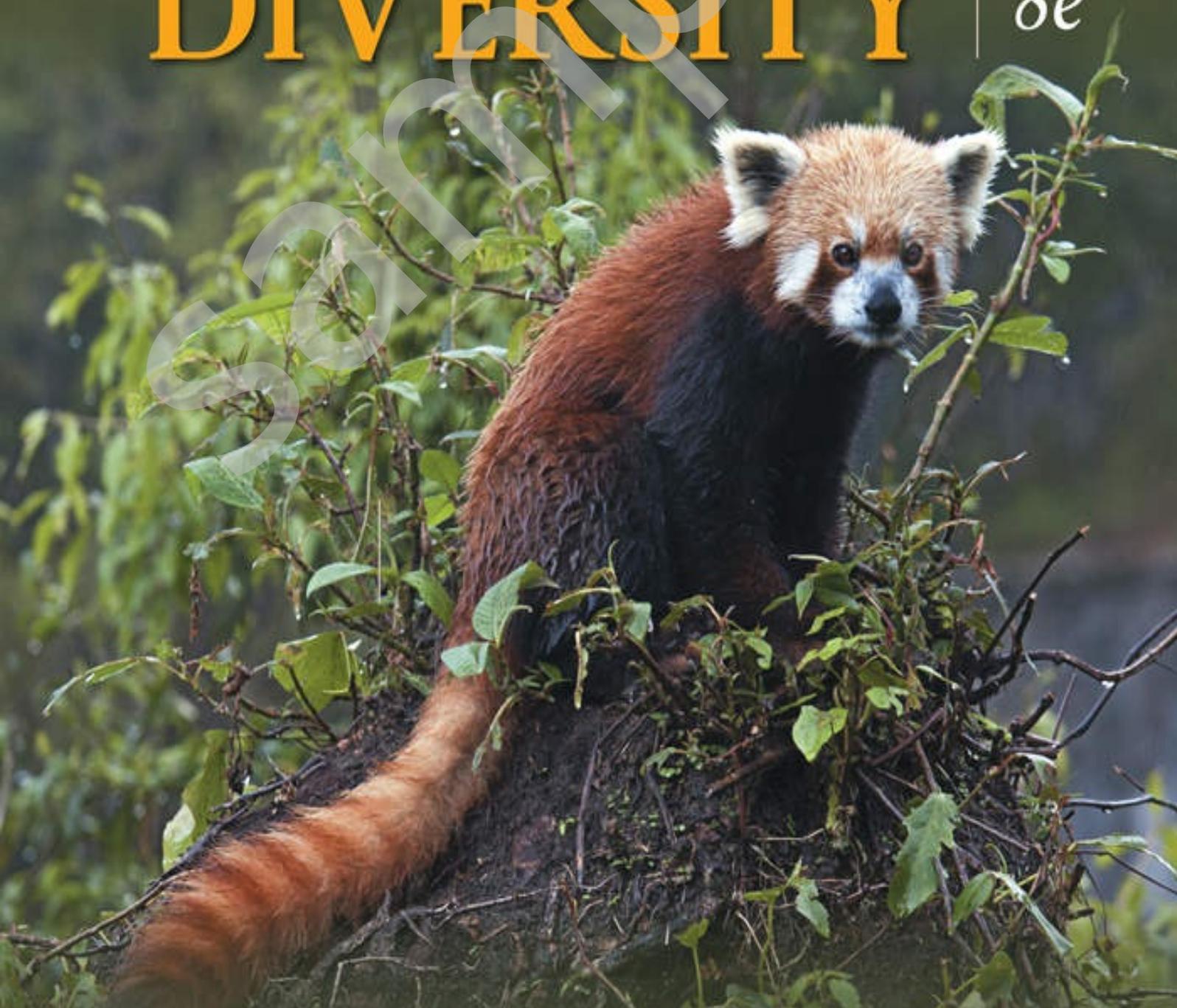


# ANIMAL DIVERSITY | 8e



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Cleveland P. Hickman, Jr.  
Susan L. Keen  
Allan Larson  
David J. Eisenhour

# Animal Diversity

EIGHTH EDITION

Cleveland P. Hickman, Jr.  
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*University of California, Davis*

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*Washington University*

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Sample



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ii

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# Brief Contents

- 1** Science of Zoology and Evolution of Animal Diversity
- 2** Animal Ecology
- 3** Animal Architecture
- 4** Taxonomy and Phylogeny of Animals
- 5** Unicellular Eukaryotes
- 6** Sponges: Phylum Porifera
- 7** Cnidarians and Ctenophores
- 8** Xenacoelomorpha, Platyzoa, and Mesozoa: Flatworms, Gastrotrichs, Gnathiferans, and Mesozoans
- 9** Polyzoa and Kryptozoa: Cyclophora,

Entoprocta, Ectoprocta, Brachiopoda, Phoronida, and Nemertea

**10** Molluscs

**11** Annelids

**12** Smaller Ecdysozoans

**13** Arthropods

**14** Chaetognaths, Echinoderms, and Hemichordates

**15** Vertebrate Beginnings: The Chordates

**16** Fishes

**17** The Early Tetrapods and Modern Amphibians

**18** Amniote Origins and Nonavian Reptiles

**19** Birds

**20** Mammals

General References  
Glossary  
Index

Sample

# Contents

## *Preface*

### Chapter 1

#### Science of Zoology and Evolution of Animal Diversity

- 1.1 Principles of Science
- 1.2 Origins of Darwinian Evolutionary Theory
- 1.3 Darwin's Theory of Evolution
- 1.4 Evidence for Darwin's Five Theories of Evolution
- 1.5 Revisions of Darwinian Evolutionary Theory
- 1.6 Microevolution: Genetic Variation and Change Within Species
- 1.7 Macroevolution: Major Evolutionary Events and Processes

*Summary*

*Review Questions*

*Selected References*

### Chapter 2

#### Animal Ecology

- 2.1 Environment and the Niche
- 2.2 Populations
- 2.3 Community Ecology
- 2.4 Ecosystems
- 2.5 Biodiversity and Extinction

*Summary*

*Review Questions*

*Selected References*

## Chapter 3

### Animal Architecture

- 3.1 The Hierarchical Organization of Animal Complexity
- 3.2 Animal Body Plans
- 3.3 How Many Body Plans Are There?
- 3.4 Components of Animal Bodies
- 3.5 Complexity and Body Size

*Summary*

*Review Questions*

*Selected References*

## Chapter 4

### Taxonomy and Phylogeny of Animals

- 4.1 Linnaeus and Taxonomy
- 4.2 Species
- 4.3 Taxonomic Characters and Reconstruction of Phylogeny
- 4.4 Theories of Taxonomy
- 4.5 Major Divisions of Life
- 4.6 Major Subdivisions of the Animal Kingdom

*Summary*

*Review Questions*

*Selected References*

## Chapter 5

### Unicellular Eukaryotes

- 5.1 Form and Function
- 5.2 Unicellular Eukaryotic Taxa
- 5.3 Phylogeny

*Summary*

*Review Questions*

*Selected References*

## Chapter 6

### Sponges: Phylum Porifera

- 6.1 Ecological Relationships
- 6.2 Form and Function

iv

- 
- 6.3 Brief Survey of Sponges
  - 6.4 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 7

### Cnidarians and Ctenophores

- 7.1 Phylum Cnidaria
- 7.2 Phylum Ctenophora
- 7.3 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 8

### Xenacoelomorpha, Platyzoa, and Mesozoa: Flatworms, Gastrotrichs, Gnathiferans, and Mesozoans

- 8.1 Phylum Xenacoelomorpha
- 8.2 Clade Platyzoa
- 8.3 Phylum Platyhelminthes
- 8.4 Phylum Gastrotricha
- 8.5 Clade Gnathifera
- 8.6 Phylum Gnathostomulida
- 8.7 Phylum Micrognathozoa
- 8.8 Phylum Rotifera
- 8.9 Phylum Acanthocephala
- 8.10 Phylum Mesozoa
- 8.11 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 9

## Polyzoa and Kryptozoa: Cycliophora, Entoprocta, Ectoprocta, Brachiopoda, Phoronida, and Nemertea

- 9.1 Clade Polyzoa
- 9.2 Phylum Cycliophora
- 9.3 Phylum Entoprocta
- 9.4 Phylum Ectoprocta
- 9.5 Clade Brachiozoa
- 9.6 Phylum Brachiopoda
- 9.7 Phylum Phoronida
- 9.8 Phylum Nemertea (Rhynchocoela)
- 9.9 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 10

### Molluscs

- 10.1 Ecological Relationships
- 10.2 Economic Importance
- 10.3 Function
- 10.4 Classes Caudofoveata and Solenogastres
- 10.5 Class Monoplacophora
- 10.6 Class Polyplacophora: Chitons
- 10.7 Class Scaphopoda
- 10.8 Class Gastropoda
- 10.9 Class Bivalvia (Pelecypoda)
- 10.10 Class Cephalopoda
- 10.11 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 11

### Annelids

- 11.1 Phylum Annelida
- 11.2 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 12

### Smaller Ecdysozoans

- 12.1 Phylum Nematoda: Roundworms
- 12.2 Phylum Nematomorpha
- 12.3 Phylum Loricifera
- 12.4 Phylum Kinorhyncha
- 12.5 Phylum Priapulida
- 12.6 Clade Panarthropoda
- 12.7 Phylum Onychophora
- 12.8 Phylum Tardigrada
- 12.9 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

v

## Chapter 13

### Arthropods

- 13.1 Ecological Relationships
- 13.2 Why Are Arthropods So Diverse and Abundant?
- 13.3 Subphylum Trilobita
- 13.4 Subphylum Chelicerata
- 13.5 Subphylum Myriapoda
- 13.6 Subphylum Crustacea
- 13.7 Subphylum Hexapoda
- 13.8 Phylogeny and Adaptive Diversification

*Summary*

*Review Questions*

*Selected References*

## Chapter 14

### Chaetognaths, Echinoderms, and Hemichordates

- 14.1 Phylum Chaetognatha: Arrow Worms
- 14.2 Clade Ambulacraria
- 14.3 Phylum Echinodermata

#### 14.4 Phylum Hemichordata

*Summary*

*Review Questions*

*Selected References*

## Chapter 15

### Vertebrate Beginnings: The Chordates

#### 15.1 Traditional and Cladistic Classification of the Chordates

#### 15.2 Five Chordate Hallmarks

#### 15.3 Ancestry and Evolution

#### 15.4 Subphylum Urochordata (Tunicata)

#### 15.5 Subphylum Cephalochordata

#### 15.6 Subphylum Vertebrata

*Summary*

*Review Questions*

*Selected References*

## Chapter 16

### Fishes

#### 16.1 Ancestry and Relationships of Major Groups of Fishes

#### 16.2 Living Jawless Fishes: Cyclostomata

#### 16.3 Cartilaginous Fishes: Chondrichthyes

#### 16.4 Bony Fishes and Tetrapods: Osteichthyes

#### 16.5 Structural and Functional Adaptations of Fishes

*Summary*

*Review Questions*

*Selected References*

## Chapter 17

### The Early Tetrapods and Modern Amphibians

#### 17.1 Devonian Origin of Tetrapods

#### 17.2 Modern Amphibians

*Summary*

*Review Questions*

*Selected References*

## Chapter 18

### Amniote Origins and Nonavian Reptiles

18.1 Origin and Early Evolution of Amniotes

18.2 Characteristics and Natural History of Reptilian Orders

*Summary*

*Review Questions*

*Selected References*

## Chapter 19

### Birds

19.1 Origin and Relationships

19.2 Structural and Functional Adaptations for Flight

19.3 Flight

19.4 Migration and Navigation

19.5 Social Behavior and Reproduction

19.6 Humans and Bird Populations

*Summary*

*Review Questions*

*Selected References*

## Chapter 20

### Mammals

20.1 Origin and Evolution of Mammals

20.2 Structural and Functional Adaptations of Mammals

20.3 Mammalian Populations

20.4 Human Evolution

*Summary*

*Review Questions*

*Selected References*

*General References*

*Glossary*

*Index*

# About the Authors

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Cleveland P. Hickman, Jr., Professor Emeritus of Biology at Washington and Lee University in Lexington, Virginia, has taught zoology and animal physiology for more than 30 years. He received his Ph.D. in comparative physiology from the University of British Columbia, Vancouver, B.C., in 1958 and taught animal physiology at the University of Alberta before moving to Washington and Lee University in 1967. He has published numerous articles and research papers on fish physiology, in addition to co-authoring these highly successful texts: *Integrated Principles of Zoology*, *Biology of Animals*, *Animal Diversity*, *Laboratory Studies in Animal Diversity*, and *Laboratory Studies in Integrated Principles of Zoology*.

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 four field guides in the Galápagos Marine Life Series for the identification of echinoderms, marine molluscs, marine crustaceans and corals and other radiates. (To read more about these field guides, visit <http://www.galapagosmarine.com>.)

His interests include scuba diving, woodworking, and participating in chamber music ensembles.

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Dr. Keen has been teaching evolution and animal diversity within the Introductory Biology series for 22 years. She enjoys all facets of the teaching process, from lectures and discussions to the design of effective laboratory exercises. In addition to her work with introductory biology, she offers seminars on teaching methods in biology, and works with an animator to create self-guided teaching modules on animal development. She has won awards for Excellence in Education from the Associated Students group at Davis. She attended the National Academies Summer Institute on Undergraduate Education in Biology, and was a National Academies Education Fellow in the Life Sciences for 2005–2006. Her interests include horseback riding, gardening, travel, and mystery novels.

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Allan Larson is a professor at Washington University, St. Louis, MO. He received his Ph.D. in genetics at the University of California, Berkeley, following B.S. and M.S. degrees in zoology from the University of Maryland. His fields of specialization include evolutionary biology, molecular population genetics and systematics, and amphibian systematics. He teaches courses in zoology, genetics, macroevolution, molecular evolution, and the history of evolutionary theory, and has organized and taught a special course in evolutionary biology for high-school teachers.

Dr. Larson's research uses DNA sequences to examine

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vii

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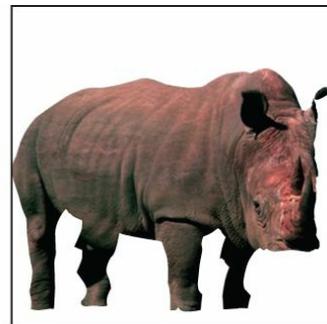
David J. Eisenhour is a professor of biology at Morehead State University in Morehead, Kentucky. He received his Ph.D. in zoology from Southern Illinois University, Carbondale. He teaches courses in environmental science, general biology, mammalogy, human anatomy, general zoology, comparative anatomy, ichthyology, and vertebrate zoology. David has an active research program that focuses on systematics, conservation biology, and natural history of North American freshwater fishes. He has a particular interest in the diversity of Kentucky's fishes and is writing a book about that subject. He and his undergraduate and graduate students have authored several publications. In 2001 he was given a Master Teacher Award by a student group at MSU, and in 2016 he was given the Distinguished Researcher Award at MSU. David serves as an academic advisor to prepharmacy students.

His interests include fishing, landscaping, softball, hiking, and entertaining his three children, who, along with his wife Lynn, are enthusiastic participants in fieldwork.

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viii

# Preface



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*Animal Diversity* is tailored for the restrictive requirements of a one-semester or one-quarter course in zoology, and is appropriate for both nonscience and science majors of varying backgrounds. This eighth edition of *Animal Diversity* presents a survey of the animal kingdom with emphasis on diversity, evolutionary relationships, functional adaptations, and environmental interactions.

