* small tube, + *in,* belonging to). Globular protein forming the hollow cylinder of microtubules.

tumor necrosis factor A cytokine, the most important source of which is macrophages, that is a major mediator of inflammation.

tumor suppressor gene A gene whose products act as restraints on cell division by triggering apoptosis, controlling transcription of other genes, restraining progression in phases of the cell cycle, or by other means.

tundra (tun′drə) (Russ. from Lapp, *tundar,* hill). Terrestrial habitat zone, located between taiga and polar regions; characterized by absence of trees, short growing season, and mostly frozen soil during much of the year.

tunic (L. *tunica,* tunic, coat). In tunicates, a cuticular, cellulose-containing covering of the body secreted by the underlying body wall.

tympanic (tim-pan′ik) (Gr. *tympanon,* drum). Relating to the tympanum that separates the outer and middle ear (eardrum).

type specimen A specimen deposited in a museum that formally defines the name of the species that it represents.

typhlosole (tif′lə-sōl′) (Gr. *typhlos,* blind, + *sōlēn,* channel, pipe). A longitudinal fold projecting into the intestine in certain invertebrates such as the earthworm.

typology (tī-päl′ə-jē) (L. *typus,* image). A classification of organisms in which members of a taxon are perceived to share intrinsic, essential properties, and variation among organisms is regarded as uninteresting and unimportant.

U

ulcer (ul-sər) (L. *ulcus,* ulcer). An abscess that opens through the skin or a mucous surface.

ultimate cause (L. *ultimatus,* last, + *causa*). The evolutionary factors responsible for the origin, state of being, or purpose of a biological system.

umbilical (L. *umbilicus,* navel). Refers to the navel, or umbilical cord.

umbo (um′bō), pl. **umbones** (əm-bō′nēz) (L. boss of a shield). One of the prominences on either side of the hinge region in a bivalve mollusc shell. Also, the "beak" of a brachiopod shell.

ungulate (un′gū-lət) (L. *ungula,* hoof). Hooved. Noun, any hooved mammal.

uniformitarianism (ū′nə-fōr′mə-ter′ē-ə-niz′əm). Methodological assumptions that the laws of chemistry and physics have remained constant throughout the history of the earth, and that past geological events occurred by processes that can be observed today.

ureter (ūr′ə-tər) (Gr. *ouētēr,* ureter). Duct carrying urine from kidney to bladder.

urethra (ū-rē′thrə) (Gr. *ourethra,* urethra). The tube from the urinary bladder to the exterior in both sexes.

uropod (ū′rə-pod) (Gr. *oura,* tail, + *pous, podos,* foot). Posteriormost appendage of many crustaceans.

utricle (ū′trə-kəl) (L. *utriculus,* little bag). That part of the inner ear containing the receptors for dynamic body balance; the semicircular canals lead from and to the utricle.

V

vacuole (vak′yə-wōl) (L. *vacuus,* empty, + Fr. *ole,* dim.). A membrane-bound, fluid-filled space in a cell.

valence (vā′ləns) (L. *valere,* to have power). Degree of combining power of an element as expressed by the number of atoms of hydrogen (or its equivalent) that the element can hold (if negative) or displace in a reaction (if positive). The oxidation state of an element in a compound. The number of electrons gained, shared, or lost by an atom when forming a bond with one or more other atoms.

valve (L. *valva,* leaf of a double door). One of the two shells of a typical bivalve mollusc or brachiopod.

variation (L. *varius,* various). Differences among individuals of a group or species that cannot be ascribed to age, sex, or position in the life cycle.

vector (L. a bearer, carrier, from *vehere, vectum,* to carry). Any agent that carries and transmits pathogenic microorganisms from one host to another host. Also, in molecular biology, an agent such as bacteriophage or plasmid that carries recombinant DNA.

veins (vānz) (L. *vena,* a vein). Blood vessels that carry blood toward the heart; in insects, fine extensions of the tracheal system that support the wings.

velarium (və-la′rē-əm) (L. *velum,* veil, covering). Shelf-like extension of the

subumbrella edge in cubozoans (phylum Cnidaria).

veliger (vēl′ə-jər, vel-) (L. *velum,* veil, covering). Larval form of certain molluscs; develops from the trochophore and has the beginning of a foot, mantle, shell, and so on.

velum (vē′ləm) (L. veil, covering). A membrane on the subumbrella surface of jellyfish of class Hydrozoa. Also, a ciliated swimming organ of the veliger larva.

ventral (ven′trəl) (L. *venter,* belly). Situated on the lower or abdominal surface.