## Organization and Coverage

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The sixteen survey chapters of animal diversity are prefaced by four chapters presenting the principles of evolution, ecology, animal architecture, and taxonomy. Throughout this revision, we updated references and worked to improve pedagogy.

Chapter 1 begins with a brief explanation of the scientific method—what science is (and what it is not)—and then introduces evolutionary principles. Following a historical account of Charles Darwin’s life and discoveries, we present the five major components of Darwin’s

evolutionary theory, the important challenges and revisions to his theory, and an assessment of its current scientific status. This approach reflects our understanding that Darwinism is a composite theory whose component parts guide active research and can be modified by new discoveries. It also prepares the student to dismiss the arguments of creationists who misconstrue scientific challenges to Darwinism as contradictions to the validity of organic evolution. The chapter summarizes the major principles of molecular genetics, population genetics, and macroevolution.

Chapter 2 explains the principles of ecology, with emphasis on populations, community ecology, and variations in the life-history strategies of natural populations. The treatment includes discussions of niche, population growth and its regulation, limits to growth, competition, energy flow, nutrient cycles, and extinction.

Chapter 3, on animal architecture, is a short but important chapter that describes the organization and development of the body plans that distinguish major groups of animals. This chapter includes a picture essay of tissue types and a section explaining important developmental processes responsible for the evolutionary diversification of the bilateral animals.

Chapter 4 treats taxonomy and phylogeny of animals. We present a brief history of how animal diversity has been organized for systematic study, emphasizing current use of Darwin's theory of common descent as the major principle underlying animal taxonomy. Our summary of continuing controversies over concepts of species and higher taxa includes discussion of how alternative taxonomic philosophies guide our study of evolution. We give special attention to phylogenetic systematics (cladistics) and the interpretation of cladograms. Chapter 4 also emphasizes that current issues in ecology and conservation biology depend upon our taxonomic system.

The sixteen survey chapters provide comprehensive, current, and thoroughly researched coverage of the animal phyla in the context of eukaryotic diversity and evolution. We emphasize the unifying phylogenetic, architectural, and functional themes of each group, and illustrate them with detailed coverage of representative forms. Each chapter includes succinct statements of the diagnostic characteristics and major subgroups of the focal taxa. Discussions of phylogenetic relationships take a cladistic viewpoint, with cladograms showing the structure of each group's history and the origin of the principal shared

derived characters. Phylogenetic trees add temporal evolutionary hypotheses to the cladistic analyses.

## Changes in the Eighth Edition

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We continue in updated form the major new structural feature of the previous two editions: a cladogram depicting phylogenetic relationships among animal taxa appears in the inside front cover and serves to order our coverage of animal diversity in Chapters 5–20. The reformatted cladogram from the inside front cover appears in small form at the start of each taxonomic chapter, with the chapter's taxonomic coverage highlighted on it. Following our seventh edition, two phyla were merged with others, reducing the number of phyla from 34 to 32. Sipuncula is now placed within Annelida, and Xenoturbellida is merged

ix

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with Acoelomorpha to form the new taxon Xenacoelomorpha. Our summary cladogram is adjusted accordingly.

A major new feature of the eighth edition is a list of learning objectives at the start of each chapter. These objectives help students to place a chapter's detailed information into the context of its major organizing principles.

Many revisions to the eighth edition are primarily to improve pedagogy. The content of *Animal Diversity* is condensed from the more comprehensive textbook, *Integrated Principles of Zoology*. The recently completed seventeenth edition of *Integrated Principles of Zoology* was guided by an electronic tabulation of students' responses to questions linked to the book. Authors received a "heat map" showing for each paragraph the percentage of correct student responses for the material covered. We focused our revisions on improving explanations wherever the heat map showed that correct responses were below 50%. With this detailed and insightful guidance, we made our text more accessible and memorable to its readers. We import these pedagogical improvements from the seventeenth edition of *Integrated Principles of Zoology* to the corresponding sections of the eighth edition of *Animal Diversity*.

Most of these revisions comprise more detailed explanations, including new illustrative examples. For example, to reinforce the

statement in Chapter 1 that Charles Lyell's geological studies convinced him that earth's age must be measured in hundreds of millions of years, we add the supporting information "For example, as skeletal remains of corals, foraminiferans, and mollusks accumulate on the sea floor, they form sediments of calcium carbonate that eventually become compressed into limestone. Measured rates of sedimentation are much too slow to have produced earth's sedimentary rock formations in a shorter period of time." Potassium-argon dating of rock strata was another point that required some further explanation to be fully accessible, "to our explanation in Chapter 1 we added". "Argon is a noble gas that evaporates from liquid media. It accumulates in the crystal structure of rock only after the rock has solidified and the nuclear decay of potassium-40 produces a trapped atom of argon." Comparable changes occur throughout our eighth edition.

Additional changes to Chapter 1 include greater explanation of adaptive radiation in oceanic islands and in lakes. The classic example of adaptive radiation of Galápagos finches is updated to include new information that questions whether the ecologically discrete forms are in fact discrete species, as traditionally interpreted, or whether they are alternative developmental modes that constitute polymorphisms within a set of genetically connected, geographic populations. To illustrate punctuated equilibrium, we replace an earlier example that was not well understood by students with the best-documented case: evolutionary history of the ectoproct genera *Metrarhabdotos* and *Stylopoma* in the Caribbean Sea. We reorder and expand our coverage of microevolutionary processes under a new heading "Forces of Evolutionary Change" near the end of Chapter 1.

Revisions to Chapter 2 include a greater emphasis on process of inquiry, explaining that "population" and "metapopulation" constitute conceptual models that investigators use to measure distributions and abundances of diverse organisms. We increase consistency in terminology; for example, we use "sigmoid" rather than a mix of "sigmoid" and "logistic" in text discussions of population growth, while explaining the relationship between these concepts in a boxed essay. Likewise, use of "abundance" rather than "fitness" in some places avoids confounding the ecological concept with population-genetic "fitness" as discussed in Chapter 1. We expand the explanation of how primary producers fix carbon and nitrogen from atmospheric gases, following evidence from our heat map that this concept often is not an

intuitive one.

In Chapters 3 and 4, many revisions increase precision and consistency in key concepts. For example, “cytoplasmic” replaces the more nebulous term “protoplasmic” in Chapter 3, and references to current taxonomic groups replace the now archaic terms “protozoan” and “metazoan.” Chapter 4 makes a stronger distinction between “classification” and “taxonomy” as central concepts. Chapter 4 also expands examples drawn from human evolution and the salamander genus *Ensatina* to illustrate the main issues that separate contrasting concepts of the species category. In asking how contrasting concepts of species would yield different species-level taxonomies of *Ensatina* populations, we lead students through the actual debates from relevant literature. Revisions clarify the relationship between the key phylogenetic concepts of clade and synapomorphy; definition of a clade makes no reference to synapomorphy, but synapomorphy is critical for testing the hypothesis that a particular grouping of species constitutes a clade. The explanation of evolutionary taxonomy is revised to emphasize that it retains pre-evolutionary Linnaean taxonomic principles that cladistic taxonomy rejects. Subsections “Major Divisions of Life” and “Major Subdivisions of the Animal Kingdom” are greatly rewritten, replacing archaic schemes (such as Whittaker’s five kingdoms) with newer rank-free taxonomies that follow cladistic principles and current molecular phylogenetic results.

The remaining chapters cover the details of animal evolutionary origins and diversification using the theoretical framework presented in Chapters 1-4. In each case, updates to species diversity and taxonomic relationships replace earlier hypotheses that new data have rejected. New opening essays for Chapters 5 and 6 reflect new ideas on the origin of the eukaryotic cell and the advent of multicellularity, respectively. Chapter 7 presents a new phylogenetic hypothesis for parasitic cnidarians of the clade Myxozoa. Chapter 8 now includes coverage and illustrations of the new taxon Xenacoelomorpha, consolidating some material on the former Xenoturbellida from Chapter 14. A new cladogram in Chapter 11 illustrates new phylogenetic results that place Sipuncula within Annelida.

Updates to Chapter 14 include new hypotheses on early evolution of deuterostomes and of echinoderms, with correspondingly revised cladograms. Revisions to Chapter 15 update phylogenies for the early chordates and fishes using new paleontological results. Coverage of the

role of *Hox* genes is reduced following rejection of some earlier hypotheses that overestimated their roles in chordate evolutionary diversification, and coverage of paraphyly of the traditional Class Reptilia is

x

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consolidated with related material in Chapter 18. Changes to Chapter 16 include extensive replacement of photographs with improved ones, plus a new figure describing aestivation in lungfishes. Changes to the narrative on the origin of terrestrial vertebrates in Chapter 17 emphasize that this was a fortuitous rather than a directed, progressive process. Chapter 18 incorporates new information on early events in turtle evolution, and Chapter 19 updates the species inventory and taxonomy of birds. In Chapter 20, early diversification of mammals is revised in light of data rejecting the hypothesis that most mammal groups arose after the end-Cretaceous mass extinction. Chapter 20 also includes an expanded and clarified discussion of mammalian feeding specializations, and incorporation of new fossil finds in understanding human evolution. Some material formerly included on density-dependent versus density-independent control of mammal populations is now consolidated with coverage of that topic in Chapter 2.

## **Teaching and Learning Aids**

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### **Vocabulary Development**

Key words are boldfaced, which serves as a cross-reference to the glossary for definition, pronunciation, and derivation of each term. Derivations of generic names of animals are given where they first appear in the text. In addition, derivations of many technical and zoological terms are provided, allowing students to recognize the more common roots that recur in many technical terms.

### **Learning Objectives**

Each chapter begins with a list of learning objectives that identify the major organizing principles of the chapter. Students enhance their understanding by using these guiding principles as they read a

chapter's detailed material.

## **Chapter Prologues**

A distinctive feature of this text is an opening essay at the beginning of each chapter. Each essay presents a theme or topic relating to the subject of the chapter to stimulate interest. Some present biological, particularly evolutionary, principles; others illuminate distinguishing characteristics of the animal group treated in the chapter.

## **Chapter Notes**

Chapter notes, which appear throughout the book, augment the text material and offer interesting sidelights without interrupting the narrative.

## **For Review**

Each chapter ends with a concise summary, review questions, and a list of annotated selected references. The review questions enable students to test themselves for retention and understanding of the more important chapter material.

## **Art Program**

The appearance and usefulness of this text are much enhanced by numerous full-color paintings by William C. Ober and Claire W. Garrison. Bill's artistic skills, knowledge of biology, and experience gained from an earlier career as a practicing physician have enriched the authors' zoology texts through many 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. Bill and Claire also are recipients of the Art Directors Award.

## **Supplements**

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## **Instructor's Manual**

Each chapter of the Instructor's Manual provides a detailed chapter outline, lecture enrichment suggestions, a commentary, and critical thinking questions. This material should be particularly helpful for first-time users of the text, although experienced teachers also may find much of value. The Instructor's Manual is available on this text's Online Learning Center through Connect.

## **Acknowledgments**

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xi

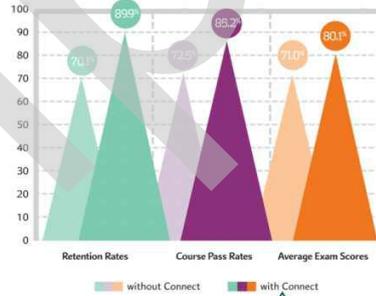
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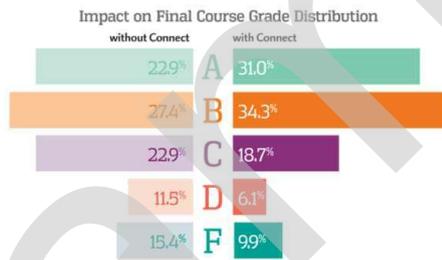
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xiii

xiv

1

# Science of Zoology and Evolution of Animal Diversity



Evolutionary diversification of Hawaiian honeycreepers.

Source: Haeckel, Ernst, *The Evolution of Man*, New York, NY: D. Appleton, 1886.

## LEARNING OBJECTIVES

Readers will be able to:

- 1** Explain that science consists in testing, possibly rejecting, and improving our simplest and best explanations using data, not in proving the correctness of a conjecture.
- 2** Describe the five major conjectures of Darwin's evolutionary theory: perpetual change, common descent, multiplication of species, gradualism, and natural selection.
- 3** Explain how Darwin's theories of perpetual change, common descent, and multiplication of species are supported by all relevant data, and why continuing controversies about the roles of gradualism and natural selection do not challenge these first three theories.

- 4 Explain the changes to Darwin's theory contributed by subsequent work in genetics and paleontology.
  - 5 Explain why the population, not the organism, is the unit of evolution.
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## A Legacy of Change

Life's history is a legacy of perpetual change. Despite the apparent permanence of the natural world, change characterizes all things on earth and in the universe. Countless kinds of animals and plants have flourished and disappeared, leaving behind an imperfect fossil record of their existence. Many, but not all, have left living descendants that resemble them to varying degrees.

We observe and measure life's changes in many ways. On a short evolutionary timescale, we see changes in the frequencies of different genetic traits within populations. For example, evolutionary changes in the relative frequencies of light- and dark-colored moths occurred within a single human lifetime in polluted areas of industrial England. On the other hand, formation of new species and dramatic changes in organismal appearance, as shown by evolutionary diversification of Hawaiian birds, require longer timescales covering 100,000 to 1 million years. Major evolutionary trends and episodic mass extinctions occur on even larger timescales, covering tens of millions of years. The fossil record of horses through the past 50 million years shows a series of different species replacing older ones. The fossil record of marine invertebrates shows episodic mass extinctions separated by intervals of approximately 26 million years.

Organic evolution is the irreversible, historical change that we observe in living populations and in the earth's fossil record. Because every feature of life is a product of evolutionary processes, biologists consider organic evolution the keystone of all biological knowledge.

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**Z**oology (Gr. *zōon*, animal, + *logos*, discourse on, study of) is the scientific study of animals. It is part of biology (Gr. *bios*, life, + *logos*), the study of all life. Explaining the panorama of animal diversity—how animals function, live, reproduce, and interact—is exciting and challenging.

To explain the diversity of animal life, we must study its long history, whose fossil evidence spans more than 540 million years. From the earliest animals to the millions of animal species living today, this

history demonstrates extensive and ongoing change, which we call **evolution**. We depict the history of animal life as a branching genealogical tree, called a **phylogeny** or **phylogenetic tree**. We place the earliest species ancestral to all animals at the trunk; all living animal species fall at the growing tips of the branches. Each successive branching event represents the historical splitting of an ancestral species to form new ones. Newly formed species inherit many characteristics from their immediate ancestor, but they also evolve new features that appear for the first time in the history of animal life. Each branch therefore has its own unique combination of characteristics and contributes a new dimension to the spectrum of animal diversity.

The scientific study of animal diversity has two major goals. The first is to reconstruct a phylogeny of animal life and to find where in evolutionary history we can locate the origins of major characteristics—multicellularity, a **coelom**, **spiral cleavage**, vertebrae, **homeothermy**—and all other dimensions of animal diversity as we know it. The second major goal is to understand historical processes that generate and maintain diverse species and adaptations throughout evolutionary history. Darwin's theory of evolution allows us to apply scientific principles to attain both goals.

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## 1.1 Principles of Science

A basic understanding of zoology requires understanding what science is, what it excludes, and how one gains knowledge using the scientific method. In this section we examine the methodology that zoology shares with science as a whole. These features distinguish the sciences from other disciplines, such as art and religion.

Despite an enormous impact of science on our lives, many people have only a minimal understanding of science. Public misunderstanding of scientific principles as applied to animal diversity revealed itself to us on March 19, 1981, when 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. Further legal scrutiny revealed that creation-science was not science, but rather a religious position advocated by a minority of America's religious community.

Enactment of this law incited a historic lawsuit tried in December 1981 in the court of Judge William R. Overton, U.S. District Court,

Eastern District of Arkansas. The American Civil Liberties Union filed the suit on behalf of 23 plaintiffs, including religious leaders and groups representing several denominations, individual parents, and educational associations. Plaintiffs contended that this law violated the First Amendment to the U.S. Constitution, which prohibits establishment of religion by government. This amendment prohibits passing a law that would favor one religious position over another one. On January 5, 1982, Judge Overton permanently prohibited Arkansas from enforcing Act 590.

Considerable testimony during the trial clarified the nature of science. On the basis of testimony by scientists, Judge Overton stated explicitly these essential characteristics of science:

1. It is guided by natural law.
2. It must be explanatory by reference to natural law.
3. Its conjectures are testable against the empirical world.
4. Its conclusions are tentative and not necessarily the final word.
5. It is falsifiable.

Pursuit of scientific knowledge is guided by physical and chemical laws that govern the state of existence. Scientific knowledge must explain observations by reference to natural law without intervention of any supernatural being or force. We must record observations that directly or indirectly test hypotheses about nature. We must discard or modify any 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 lies outside religion, and scientific knowledge does not favor one religious position over another.

Unfortunately, the religious position formerly called creation-science later reappeared in American politics with the name "intelligent design theory." We once again defended science education against this scientifically meaningless doctrine. On December 20, 2005, Judge John E. Jones III of the U.S. District Court for the Middle District of Pennsylvania ruled unconstitutional the teaching of intelligent design, which had been mandated by the Dover school board. The local voters already had rejected the eight board members who supported the intelligent-design requirement, replacing them with candidates

who actively opposed teaching intelligent design as science.

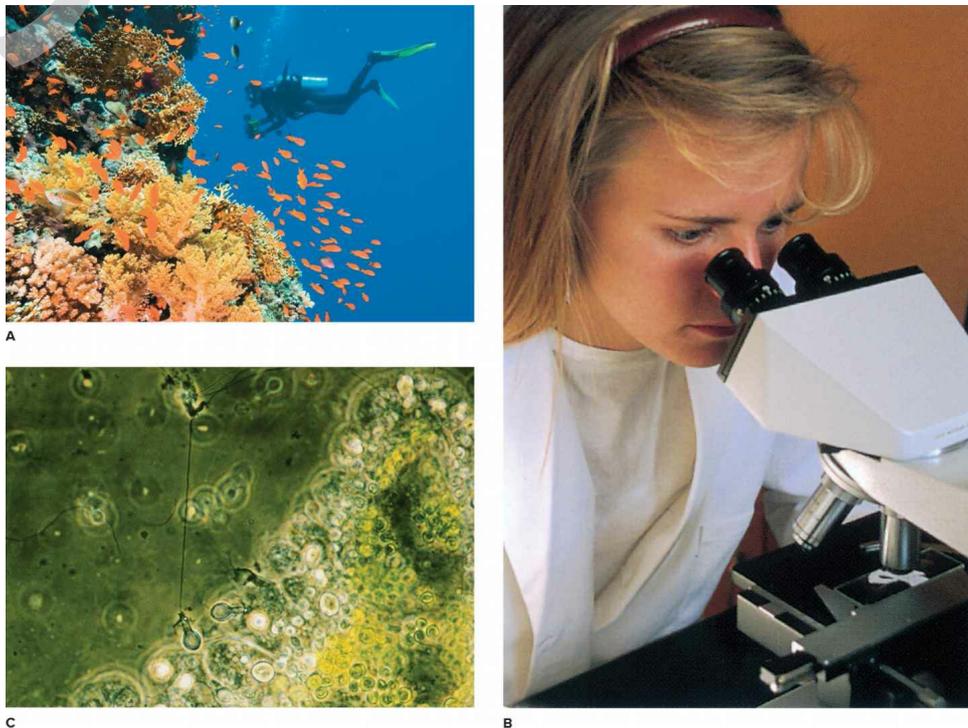
## Scientific Method

The essential criteria of science form the **hypothetico-deductive method**. One begins this process by generating **hypotheses**, or potential explanations of a phenomenon of nature. These hypotheses are usually based on prior observations of nature (figure 1.1) or on theories derived from such observations. Scientific hypotheses often constitute general statements that might explain a large number of diverse observations. The hypothesis of natural selection, for example, explains our observations that many different species have accumulated favorable characteristics that adapt them to their environments. Based on a hypothesis, a scientist must say, “If my hypothesis

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correctly explains past observations, then future observations must match specific expectations.”



**figure 1.1**

Examples of observation in zoological research. **A**, Observing a coral reef. **B**, Observing nematocyst discharge, **C**, from cnidarian tentacles (see p. 147).

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The scientific method comprises six steps:

1. Observation
2. Question
3. Hypothesis
4. Empirical test
5. Conclusions
6. Publication

Observations are a critical first step in evaluating the biological characteristics and evolutionary histories of animal populations. For example, observations of moth populations in industrial areas of England for more than a century have revealed that moths in polluted areas mostly have darkly colored wings and body, whereas moths of the same species in unpolluted areas are more lightly colored. This observation pertains to multiple moth species, but we focus here on *Biston betularia* (figure 1.2).



**figure 1.2**

Light and melanic forms of peppered moths, *Biston betularia*, on **A**, an unpolluted lichen-covered tree and **B**, a soot-covered tree near industrial Birmingham, England. These color variants have a simple genetic basis. **C**, Recent decline in frequency of the melanic form due to diminished air pollution in industrial areas of England. Frequency of the melanic form 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 tree trunks, the melanic form became more conspicuous to predators. By 1986, only 50% of the moths were melanic, the rest having been replaced by the light form.

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Our question is, Why do pigmentation patterns vary according to habitat? With no prior knowledge of the biology of these moth populations, one might hypothesize that coloration is influenced somehow by a direct action of the environment. Does consumption of soot by caterpillars somehow darken pigmentation of the adult moth? One could test this hypothesis by rearing moths under artificial conditions. If darkly pigmented moths and lightly pigmented moths are allowed to reproduce in unpolluted conditions, our hypothesis predicts that offspring of both will be lightly pigmented; by contrast, offspring of both groups would be darkly pigmented if raised in polluted conditions.

To test our hypothesis, we construct a null hypothesis. A null hypothesis is one that permits a statistical test of our data

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to reject its predictions if the hypothesis is false. We can choose as our null hypothesis the prediction that population of origin has no effect on moth color: moths reared in unpolluted conditions should be lightly pigmented regardless of whether their parents were from light or dark populations, and offspring from both populations reared in polluted conditions should be dark. This experiment is a special case of a “common garden” experiment as used in agriculture. Do contrasting populations from different habitats retain their contrasting characteristics when reared in a common garden?

For *Biston betularia*, a common garden experiment reveals that the contrasting wing colors of populations from polluted and unpolluted environments are maintained in the common garden. Offspring of moths from polluted populations retain the dark pigmentation of their parents, whereas offspring of lightly pigmented moths are lightly colored like their parents. We thereby reject the hypothesis that the color contrasts represent a direct action of environmental conditions.

We have gained important knowledge by rejecting our initial hypothesis, and we now test an alternative hypothesis, that pigmentation is a genetic trait in *Biston betularia*. Using standard genetic methodology, we cross the darkly and lightly colored populations and trace the inheritance of pigmentation in subsequent generations. Experimental results reveal that the offspring produced by crossing light and dark populations have dark pigmentation, and that

the second-generation progeny include both dark and light moths in the 3:1 ratio predicted by the null hypothesis for a single-gene trait with dark pigmentation being genetically dominant.

We still have not answered our initial question, why pigmentation differs between populations in polluted versus unpolluted environments. We have learned, however, that the critical question is why different forms of a single gene have contrasting frequencies in these two areas. We know that the moth populations have inhabited England since well before the introduction of industrial pollution. The lightly pigmented populations most likely resemble the ancestral condition, so why have darkly pigmented moths accumulated in the polluted environments? The simplest hypothesis is that darkly pigmented individuals are more likely to survive and to reproduce in polluted environments.

Further observations reveal that *Biston betularia* is typical of moths in being active at night and inactive during the day, resting on the bark of trees. Contrasting photographs of light and dark moths resting on unpolluted, lichen-covered tree bark versus sooty tree bark lead us to a hypothesis that might explain why dark moths predominate in polluted areas. Figure 1.2 shows that the lightly colored moth is camouflaged against the unpolluted substrate, whereas the dark moth is highly visible; by contrast, the dark moth is camouflaged against the sooty bark, whereas the light moth is highly visible. Camouflage suggests that a predator using vision to find its prey preferentially kills moths that contrast with the background color of their diurnal resting place. How can we test this hypothesis?

Many birds are diurnal predators guided to their prey by vision. Many experiments have revealed that birds will attack clay models that closely resemble their favored prey items. We can test our hypothesis by constructing clay models of light and dark moths. We place equal numbers of the light and dark models against the bark of unpolluted trees and equal numbers of light and dark models against sooty tree bark. When a bird attacks a clay model, it typically leaves an imprint of its beak in the clay. Because beak shape varies among bird species, the beak shape marked in the clay often reveals which species attacked the model. Our null hypothesis is that equal numbers of dark and light models have beak impressions on both the unpolluted and the polluted substrates. We reject this hypothesis if we find a large excess of beak marks in the uncamouflaged models relative to the camouflaged ones;

dark models should be attacked preferentially in unpolluted conditions and light models attacked preferentially in polluted conditions. Note that in this case, we use a null hypothesis that is the *opposite* of our favored explanation, that birds preferentially

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destroy uncamouflaged moths. In this case, data that reject the null hypothesis serve to verify our favored explanation.

Experiments of this kind have rejected the null hypothesis as expected, verifying our explanation that dark moths prevail in polluted environments because the dark color protects them from predation by birds during the day. Note that our experiments led us to a strong, specific explanation for the initial observations. It is a strong working hypothesis, but our experiments have not proven the correctness of this hypothesis. We can test it further in various ways. For example, we might raise light and dark moths in equal numbers in an outdoor enclosure that excludes birds; our null hypothesis is then that the dark and light forms should persist in equal numbers regardless of whether the tree bark is polluted or unpolluted. Rejection of this null hypothesis would tell us that our favored explanation was not the full answer to our original question.

We publish our results and conclusions to guide other researchers further to test our hypotheses. Over the past century, many research papers have reported results and conclusions to explain “industrial melanism” in moths. With some ambiguities, the favored explanation is that differential bird predation on uncamouflaged moths best explains industrial melanism. These studies have drawn much attention because this explanation illustrates Darwin’s theory of natural selection (p. 12).

## Experimental Versus Comparative Methods

One can group the many questions raised about animal life into two major categories. The first category seeks to explain **proximate causes** (also called immediate causes) that guide biological systems at all levels of complexity. It includes explaining how animals perform their metabolic, physiological, and behavioral functions at molecular, cellular, organismal, and even population levels. For example, how is genetic information expressed to guide the synthesis of proteins? What signal causes cells to divide to produce new cells? How does population

density affect the physiology and behavior of organisms?

We test hypotheses of proximate causes using the **experimental method**. This method has three steps: (1) predicting from a tentative explanation how a system being studied would respond to a treatment, (2) making the treatment, and (3) comparing observed results to predicted ones. An investigator repeats the experiment multiple times to eliminate chance occurrences that might produce errors. **Controls** (repetitions of an experimental procedure that lack the treatment) eliminate any unperceived conditions that might bias an experiment's outcome.

Our example in the preceding section of using clay models of moths to test avian predation on differently colored forms illustrates experimental testing of a hypothesis. By placing darkly colored models on both light and dark backgrounds, we see that birds attack the ones on light backgrounds much more frequently than they do dark models on dark backgrounds. Our interpretation that dark moths on dark backgrounds avoid predation by camouflage requires a control. Perhaps birds choose to feed only on light, unpolluted branches. Our control is to place light moths on both light and dark backgrounds. When we observe that birds preferentially attack the light models placed on dark backgrounds, we reject the hypothesis that birds choose not to feed on dark, polluted substrates. The simplest interpretation of the results as described here is that birds will eat both dark and light moths that fail to match their backgrounds, and that camouflage conceals potential prey items from avian predators.

Processes by which animals maintain their body temperature under different environmental conditions, digest food, migrate to new habitats, or store energy are additional examples of phenomena studied by experimentation. Experimental sciences in biology include molecular biology, cell biology, endocrinology, immunology, physiology, developmental biology, and community ecology.

In contrast to proximate causes, ultimate causes are the processes that have produced biological systems and their properties through evolutionary time. For example, what evolutionary factors cause some birds to make complex seasonal migrations between temperate and tropical regions? Why do different species of animals have different numbers of chromosomes in their cells? Why do some animal species maintain complex social systems, whereas individuals of other species remain largely solitary?

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A scientist's use of the phrase "ultimate cause," unlike Aristotle's usage, does not imply a preconceived goal for natural phenomena. An argument that nature has a predetermined goal, such as evolution of the human mind, is termed teleological. **Teleology** is the mistaken notion that the evolution of living organisms is guided by purpose toward an optimal design. A major success of Darwinian evolutionary theory is its rejection of teleology in explaining biological diversification.

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Tests of hypotheses of ultimate causality require the **comparative method**. Characteristics of molecular biology, cell biology, organismal structure, development, and ecology are compared among species to identify patterns of variation. Scientists then use patterns of similarity and dissimilarity to test hypotheses of relatedness and thereby to reconstruct the phylogenetic tree that relates the species being compared. Systematics is the ordering of organisms according to their inferred evolutionary relationships for comparative study. Recent advances in DNA sequencing technology permit precise tests of evolutionary relationships among all animal species. Comparative studies also serve to test hypotheses of evolutionary processes that have molded diverse animal species.

We use the evolutionary tree to examine hypotheses of the evolutionary origins of the diverse molecular, cellular, organismal, and populational characteristics observed in the animal world. For example, comparative methodology rejects the hypothesis of a common origin for flight in bats and birds. Comparative morphology of vertebrates and comparisons of DNA sequences from living species clearly place bats within the mammals (Chapter 20) and birds within a separate group that also includes crocodilians, lizards, snakes, and turtles (see figure 18.2). The most recent common ancestor of these vertebrates clearly could not fly, and close inspection reveals that bats and birds evolved flight via very different modifications of their bodies and forelimbs (pp. 404, 424). The ultimate causes of flight in bats and birds thus require separate explanations, not a shared one. The comparative method likewise reveals that **homeothermy** evolved in a lineage ancestral to birds and separately in a lineage ancestral to mammals. Furthermore, comparative studies of fossil birds reject the hypothesis that feathers arose for the purpose of flight, because feathers preceded evolution of the flight apparatus in avian ancestry. Feathers most likely served initially primarily for insulation and only

later acquired a role in aerodynamics. It should be clear that none of these important historical questions could have been answered by experiment.

5

## The Power of a Theory

Darwin's theory of common descent (p. 11) illustrates the scientific importance of general theories that give unified explanations to diverse kinds of data. Darwin proposed his theory of descent with modification of all living forms because it explained the patterns of similarity and dissimilarity among organisms in anatomical structures and cellular organization.