venule (ven′ūl) (L. *venula,* dim. of *vena,* vein). Small vessel conducting blood from capillaries to vein; small vein of insect wing.

vermiform (ver′mə-form) (L. *vermis,* worm, + *forma,* shape). Adjective to describe any wormlike organism; an adult (nematogen) rhombozoan (phylum Mesozoa).

vestige (ves′tij) (L. *vestigium,* footprint). A rudimentary organ that may have been well developed in some ancestor or in the embryo.

vibrissa (vī-bris′ə), pl. **vibrissae** (L. nostril-hair). Stiff hairs that grow from the nostrils or other parts of the face of many mammals and that serve as tactile organs; "whiskers."

vicariance (vī-kar′ē-ənts) (L. *vicarius,* a substitute). Geographical separation of populations, especially as imposed by discontinuities in the physical environment that fragmented populations that were formerly geographically continuous.

villus (vil′əs), pl. **villi** (L. tuft of hair). A small fingerlike, vascular process on the wall of the small intestine. Also one of the branching, vascular processes on the embryonic portion of the placenta.

virus (vī′rəs) (L. slimy liquid, poison). A submicroscopic noncellular particle composed of a nucleoprotein core and a protein shell; parasitic; will grow and reproduce in a host cell.

viscera (vis′ər-ə) (L. pl. of *viscus,* internal organ). Internal organs in the body cavity.

visceral (vis′ər-əl). Pertaining to viscera.

vitalism (L. *vita,* life). The discredited viewpoint that natural processes are controlled by supernatural forces and cannot be explained through the laws of physics and chemistry alone, as opposed to mechanism.

vitamin (L. *vita,* life, + *amine,* from former supposed chemical origin). An organic substance required in small amounts for normal metabolic function; must be supplied in the diet or by intestinal flora because the organism cannot synthesize it.

vitellaria (vi′təl-lar′e-ə) (L. *vitellus,* yolk of an egg). Structures in many flatworms that produce vitelline cells, that is, cells that provide eggshell material and nutrient for the embryo.

vitelline gland See **vitellaria.**

vitelline membrane (və-tel′ən, vī′təl-ən) (L. *vitellus,* yolk of an egg). The noncellular membrane that encloses the egg cell.

viviparity (vī′və-par′ə-dē) (L. *vivus,* alive, + *parere,* to bring forth). Reproduction in which eggs develop within the female body, with nutritional aid of maternal parent as in therian mammals, many reptiles, and some fishes; offspring are born as juveniles. Adj., **viviparous** (vī-vip′ə-rəs).

W

water-vascular system System of fluid-filled closed tubes and ducts peculiar to echinoderms; used to move tentacles and tube feet that serve variously for clinging, food handling, locomotion, and respiration.

weir (wer) (Old English *wer,* a fence placed in a stream to catch fish). Interlocking extensions of a flame cell and a collecting tubule cell in some protonephridia.

X

xanthophore (zan′thə-fōr) (Gr. *xanthos,* yellow, + *pherein,* to bear). A chromatophore containing yellow pigment.

xenograft (zē′nə-graft). Graft of tissue from a species different from the recipient.

X-organ Neurosecretory organ in eyestalk of crustaceans that secretes molt-inhibiting hormone.

Y

Y-organ Gland in the antennal or maxillary segment of some crustaceans that secretes molting hormone.

Z

zoecium, zooecium (zō-ē′shē-əm) (Gr. *zōon,* animal, + *oikos,* house). Cuticular sheath or shell of Ectoprocta.

zoochlorella (zō′ə-klōr-el′ə) (Gr. *zōon,* life, + *Chlorella*). Any of various minute green algae (usually *Chlorella*) that live symbiotically within the cytoplasm of some protozoa and other invertebrates.

zooflagellates (zō′ə-fla′jə-lāts). Members of the Zoomastigophora, the animal-like flagellates (phylum Sarcomastigophora).

zooid (zō-id) (Gr. *zōon,* life). An individual member of a colony of animals, such as colonial cnidarians and ectoprocts.

zooxanthella (zo′ə-zan-thəl′ə) (Gr. *zōon,* animal, + *xanthos,* yellow). A minute dinoflagellate alga living in the tissues of many types of marine invertebrates.

zygote (Gr. *zygōtos,* yoked). The fertilized egg.

zygotic meiosis Meiosis that takes place within the first few divisions after zygote formation; thus all stages in the life cycle other than the zygote are haploid.

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INDEX

Note: **Boldface** page numbers refer to figures, illustrations, or tables.

Italic page numbers refer to chapter opener illustrations.

D

E

F

G

H

M

N

O

P

X

Y

Z