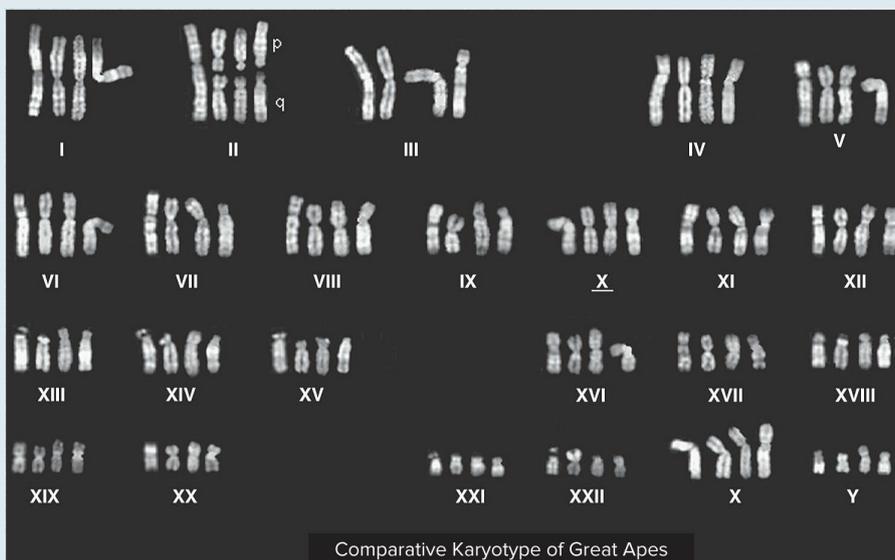
Anatomical similarities between humans and apes led Darwin to propose that humans and apes share more recent common ancestry with each other than they do with any other species. Darwin was unaware that his theory, a century later, would provide the primary explanation for similarities and dissimilarities among species in the structures of their chromosomes, sequences of amino acids in homologous proteins, and sequences of bases in homologous genomic DNA.

The accompanying figure shows photographs of a complete haploid set of chromosomes from each of four ape species: human (*Homo sapiens*), bonobo (the pygmy chimpanzee, *Pan paniscus*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo pygmaeus*). Each chromosome in the human genome has a corresponding chromosome with similar structure and gene content in the genomes of other ape species. The most obvious difference between human and ape chromosomes is that the large second chromosome in the human nuclear genome was formed evolutionarily by a fusion of two smaller chromosomes characteristic of the ape genomes. Detailed study of the human and other ape chromosomes shows remarkable correspondence between them in genic content and organization. Ape chromosomes are more similar to each other than they are to chromosomes of any other animals.

Comparison of DNA and protein sequences among apes likewise confirms their close genetic relationships, with humans and the two chimpanzee species being closer to each other than any of these species are to other apes. DNA sequences from the

nuclear and mitochondrial genomes independently support the close relationships among ape species and especially the grouping of humans and chimpanzees as close relatives. Homologous DNA sequences of humans and chimpanzees are approximately 99% similar in base sequence.

Studies of variation in chromosomal structure, mitochondrial DNA sequences, and nuclear DNA sequences produced multiple independent data sets, each one potentially capable of rejecting Darwin's theory of common descent. Darwin's theory would be rejected, for example, if the chromosomal structures and DNA sequences of apes were no more similar to each other than to those of other animals. The data in this case support rather than reject predictions of Darwin's theory. The ability of Darwin's theory of common descent to make precise predictions of genetic similarities among these and other species, and to have those predictions confirmed by numerous empirical studies, illustrates its great strength. As new kinds of biological data have become available, the scope and strength of Darwin's theory of common descent have increased enormously. Indeed, nothing in biology makes sense in the absence of this powerful explanatory theory.



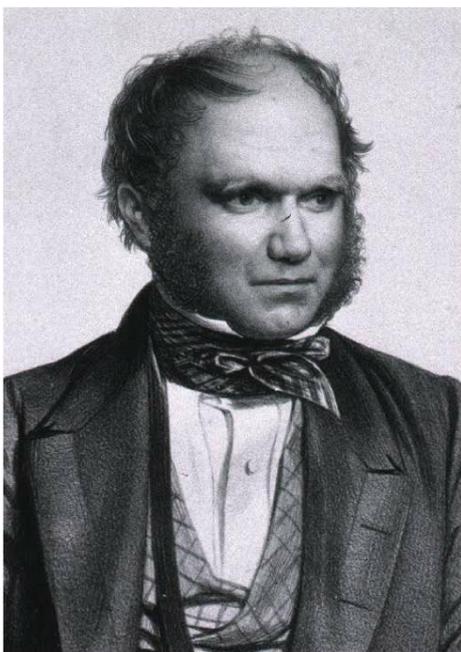
The human haploid genome contains 22 autosomes (I–XXII) and a sex chromosome (X or Y). The human chromosome is shown first in each group of four, followed by the corresponding chromosomes of bonobo, gorilla, and orangutan, in that order. Note that the chromatin of human chromosome II corresponds to that of two smaller chromosomes (marked p and q) in other apes.

©Dr. Mariano Rocchi

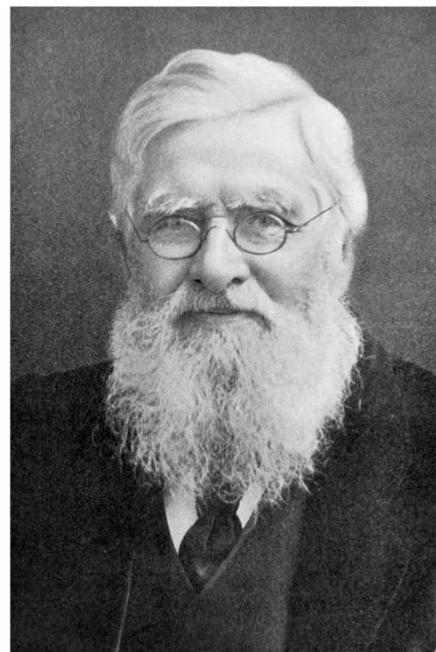
Clearly, the comparative method often relies on results of experimental sciences to reveal the characteristics being compared among animals. The comparative method utilizes all levels of biological complexity, as illustrated by the fields of comparative biochemistry, molecular evolution, comparative cell biology, comparative anatomy, comparative physiology and behavior, and phylogenetic systematics.

## 1.2 Origins of Darwinian Evolutionary Theory

Charles Robert Darwin and Alfred Russel Wallace (figure 1.3) were the first to establish evolution as a powerful scientific theory. Today, evolution can be denied only by abandoning reason. As the English biologist Sir Julian Huxley wrote, “Charles Darwin effected the greatest of all revolutions in human thought, greater than Einstein’s or Freud’s or even Newton’s, by simultaneously establishing the fact and discovering the mechanism of organic evolution.” Darwinian theory allows us to explain both the genetics of populations and long-term trends in the fossil record. Darwin and Wallace did not originate the basic idea of organic evolution, which has an ancient history. We review first the history of evolutionary thinking as it led to Darwin’s theory and then discuss critical evidence supporting Darwin’s theory.



A



B

## figure 1.3

Founders of the theory of evolution by natural selection. **A**, Charles Robert Darwin (1809–1882). **B**, Alfred Russel Wallace (1823–1913) in 1895. Darwin and Wallace independently developed the same theory. A letter and essay from Wallace written to Darwin in 1858 spurred Darwin into writing *On the Origin of Species*, published in 1859.

Source: Thomas Herbert Maguire/National Library of Medicine

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## Pre-Darwinian Evolutionary Ideas

Early Greek philosophers, notably Xenophanes, Empedocles, and Aristotle, recorded the idea that life has a long history of evolutionary change. They recognized fossils as evidence for former life, which they thought had been destroyed by natural catastrophe. Despite their inquiry, ancient Greeks failed to establish an evolutionary concept that could guide a meaningful study of life's history. Evolutionary thinking declined as the metaphorical biblical account of earth's creation became accepted as requiring no mechanistic explanation. The year 4004 B.C. was fixed by Archbishop James Ussher (mid-seventeenth century) as the time of life's creation. Evolutionary views were considered heretical, but they refused to die. The French naturalist Georges Louis Buffon (1707–1788) stressed environmental influences on modifications of animal form and extended the earth's age to 70,000 years.

## Lamarckism: The First Scientific Hypothesis for Evolution

The first complete hypothesis for evolution was authored by the French biologist Jean Baptiste de Lamarck (1744–1829) (figure 1.4) in 1809, the year of Darwin's birth. He made the first convincing argument that fossils were remains of extinct animals. Lamarck's evolutionary mechanism, **inheritance of acquired characteristics**, tentatively answered the challenging question of how evolution could construct biological characteristics that seemed designed to serve their possessors' needs: By striving to make best use of their environmental resources, organisms would acquire adaptations and pass them by heredity to their offspring. According to Lamarck, giraffes evolved a

long neck because their ancestors lengthened their necks by stretching to obtain food and then passed the lengthened neck to their offspring. Lamarck proposed that over many

7

generations, these changes accumulated to produce the long necks of modern giraffes.



**figure 1.4**

Jean Baptiste de Lamarck (1744–1829), French naturalist who offered the first scientific explanation of evolution. Lamarck's hypothesis that evolution proceeds by inheritance of acquired characteristics was rejected by genetic research.

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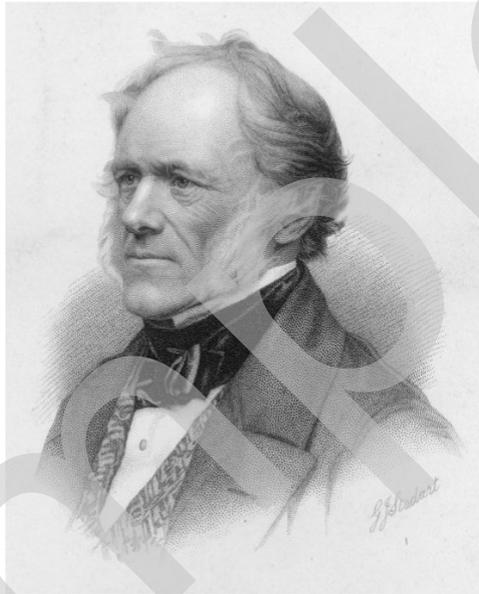
We call Lamarck's concept of evolution *transformational*, because as individual organisms transform their characteristics through the use and disuse of body parts, heredity makes corresponding adjustments to produce evolution. We now reject transformational theories because genetic studies show that traits acquired during an organism's lifetime, such as strengthened muscles, are not transmitted to offspring.

Darwin's evolutionary theory differs from Lamarck's in being a *variational* theory based in genetic differences that occur among organisms within a population. Evolution occurs at the level of the **population**, and it includes changes across generations in the organismal characteristics that prevail in the population. Darwin argued that organisms whose hereditary characteristics conferred an

advantage for survival or reproduction would contribute the greatest numbers of offspring to future generations. Populations would thus accumulate, across generations, the characteristics most favorable for the organisms possessing them. Any less favorable alternative characteristics would decline in frequency and eventually disappear.

## Charles Lyell and Uniformitarianism

The geologist Sir Charles Lyell (1797–1875) (figure 1.5) established in his *Principles of Geology* (1830–1833) the principle of **uniformitarianism**. Uniformitarianism encompasses two important assumptions that guide scientific study of the history of nature. These assumptions are (1) that the laws of physics and chemistry have not changed throughout earth's history, and (2) that past geological events occurred by natural processes similar to those that we observe in action today. Lyell showed that natural forces, acting over long periods of time, could explain the formation of fossil-bearing rocks. For example, as skeletal remains of corals (p. 157), foraminiferans (p. 122), and molluscs (p. 200) accumulate on the sea floor, they form sediments of calcium carbonate that eventually become compressed into limestone. Lyell's geological studies convinced him that earth's age must be measured in hundreds of millions of years. Measured rates of sedimentation are much too slow to have produced earth's sedimentary rock formations in a shorter period of time. These principles were important because they discredited miraculous and supernatural explanations of the history of nature and replaced them with scientific explanations. Lyell also stressed the gradual nature of geological changes that occur through time, and he argued that such changes have no inherent directionality. Both of these claims left important marks on Darwin's evolutionary theory.



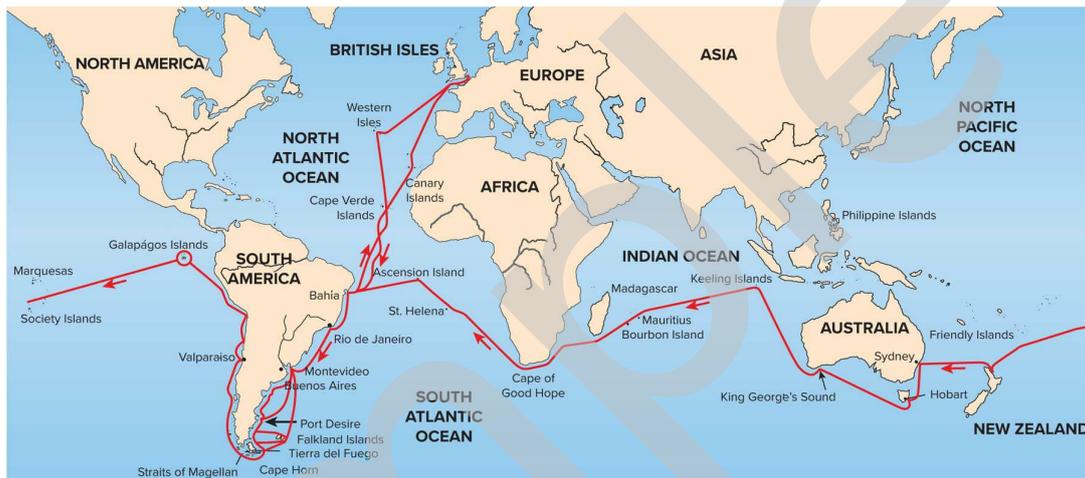
### **figure 1.5**

Sir Charles Lyell (1797–1875), English geologist and friend of Darwin. His book *Principles of Geology* greatly influenced Darwin during Darwin's formative period.

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## **Darwin's Great Voyage of Discovery**

"After having been twice driven back by heavy southwestern gales, Her Majesty's ship *Beagle*, a ten-gun brig, under the command of Captain Robert FitzRoy, R.N., sailed from Devonport on the 27th of December, 1831." Thus began Charles Darwin's account of the historic five-year voyage of the *Beagle* around the world (figure 1.6). Darwin, not quite 23 years old, had asked to accompany Captain FitzRoy on the *Beagle*, a small vessel only 90 feet in length, which was about to make an extensive surveying voyage to South America and the Pacific (figure 1.7). It was the beginning of the most important scientific voyage of the nineteenth century.



**figure 1.6**

Five-year voyage of H.M.S. *Beagle*.



A



B

**figure 1.7**

Charles Darwin and H.M.S. *Beagle*. **A**, Darwin in 1840, four years after the *Beagle* returned to England, and a year after his marriage to his cousin, Emma Wedgwood. **B**, H.M.S. *Beagle* sails in *Beagle* Channel, Tierra del Fuego, on the southern tip of South America in 1833. This watercolor was painted by Conrad Martens, one of two official artists during the voyage of the *Beagle*.

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During this voyage (1831–1836), Darwin endured sea-sickness and erratic companionship from Captain FitzRoy, but his endurance and early training as a naturalist equipped him for his work. The *Beagle* made many stops along the coasts of South America and adjacent

islands. Darwin made extensive collections and observations of the faunas and floras of these regions. He unearthed numerous fossils of animals long extinct and noted a resemblance between fossils of South American pampas and known fossils of North America. In the Andes, he encountered seashells embedded in rocks at 13,000 feet. He experienced a severe earthquake and watched mountain torrents that relentlessly wore away the earth. These observations and his reading of Lyell's *Principles of Geology* during the voyage strengthened Darwin's conviction

8

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that natural forces could explain geological features of the earth.

In mid-September of 1835, the *Beagle* arrived at the Galápagos Islands, a volcanic archipelago straddling the equator 600 miles west of Ecuador (figure 1.8). The fame of these islands stems from their oceanic isolation and rugged volcanic terrain. Circled by capricious currents, surrounded by shores of twisted lava, bearing skeletal brushwood baked by equatorial sunshine, almost devoid of vegetation, inhabited by strange reptiles and by convicts stranded by the Ecuadorian government, these islands had few admirers among mariners. By the middle of the seventeenth century, Spaniards called these islands "Las Islas Galápagos"—the tortoise islands. The giant tortoises, used for food first by buccaneers and later by American and British whalers, sealers, and ships of war, were the islands' principal attraction. At the time of Darwin's visit, these tortoises already were heavily exploited.



## figure 1.8

The Galápagos Islands viewed from the rim of a volcano.

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9

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During the *Beagle's* five-week visit to the Galápagos, Darwin documented the unique character of the Galápagos plants and animals, including the giant tortoises, marine iguanas, mockingbirds, and ground finches. Darwin later described these studies as the “origin of all my views.”

Darwin discovered that although the Galápagos Islands and Cape Verde Islands (visited earlier in this voyage) were similar in climate and topography, Galápagos plants and animals resembled most closely those of the South American mainland, and they were entirely different from the African-derived forms of the Cape Verde Islands. Each Galápagos island often contained a unique species that nonetheless resembled forms on other Galápagos islands. In short, Galápagos life must have originated in continental South America, colonized islands in rare events of trans-oceanic dispersal, and then undergone modification in various environmental conditions of different islands. He concluded that these species were neither divinely created nor immutable; they were products of a long history of evolutionary change.

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“Whenever I have found that I have blundered, or that my work has been imperfect, and when I have been contemptuously criticized, and even when I have been overpraised, so that I have felt mortified, it has been my greatest comfort to say hundreds of times to myself that ‘I have worked as hard and as well as I could, and no man can do more than this.’ ”

—Charles Darwin, in his autobiography, 1876.

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On October 2, 1836, the *Beagle* returned to England, where Darwin conducted most of his scientific work (figure 1.9). Most of Darwin's extensive collections had preceded him there, as had his notebooks and diaries kept during the cruise. Darwin's journal, published three years after the *Beagle's* return to England, was an instant success and required two additional printings within its first year. *The Voyage of the Beagle* would become one of the most popular travel books of all time.



**figure 1.9**

Darwin's study at Down House in Kent, England, is preserved today much as it was when Darwin wrote *On the Origin of Species*.

©Cleveland P. Hickman, Jr.

The main product of Darwin's voyage, his theory of evolution, would continue to develop for more than 20 years after the *Beagle's* return. In 1838, he "happened to read for amusement" an essay on populations by T. R. Malthus (1766–1834), who stated that animal and plant populations, including human populations, have the reproductive capacity to increase beyond the capacity of their environment to support them. Darwin already had been gathering information on artificial selection of animals under domestication. He was especially fascinated by artificial breeds of pigeons. Many pigeon breeds differed so much in appearance and behavior that they would be considered different species if found in nature. All clearly had been derived from a single wild species, the rock dove (*Columbia livia*). After reading Malthus's article, Darwin realized that a process of selection in nature, driven by a "struggle for existence" because of overpopulation, could be a powerful force for evolution of wild species.

Darwin allowed the idea to develop in his own mind, writing private, trial essays in 1844 and 1846. In 1856, he began to assemble his voluminous data into a work on origins of species. He expected to write four volumes, a very big book, "as perfect as I can make it." However, his plans took an unexpected turn.

In 1858, he received a manuscript from Alfred Russel Wallace (1823–1913), an English naturalist in Malaya with whom he corresponded. Darwin was stunned to find that in a few pages, Wallace summarized the main points of the natural selection theory on which Darwin had worked for two decades. Rather than withhold his own work in favor of Wallace as he was inclined to do, Darwin took the advice of two close friends, Lyell and a botanist, Hooker, to publish his views in a brief statement that would appear together with Wallace's paper in the *Journal of the Linnean Society*. Portions of both papers were read before an unresponsive audience on July 1, 1858.

10

For the next year, Darwin worked urgently to prepare an "abstract" of the planned four-volume work. This book was published in November 1859, with the title *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. The 1250 copies of the first printing were sold the first day! The book instantly generated a storm that has never abated. Darwin's views were to have extraordinary consequences on scientific and religious beliefs, and they remain among the greatest intellectual achievements of all time.

Once Darwin's caution had been swept away by publication of *On the Origin of Species*, he entered an incredibly productive period of evolutionary thinking for the next 23 years, producing five revisions of *On the Origin of Species* and a dozen new books. He died on April 19, 1882, and was buried in Westminster Abbey. The *Beagle* had already disappeared, having been retired in 1870 and sold for scrap.

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## 1.3 Darwin's Theory of Evolution

Darwin's theory of evolution is now over 150 years old. Biologists frequently are asked, "What is Darwinism?" and "Do biologists still accept Darwin's theory of evolution?" These questions do not have simple answers because Darwinism encompasses several different, although mutually connected, theories. Professor Ernst Mayr of Harvard University argued that Darwinism should be viewed as five major theories. These five theories have somewhat different origins and fates and cannot be treated as only a single hypothesis. 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. Gradualism and natural selection remain somewhat controversial among evolutionists; they are clearly important evolutionary processes, but they might not explain as much of animal evolution as Darwin thought. Creationists often misrepresent legitimate controversies regarding gradualism and natural selection as challenges to the first three theories, whose validity is strongly supported by all relevant facts.

1. **Perpetual change.** This is the basic theory of evolution on which the others depend. It states that the living world has a long history of ongoing change, with hereditary continuity from past to present life. Organismal characteristics undergo modification 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 any 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 fact.
2. **Common descent.** The second Darwinian theory, common descent, states that all forms of life propagated from a common ancestor through a branching of lineages (figure 1.10). An opposing argument, that different forms of life arose independently and descended to the present in linear, unbranched genealogies, is refuted by comparative studies of

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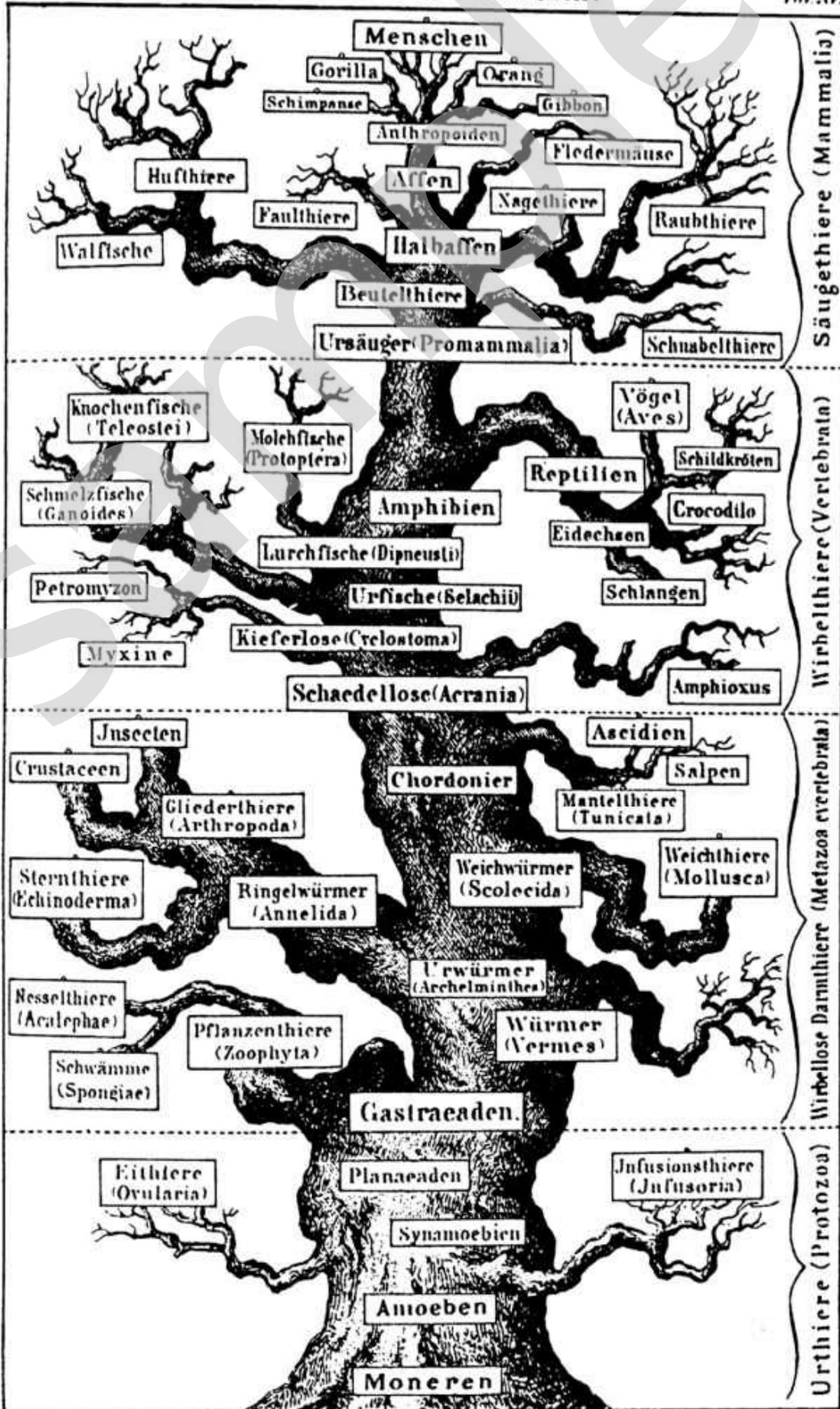
organismal form, cellular structure, and macromolecular structures (including those of the genetic material, DNA). All of these studies confirm the theory that life's history has the structure of a branching evolutionary tree, called a phylogeny. Species that share relatively recent common ancestry (within the past several million years) have more similar features at all levels than do species whose most recent common ancestor occurred tens or hundreds of millions of years ago. Darwin's theory of common descent guides much ongoing research to reconstruct life's phylogeny using patterns of similarity and dissimilarity observed among species. The resulting phylogeny provides the basis for our taxonomic

classification of animals (see Chapter 4).

Sample

Stammbaum des Menschen.

Taf. 17.



## figure 1.10

An early tree of animal life drawn in 1874 by the German biologist Ernst Haeckel, who was strongly influenced by Darwin's theory of common descent. Some hypotheses, including the grouping of humans (*Menschen*) with anthropoid apes, have been verified by subsequent testing. Other hypotheses have been rejected in favor of contrasting hypotheses; for example, humans and chimpanzees are more closely related to each other than either is to gorillas, and orangs are more closely related to the combined chimpanzees, gorillas, and humans than they are to gibbons.

Source: Haeckel, Ernst, *The Evolution of Man*, New York, NY: D. Appleton, 1886.

- 3. Multiplication of species.** Darwin's third theory states that evolution produces new species by splitting and transforming older ones. This theory adds a spatial dimension to evolutionary processes. When populations of a species become isolated from each other by geographic barriers, the isolated populations undergo separate evolutionary change and can diverge from each other. For example, when sea level was higher in the past than it is now, low areas of Cuba were inundated, dividing its land area into multiple isolates. Lizard populations that were formerly parts of a single species evolved species-level differences in isolation before another lowering of sea level reconsolidated Cuba as we know it today.

Species are reproductively distinct populations of organisms that usually but not always differ from each other in organismal form. Once species are fully formed, they propagate as separate evolutionary lineages, and interbreeding does not occur freely among members of different species, or the resulting hybrid offspring do not persist. Evolutionists generally agree that splitting and transformation of lineages produce new species, although much controversy remains concerning the details of this process and the precise meaning of the term "species" (see Chapter 4). Biologists are actively studying evolutionary processes that generate new species.

- 4. Gradualism.** Darwin's theory of gradualism states that large differences in anatomical traits among species originate by accumulation of many small incremental changes over very long periods of time. This theory opposes the notion that large

anatomical differences arise by sudden genetic changes within a generation. This theory is important because genetic changes having very large effects on organismal form are usually harmful to an organism. It is possible, however, that some genetic changes of large effect are nonetheless sufficiently beneficial to be favored by natural selection. For example, the genetic mutation that produced dark pigmentation in *Biston betularia* (see figure 1.2) and thus permitted camouflage on polluted substrates was favored in polluted environments despite causing an abrupt change. Gradual evolution of industrial melanism would have involved accumulation of slightly darker forms over many generations to produce the melanic moth, and the genetic data contradict the gradual interpretation. Therefore, although we know that gradual evolution occurs, it does not necessarily explain the origins of all structural differences among species. Scientists are studying this question actively.

5. **Natural selection.** Natural selection explains why organisms are constructed to meet the demands of their environments, a phenomenon called **adaptation**. This theory describes a natural process by which populations accumulate favorable characteristics throughout long periods of evolutionary time. Adaptation formerly was considered strong evidence against evolution. Darwin's theory of natural selection was therefore important for convincing people that a natural process, amenable to scientific study, could produce new adaptations and new species. Demonstration that natural processes could produce adaptation was important to the eventual acceptance of all five Darwinian theories. Darwin developed his theory of natural selection as a series of five observations, and he made three inferences from them (see box on page 13):

**Observation 1: Organisms have great potential fertility.** All populations produce large numbers of gametes and potentially large numbers of offspring each generation. Population size would increase exponentially at an enormous rate if all fertilized eggs produced each generation successfully completed their development to form reproductively active adult individuals. Darwin calculated that, even for slow-breeding organisms such as elephants, a single pair breeding from age 30 to 90 and having only six offspring could produce 19 million descendants

in 750 years.

**Observation 2: Natural populations normally remain constant in size, except for minor fluctuations.** Natural populations fluctuate in size across generations and sometimes go extinct, but no natural populations show the continued exponential growth that their reproductive capacity theoretically could sustain.

**Observation 3: Natural resources are limited.** Exponential growth of a natural population would require unlimited natural resources to provide food and habitat for an expanding population, but natural resources are finite.

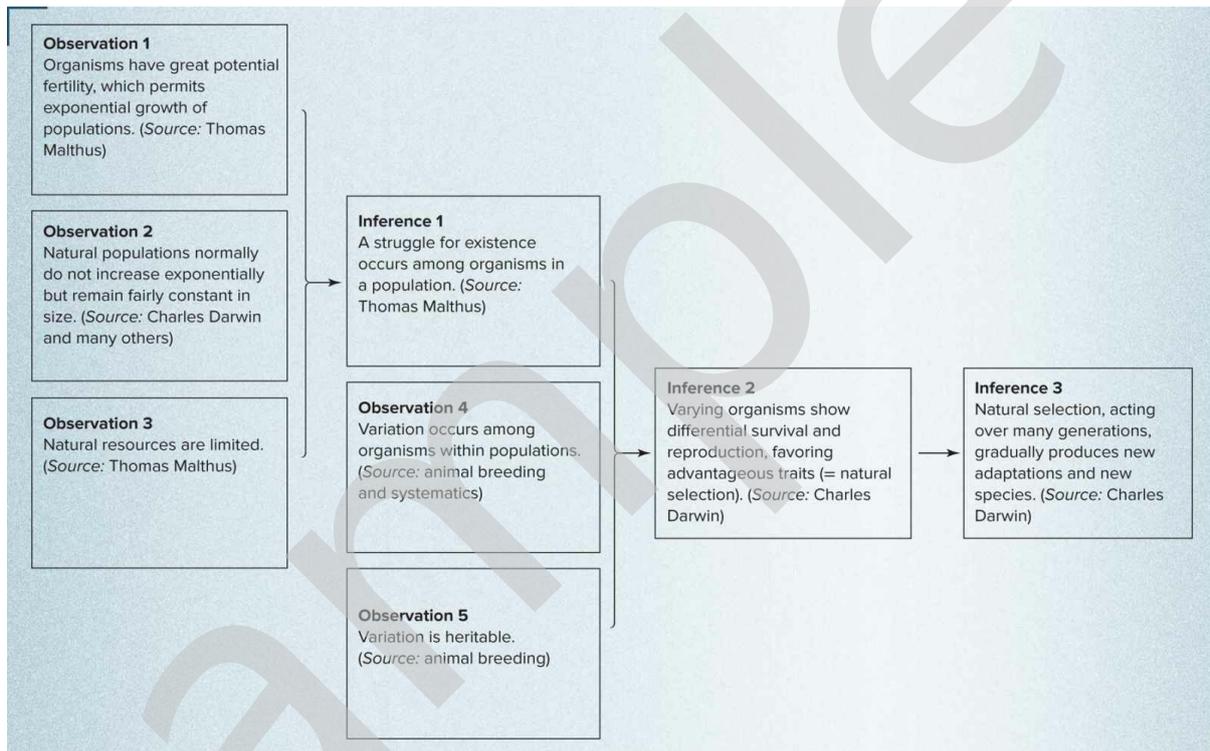
**Inference 1: A continuing *struggle for existence* occurs among members of a population.** Survivors represent only a portion, often a very small portion, of all individuals produced each

12

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generation. Darwin wrote in *On the Origin of Species* that “it is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms.” Struggle for food, shelter, and space becomes increasingly severe as overpopulation develops.

Darwin’s Explanatory Model of Evolution by  
Natural Selection



Source: E. Mayr, *One Long Argument*, 1991, Harvard University Press, Cambridge, MA.

**Observation 4: All populations show organismal *variation*.** No two individuals are exactly alike. They differ in size, color, physiology, behavior, and many other ways.

**Observation 5: Variation is heritable.** Darwin noted that offspring tend to resemble their parents, although he did not understand how. Many years later, the hereditary mechanism discovered by Gregor Mendel would be applied to Darwin's theory.

**Inference 2: Varying organisms show *differential survival and reproduction* favoring advantageous traits (= natural selection).** Survival in a struggle for existence is not random with respect to contrasting hereditary traits present in a population. Some traits give their possessors an advantage in using their environmental resources for effective survival and reproduction. Survivors transmit their favored traits to offspring, thereby causing those traits to accumulate in the population.

**Inference 3: Over many generations, natural selection gradually produces new adaptations and new species.** The preferential propagation of favorable traits across generations

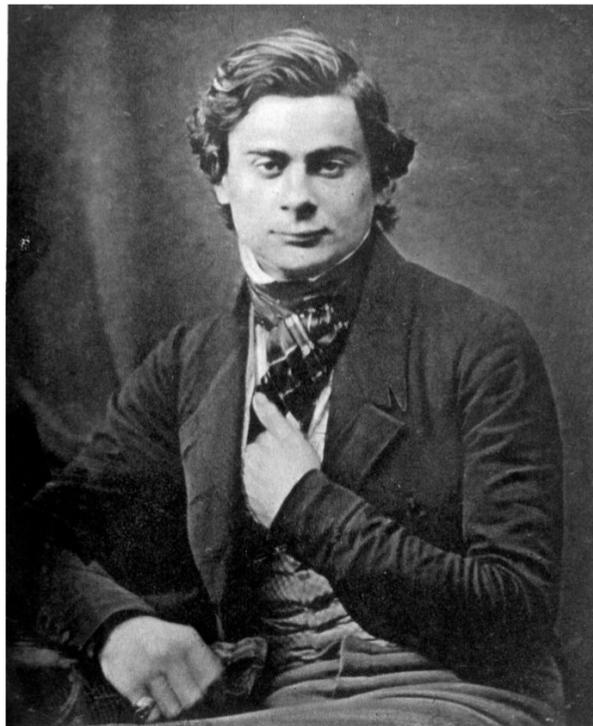
gradually transforms species and causes their long-term “improvement.” Darwin knew that people often use hereditary variation to produce useful new breeds of livestock and plants. *Natural* selection acting over millions of years should be even more effective in producing new types than *artificial* selection imposed during a human lifetime. Natural selection acting independently on geographically separated populations would cause them to diverge from each other, thereby generating reproductive barriers that lead to speciation.

13

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Natural selection can be considered a two-step process with a random component and a nonrandom component. Production of variation among organisms is the random part. Mutational processes have no inherent tendency to generate traits that are favorable to an organism. The nonrandom part is differential persistence among traits, determined by the effectiveness of contrasting traits in permitting their possessors to use environmental resources to survive and to reproduce.

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Thomas Henry Huxley (1825–1895), one of England’s greatest zoologists, on first reading the convincing evidence of natural selection in Darwin’s *On the Origin of Species*, is said to have exclaimed, “How extremely stupid not to have thought of that!” He became Darwin’s foremost advocate and engaged in often bitter debates with Darwin’s critics. Darwin, who disliked publicly defending his own work, was glad to leave such encounters to his “bulldog,” as Huxley called himself.

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Differential survival and reproduction among varying organisms is called **sorting** and should not be equated with natural selection. We now know that even random processes (genetic drift, see p. 33) can produce sorting. If a garden planted with equal numbers of red- and white-flowered plants suffers severe damage from a hurricane, it is unlikely that equal numbers of red- and white-flowered plants will survive to produce seeds. If red-flowered plants constitute 70% of the survivors, sorting has occurred in favor of the red-flowered plants. In this case, flower color provided no advantage in withstanding the hurricane damage. Most likely, a larger number of red-flowered plants happened to be growing in better-protected locations, permitting their differential survival. This sorting therefore cannot be attributed to natural selection because the character being sorted had no causal influence on the outcome. If in the same garden, white-flowered plants produced more seeds and offspring because they were more visible to a nocturnal moth pollinator, we would observe sorting favoring the white flowers and could attribute this sorting to selection; white flower color in this case provided a reproductive advantage over red color, leading the white-flowered plants to increase in frequency in the next generation. Darwin’s theory of natural selection states that sorting occurs *because certain traits give their possessors advantages in survival and reproduction* relative to others that lack those traits. Therefore, selection is one specific cause of sorting.

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The popular phrase “survival of the fittest” predates the publication of Darwin’s theory of natural selection; it was introduced by the British social philosopher Herbert Spencer, and later applied to Darwin’s theory. Unfortunately, this phrase often implies unbridled aggression and violence

in a bloody, competitive world. In fact, natural selection operates through many other characteristics of living organisms. For example, many Russian evolutionists argued that animals practicing mutual aid enjoyed the greatest survival advantages in harsh climates.

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## 1.4 Evidence for Darwin's Five Theories of Evolution

### Perpetual Change

Perpetual change in the form and diversity of animal life throughout its history reveals itself most directly in the fossil record of the past 540 million years. A **fossil** is a remnant of past life uncovered from the earth's crust (figure 1.11). Some fossils constitute complete remains (insects in amber and mammoths), actual hard parts (teeth and bones), or petrified skeletal parts infiltrated with silica or other minerals (ostracoderms and molluscs). Other fossils include footprints or other impressions, burrows of marine worms in sediment on the sea floor, and fossil excrement (coprolites). In addition to documenting organismal evolution, fossils reveal profound changes in the earth's physical environments, including major changes in the locations of lands and seas. Fossils formed on the floors of ancient seas can be quarried high atop current mountains (Burgess Shale, p. 16). Discovery of new fossils and reinterpretation of familiar ones expand our knowledge of how the forms and diversity of animals changed through geological time. Evolutionary study of the fossil record is called paleontology.



**figure 1.11**

Four examples of fossil material. **A**, Stalked crinoids (sea lilies, class Crinoidea, phylum Echinodermata; see p. 316) from Devonian rocks. The fossil record shows that these echinoderms reached their greatest diversity millions of years earlier and began a slow decline to the present. **B**, The fossil of an insect that got stuck in the resin of a tree approximately 25 million years ago, after which the resin hardened into amber. **C**, Fish fossil of the perciform genus *Priscacara* from rocks of the Green River Formation, Wyoming. Such fish swam here during the Eocene epoch, approximately 50 million years ago. **D**, Electron micrograph of tissue from a fly fossilized as shown in **B**; the nucleus of a cell is marked in red.

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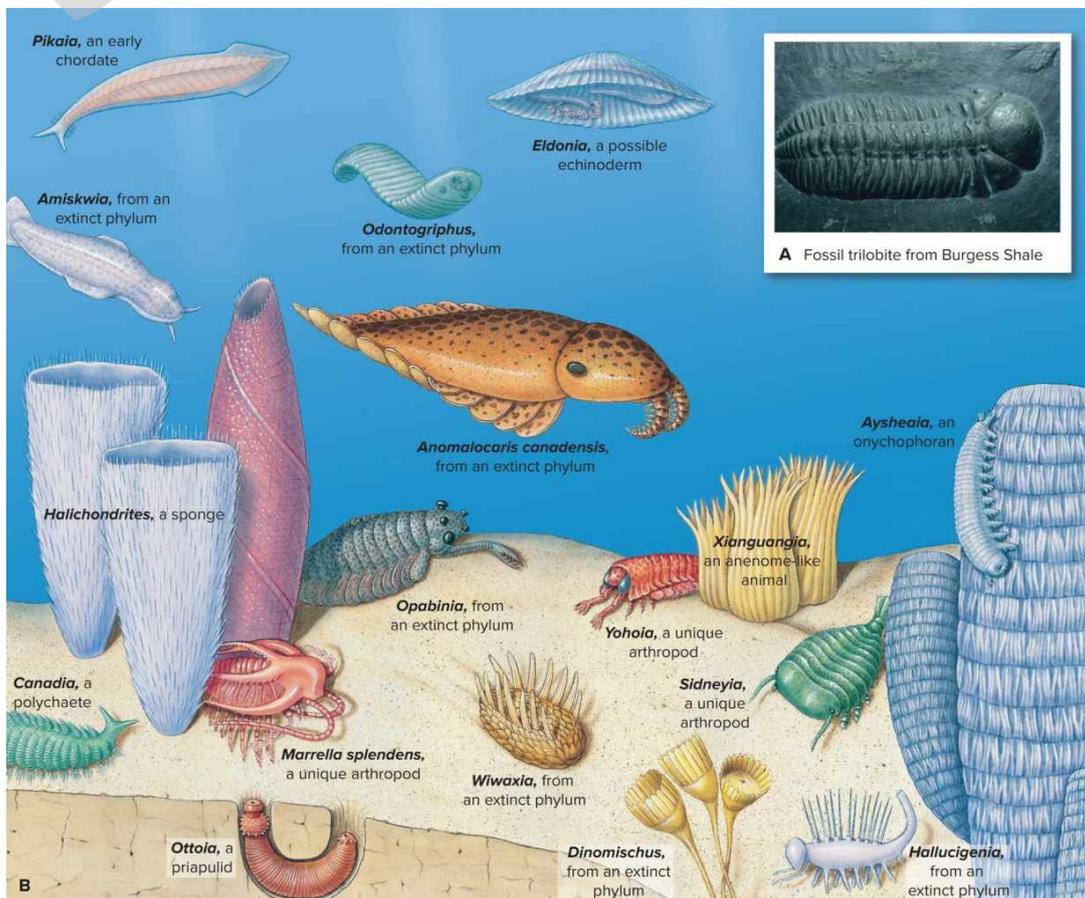
On rare occasions, fossil remains include soft tissues preserved so well that electron microscopy reveals recognizable cellular organelles! Insects and even small vertebrates, such as lizards, can be entombed in amber, the fossilized resin of trees. One study of a fly entombed in 40-million-year-old amber revealed structures corresponding to muscle fibers, nuclei, ribosomes, lipid droplets, endoplasmic reticulum, and mitochondria (figure

1.11D). This extreme case of mummification probably occurred because chemicals in the plant sap diffused into the embalmed insect's tissues. A fictional

extraction and cloning of DNA from embalmed insects that had bitten and then sucked the blood of dinosaurs was the technical basis for Michael Crichton's best-seller *Jurassic Park*.

## Interpreting the Fossil Record

The fossil record is biased because preservation is selective. Vertebrate skeletal parts and invertebrates with shells and other hard structures left the best record (figure 1.11). Soft-bodied animals, including jellyfishes and most worms, are fossilized only under very unusual circumstances, such as those that formed the Burgess Shale of British Columbia (figure 1.12). Exceptionally favorable conditions for fossilization produced a Precambrian fossil bed in South Australia, tar pits at Rancho La Brea (Hancock Park, Los Angeles), great dinosaur beds (Alberta, Canada, and Jensen, Utah; figure 1.13), the Olduvai Gorge of Tanzania, and the early Cambrian Chengjiang beds of China.



## figure 1.12

**A**, Fossil trilobite. **B**, Animals of the Cambrian period, approximately 540 million years ago, as reconstructed from fossils preserved in the Burgess Shale of British Columbia, Canada. The major body plans of living animals appeared rather abruptly at this time.

©Kevin Schafer/Alamy Stock Photo



## figure 1.13

A fossil skeleton from Dinosaur Provincial Park, Alberta, Canada.

©Cleveland P. Hickman, Jr.

Fossil deposits form stratified layers, with new deposits forming above older ones. If left undisturbed, which is rare, the ages of fossils in a preserved sequence are directly proportional to their depth in stratified layers. Stratigraphy is the study of fossil-bearing rocks. Characteristic fossils often serve to identify particular layers. Certain widespread marine invertebrate fossils, including various foraminiferans (see p. 157) and echinoderms (see p. 305), are such good indicators of specific geological periods that we call them “index,” or “guide,” fossils. Unfortunately, layers are usually tilted or folded or show faults (cracks). Old deposits exposed by erosion might be covered by new deposits in a different plane. When exposed to tremendous pressures or heat, stratified sedimentary rock metamorphoses into crystalline quartzite, slate, or marble, thereby destroying fossils.

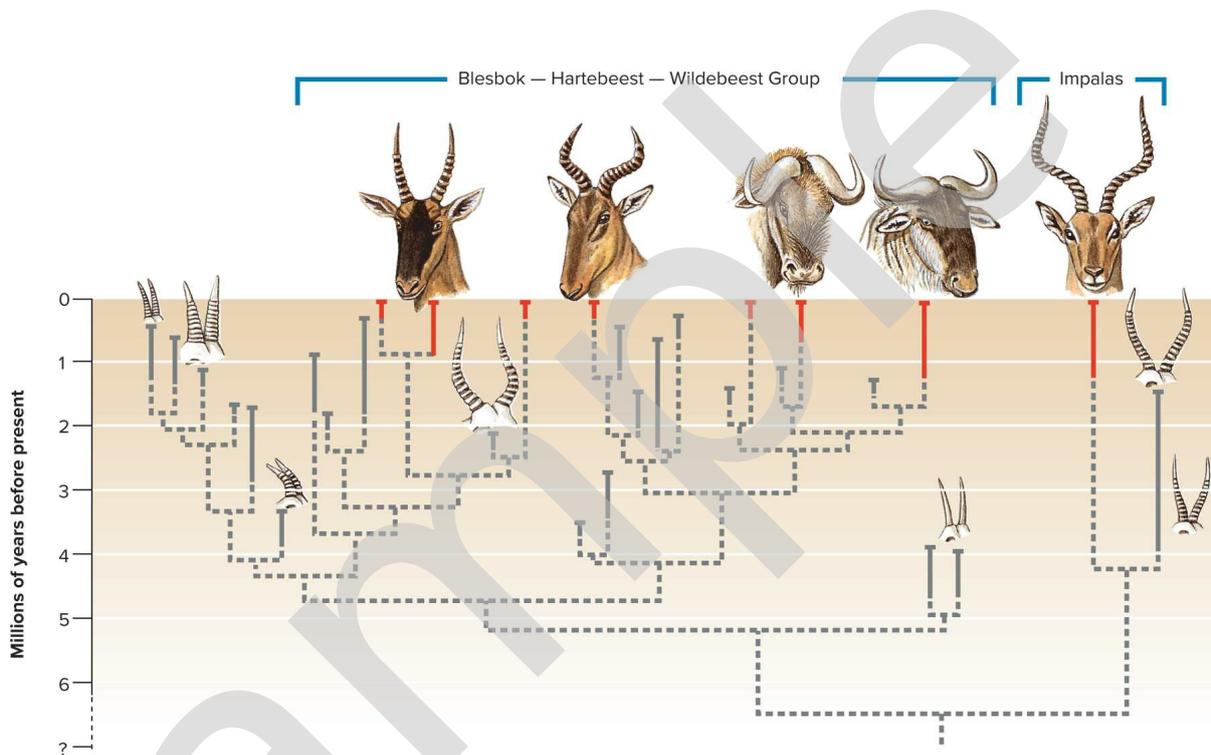
Stratigraphy of fossils for two major groups of African antelopes is in figure 1.14. These antelope species have different characteristic sizes

and shapes of their horns, which form much of the fossil record of this group. Solid vertical lines in figure 1.14 show the temporal distributions of species as determined by the presence of their characteristic horns in rock strata of various ages. Red lines denote the fossil records of living species, and gray lines denote the fossil records of extinct species. The dotted gray lines show the inferred relationships

15

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among living and fossil species based upon their sharing of homologous structural features.



**figure 1.14**

Stratigraphic record and inferred evolutionary relationships among alcelaphine (blesboks, hartebeests, wildebeests) and aepycerotine (impalas) antelopes in Africa. Species in this group are identified by characteristic sizes and shapes of horns found in rock strata of various ages. Solid vertical lines show the temporal distributions of species in rock strata whose ages are shown on the scale at the left side of the figure. Red lines show the temporal distributions of living species, and gray lines show the temporal distributions of extinct species in rock strata. Dotted gray lines show the inferred relationships among species based on their sharing of homologous structural features. The relative constancy of horn structure within species through geological time is consistent with the theory of punctuated equilibrium (see p. 27). This fossil record shows that rates of speciation and extinction are higher for alcelaphine antelopes than for impalas.

## Geological Time

Long before the earth's age was known, geologists divided its history into a table of succeeding events based on ordered layers of sedimentary rock. The "law of stratigraphy" produced a relative dating, with the oldest layers at the bottom and the most recent at the top of a sequence. Time was divided into eons, eras, periods, and epochs as shown on the endpapers inside the back cover of this book. Time during the last eon (Phanerozoic) is expressed in eras (for example,

Cenozoic), periods (for example, Cambrian), epochs (for example, Paleocene), and sometimes smaller divisions of an epoch.

In the late 1940s, radiometric dating methods were developed for determining the absolute ages (in years) of rock formations. Several independent methods are now used, all based on radioactive decay of naturally occurring elements into other elements. These “radioactive clocks” are independent of pressure and temperature changes and therefore not affected by often violent earth-building activities.

16

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One method, potassium-argon dating, uses the decay of potassium-40 ( $^{40}\text{K}$ ) to argon-40 ( $^{40}\text{Ar}$ ) (12%) and calcium-40 ( $^{40}\text{Ca}$ ) (88%). Argon is a noble gas that evaporates from liquid media. It accumulates in the crystal structure of rock only after the rock has solidified and the nuclear decay of potassium-40 produces a trapped atom of argon. The half-life of potassium-40 is 1.3 billion years, meaning that half of the original atoms will decay in 1.3 billion years, and half of the remaining atoms will be gone at the end of the next 1.3 billion years. This decay continues until all radioactive potassium-40 atoms are gone. To measure the age of a rock, one calculates the ratio of remaining potassium-40 atoms to the amount of potassium-40 originally there (the remaining potassium-40 atoms plus the argon-40 and calcium-40 into which they have decayed). A standard equation converts these data to the time elapsed since the formation of the rock as a function of the half life of potassium-40. Several other isotopes can be used in a similar manner to date the ages of rock formations, some for dating the age of the earth itself.

17

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One of the most useful radioactive clocks depends on decay of uranium into lead. With this method, rocks over 2 billion years old can be dated with a probable error of less than 1%.

The fossil record of macroscopic organisms begins near the start of the Cambrian period of the Paleozoic era, approximately 540 million years before present (BP). Geological time before the Cambrian period is called the Precambrian era or the Proterozoic eon. Although the Precambrian era occupies 85% of all geological time, it receives much less attention than do later eras, partly because oil, which provides a commercial incentive for much geological work, seldom exists in Precambrian formations. The Precambrian era contains well-preserved

fossils of bacteria and algae, and casts of jellyfishes, sponge spicules, soft corals, segmented flatworms, and worm trails. Most, but not all, are microscopic fossils.

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The more well-known carbon-14 ( $^{14}\text{C}$ ) dating method is of little help in estimating ages of geological formations because its short half-life restricts the use of  $^{14}\text{C}$  to quite recent events (less than about 40,000 years). It is especially useful, however, for archaeological studies. This method is based on the production of radioactive  $^{14}\text{C}$  (half-life of approximately 5570 years) in the upper atmosphere by bombardment of nitrogen-14 ( $^{14}\text{N}$ ) with cosmic radiation. Radioactive  $^{14}\text{C}$  enters the tissues of living animals and plants, and an equilibrium is established between atmospheric  $^{14}\text{C}$  and  $^{14}\text{N}$  in living organisms. At death,  $^{14}\text{C}$  exchange with the atmosphere stops. In 5570 years, only half of the original  $^{14}\text{C}$  remains in a preserved fossil. One estimates a fossil's age by comparing the  $^{14}\text{C}$  content of the fossil with that of living organisms.

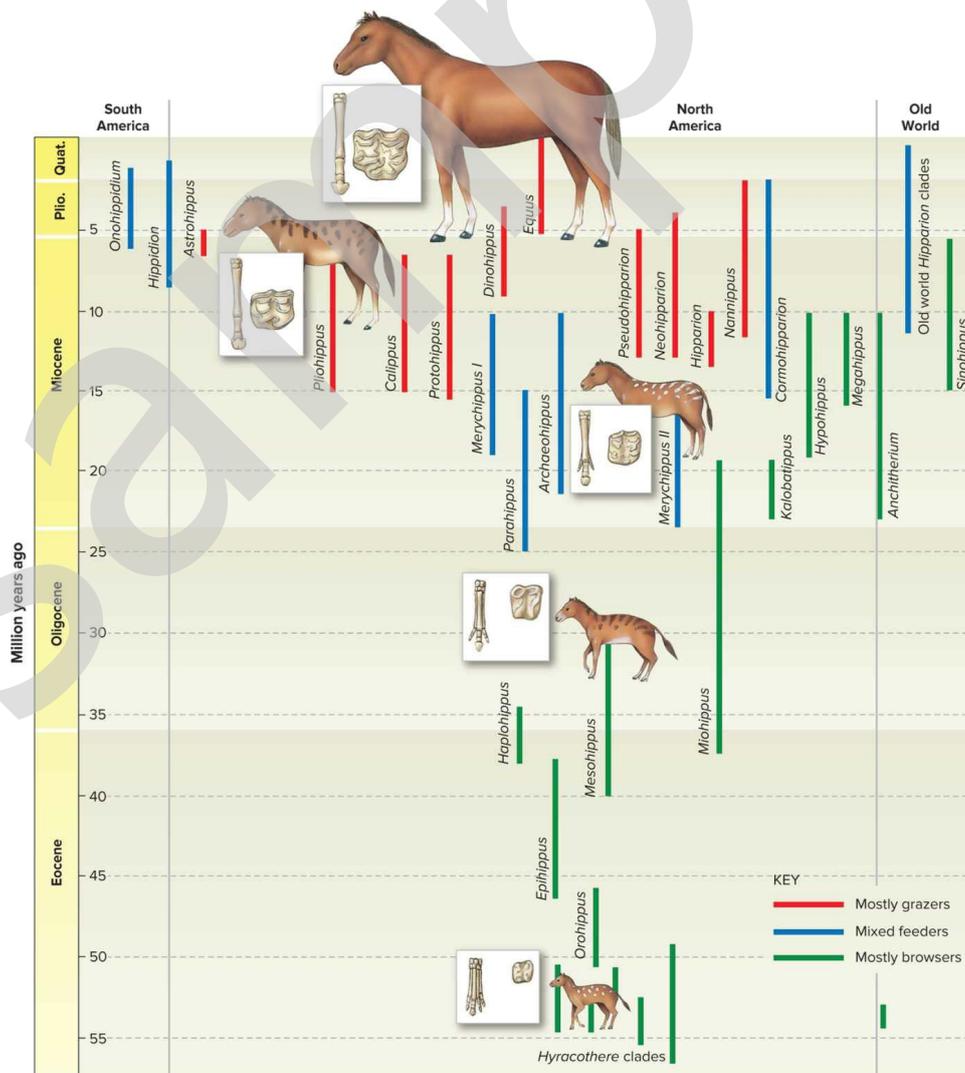
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## Evolutionary Trends

The fossil record reveals evolutionary change across the broadest scale of time. Throughout the geological history recorded by the fossil record, millions of species have arisen and almost as many have gone extinct. Animal species typically survive approximately 1 million to 10 million years, although their durations are highly variable. We can summarize patterns of species or taxon replacement through time as **trends**. Trends are directional changes in characteristic features or patterns of diversity in a group of organisms. Fossil trends clearly demonstrate Darwin's principle of perpetual change.

A well-studied fossil trend is the evolution of horses from the Eocene epoch to the present. Looking back to the Eocene epoch, we see many different genera and species of horses that replaced each other through time (figure 1.15). George Gaylord Simpson (see p. 90) showed that this trend is compatible with Darwinian evolutionary theory. Three characteristics that show the clearest trends in horse evolution are body size, tooth structure, and foot structure. Compared to modern horses, those of extinct genera were small, their teeth had a relatively small grinding surface, and their feet had a relatively large number of toes (four). Throughout the subsequent Oligocene, Miocene, Pliocene, and Pleistocene epochs, new genera arose and old ones went

extinct. In each case, there was a net increase in body size, expansion of the grinding surface of teeth, and reduction in number of toes. As the number of toes declined, the central digit became increasingly more prominent in the foot, and eventually only this central digit remained.

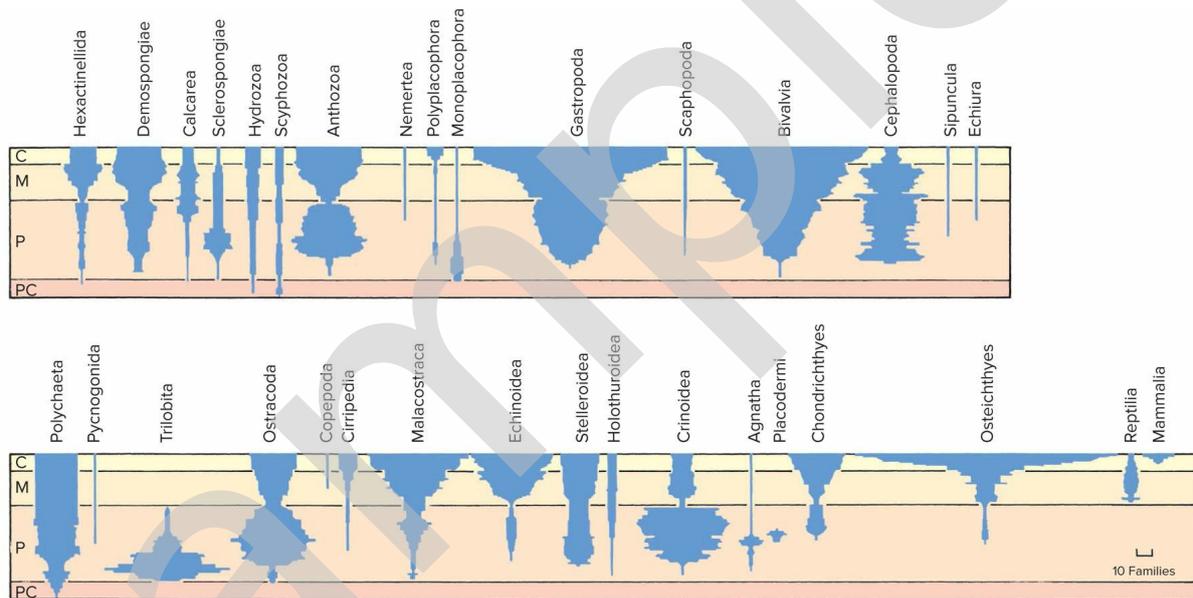


**figure 1.15**

Stratigraphy of genera of horses from the Eocene epoch to the present. Evolutionary trends toward increased size, elaboration of molars, and loss of toes are shown along with bars denoting temporal durations and continental locations of genera.

The fossil record shows a net change not only in the characteristics of horses but also in the numbers of different horse genera (and numbers of species) that exist through time. Many horse genera of past epochs have been lost to extinction, leaving only a single survivor.

Evolutionary trends in diversity are observed in fossils of many different groups of animals (figure 1.16).



**figure 1.16**

Diversity profiles of taxonomic families from different animal groups in the fossil record. A scale marks the Precambrian (PC), Paleozoic (P), Mesozoic (M), and Cenozoic (C) eras. The number of families is indicated by the width of each profile.

Our use of “evolutionary trend” does not imply that more recent forms are superior to older ones or that the changes represent progress in adaptation or organismal complexity. Although Darwin predicted that such trends would show progressive adaptation, many contemporary paleontologists consider progressive adaptation rare among evolutionary trends. Observed trends in the evolution of horses do not imply that contemporary horses are superior in any general sense to their Eocene predecessors.

Different rates of species formation versus extinction through time produce trends in fossil species diversity. Why do some lineages generate large numbers of new species whereas others generate relatively few? Why do different animal groups undergo higher or lower rates of extinction (of species, genera, or families) throughout evolutionary time? To answer these questions, we must turn to Darwin’s other four theories of evolution. Regardless of how we answer these questions, however, observed trends in animal diversity

clearly illustrate Darwin's principle of perpetual change. Because Darwin's remaining four theories rely on perpetual change, evidence supporting these theories strengthens Darwin's theory of perpetual change.

## Common Descent

Darwin proposed that all plants and animals have descended from some one form into which life was first "breathed." Life's history forms a branching tree, called a phylogeny, that gives all of life a unified evolutionary history. Pre-Darwinian evolutionists, including Lamarck, advocated multiple independent origins of life, each of which gave rise to lineages that changed through time without the extensive branching required by Darwin's theory. Like all good scientific theories, common descent makes several important predictions that can be tested and potentially used to reject it. According to this theory, one should be able to trace the genealogies of all modern species backward until they converge on ancestral lineages shared with other species, both living and extinct. We continue this process, moving farther backward through evolutionary time, to reach a primordial ancestor of all life on earth. All forms of life, including many extinct forms that represent dead branches, connect to this tree somewhere. Although reconstructing a history of life

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in this manner may seem almost impossible, it has in fact been extraordinarily successful. How has this difficult task been accomplished?

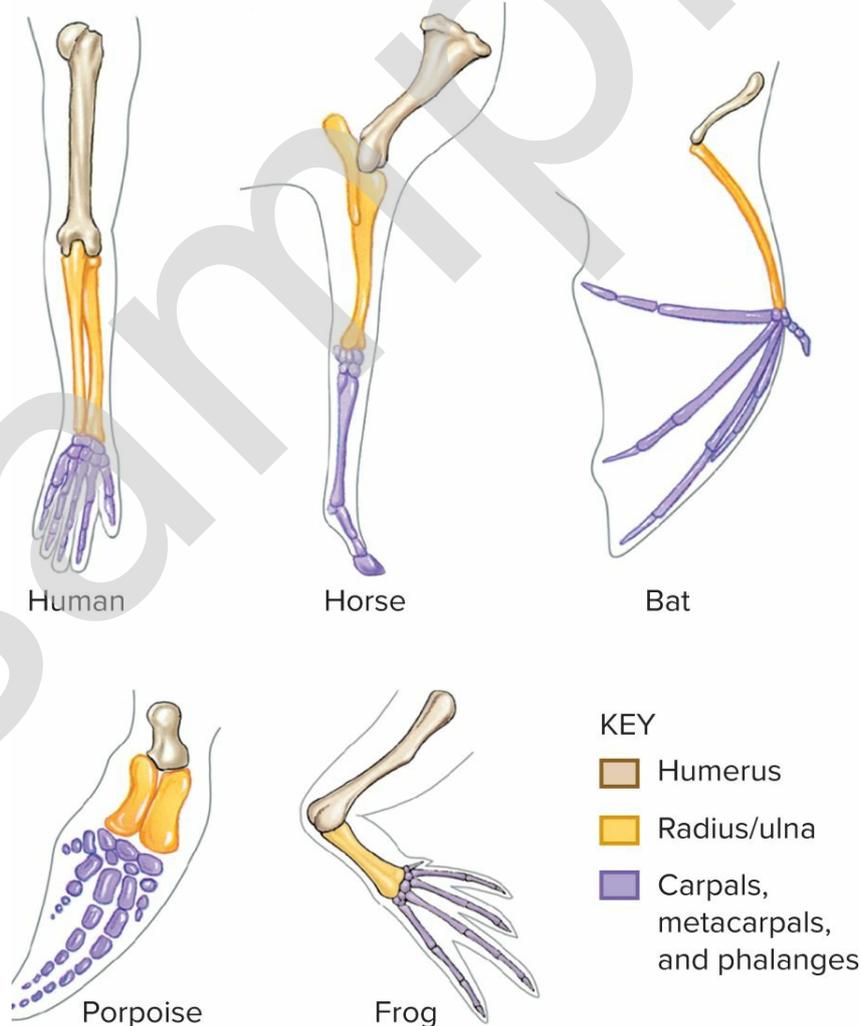
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## Homology and Reconstruction of Phylogeny

Darwin recognized a major source of evidence for common descent in the concept of **homology**. Darwin's contemporary, Richard Owen (1804–1892), used this term to denote "the same organ in different organisms under every variety of form and function." A classic example of homology is the limb skeleton of vertebrates. Bones of vertebrate limbs maintain characteristic structures and patterns of connection despite diverse modifications for different functions (figure 1.17).

According to Darwin's theory of common descent, structures that we call homologies represent characteristics inherited with some modification from a corresponding feature in a common ancestor.

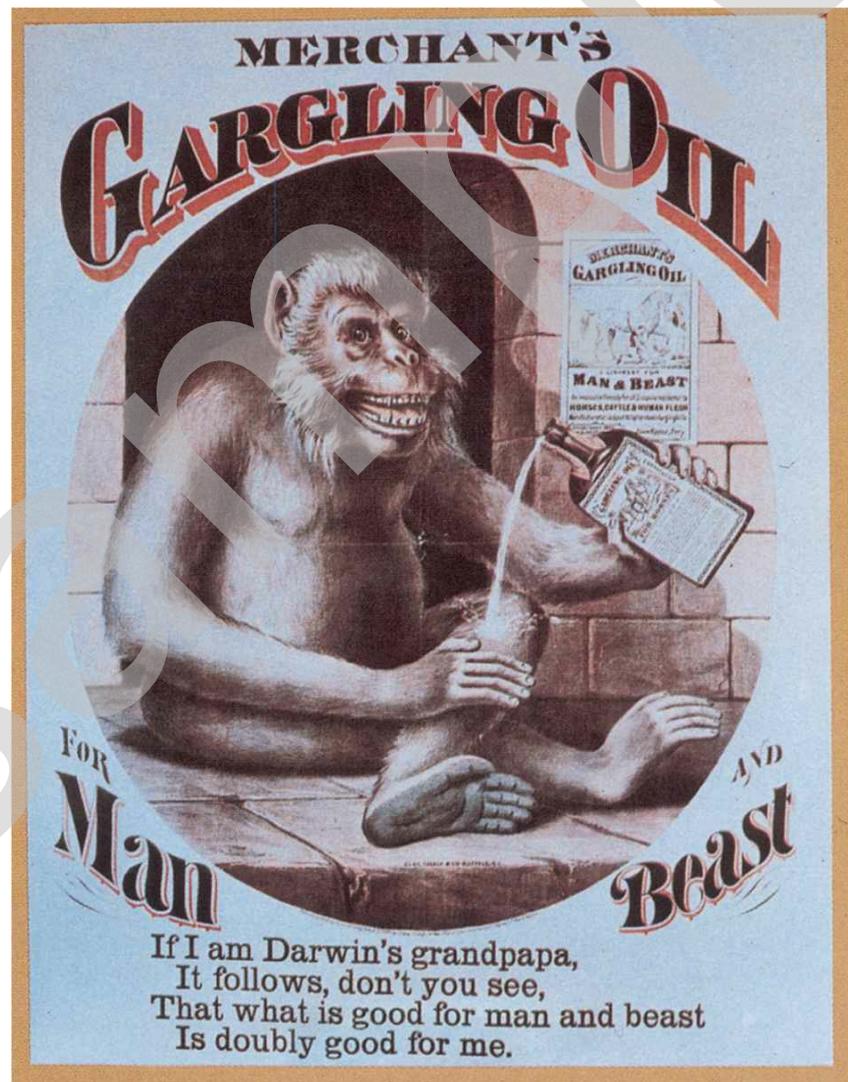


**figure 1.17**

Forelimbs of five vertebrates show skeletal homologies: brown, humerus; orange, radius and ulna; purple, “hand” (carpals, metacarpals, and phalanges). Homologies of bones and patterns of connection are evident despite evolutionary modification for various uses.

Darwin devoted an entire book, *The Descent of Man and Selection in Relation to Sex*, largely to the idea that humans share common descent with apes and other animals. This idea was repugnant to many Victorians, who responded with outrage (figure 1.18). Darwin built his case mostly on anatomical comparisons that revealed homology between humans and apes. To Darwin, the close resemblances

between apes and humans could be explained only by common descent.



**figure 1.18**

This 1873 advertisement for Merchant's Gargling Oil ridicules Darwin's theory of the common descent of humans and apes, which was widely doubted by the general public during Darwin's lifetime.

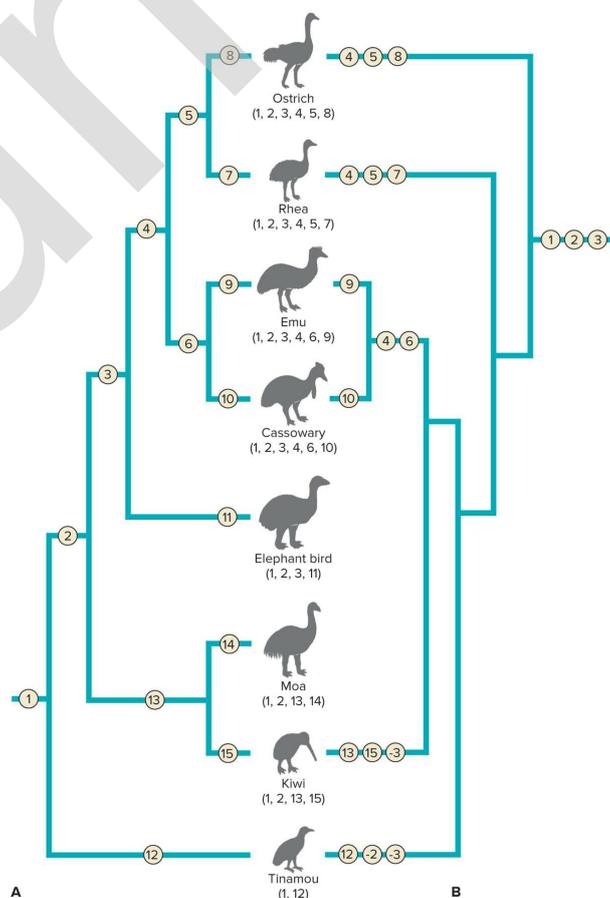
Source: Library of Congress Prints and Photographs Division, [LC-USZ62- 48534]

Throughout the history of all forms of life, evolutionary processes generate new characteristics that are transmitted across generations. Every time a new feature becomes established in a lineage destined to be ancestral to others, a new homology

20

originates. The sharing of these homologies among species provides

evidence for common descent and allows us to reconstruct a branching evolutionary history of life. We illustrate such evidence using a phylogenetic tree of ground-dwelling flightless birds (figure 1.19). A new skeletal homology (figure 1.19) arises on each of the lineages shown (descriptions of these homologies are not included because they are highly technical). The different groups of species located at the tips of the branches contain different combinations of these homologies, thereby revealing common ancestry. For example, ostriches show homologies 1 through 5 and 8, whereas kiwis show homologies 1, 2, 13, and 15.



**figure 1.19**

**A**, The phylogenetic pattern specified by 15 homologous structures in the skeletons of a group of flightless birds. Homologous features are numbered 1 through 15 and are marked both on the branches of the tree on which they arose and on the birds that have them. If you were to erase the tree structure, you would be able to reconstruct it without error from the distributions of homologous features shown for the birds at the terminal branches. **B**, A phylogenetic analysis of molecular data suggests a different pattern of relationships among the living flightless birds (all except moas and elephant

birds). If the molecular analysis is correct, then one must reinterpret evolution of skeletal characters 2, 3, 4, and 5. In the interpretation shown, character 2 is lost by tinamous (-2), and character 3 is lost by both kiwis and tinamous (-3). Character 4 arises independently in ostriches, rheas, and a common ancestor of cassowaries and emus. Character 5 originates separately in ostriches and rheas. Multiple origins and losses complicate phylogenetic analysis, as explained in Chapter 4.

The tree structure inferred from analysis of skeletal structures of flightless birds can be tested by data gathered independently from DNA-sequence information (see Chapter 4). The phylogeny of flightless birds inferred from DNA-sequence data does not agree completely with the one inferred from skeletal structures (figure 1.19); if we choose the hypothesis favored by DNA-sequence data, then we must hypothesize that some of the skeletal structures either arose multiple times or were lost on some lineages as shown in figure 1.19B. Conflict between the phylogenetic hypotheses derived from skeletal structures and from DNA sequences guides systematists to examine their phylogenetic characters and analyses for sources of error in inferring the detailed phylogenetic relationships among these species. All of the phylogenetic data support the hypothesis that these flightless birds are more closely related to each other than they are to any other living species.

Branches of an evolutionary tree combine species into a **nested hierarchy** of groups within groups (see Chapter 4). Smaller groups (species grouped near terminal branches) are contained within larger ones (species grouped by basal branches, including the trunk of the tree). If we erase the tree structure but retain the patterns of homology observed in the terminal groups of species, we can reconstruct the branching structure of the entire tree. Evolutionists test the theory of common descent by observing patterns of homology present in all groups of organisms. The pattern formed by all homologies taken together should specify a single branching tree that represents the evolutionary genealogy of all living organisms.

The nested hierarchical structure of homology is so pervasive in animals that it forms the basis for our systematic groupings (genera grouped into families, families grouped into orders, orders into classes, classes into phyla, and phyla into the animal kingdom). Plants and fungi show similar hierarchical patterns of homology and corresponding systematic groupings. Hierarchical classification even

preceded Darwin's theory because this pattern was so evident, but it was not explained scientifically before Darwin. Once common descent was understood, biologists began investigating structural, molecular, and/or chromosomal homologies of animal groups to infer evolutionary relationships. Taken together, the nested hierarchical patterns uncovered by these studies permit us to reconstruct the evolutionary trees of many groups and to continue testing our phylogenetic hypotheses with new data. Methods presented in Chapter 4 show how we use Darwin's theory of common descent to reconstruct the evolutionary history of life and to construct a taxonomic system that summarizes evolutionary relationships among species.

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Characters of different organisms that perform similar functions are not necessarily homologous. The wings of bats and birds, although homologous as vertebrate forelimbs, are not homologous as wings. The most recent common ancestor of bats and birds had forelimbs, but the forelimbs were not in the form of wings. The wings of bats and birds evolved independently and have only superficial similarity in their flight structures.

Bat wings are formed by skin stretched over elongated digits, whereas bird wings are formed by feathers attached along the forelimb. Such functionally similar but nonhomologous structures are often called *analogues*.

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Note that the earlier evolutionary hypothesis that life arose many times, forming unbranched lineages, predicts linear sequences of evolutionary change with no nested hierarchy of homologies among species. Because we do observe nested hierarchies of homologies, that hypothesis is rejected. Note also that a supernatural creationist argument can make no testable predictions about any pattern of homology and therefore fails the criteria of a scientific theory of animal diversity.

21

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## Ontogeny, Phylogeny, and Recapitulation

Zoologists find in animal development important clues to an animal's evolutionary history. **Ontogeny** is the development of an organism through its entire life, from its origin as a fertilized egg or bud

throughout adulthood to death. Early developmental and embryological features contribute greatly to our knowledge of homology and common descent. Comparative studies of ontogeny show how evolutionary changes in developmental timing generate new body forms and structures.

Comparisons of gene expression among animals show that in forms as dissimilar as insects and humans, homologous genes may guide developmental differentiation of anterior versus posterior body segments. For example, mutations of such genes, termed **homeotic genes**, in fruit flies can cause awkward developmental changes such as legs in the place of antennae or an extra pair of wings. Such genes provide an evolutionary “tool kit” that can be used to construct new body parts by relocating patterns of gene expression to different parts of a developing embryo. Perhaps the most famous homeotic genes are those containing a sequence of 180 base pairs, called the **homeobox**, which encodes a protein sequence that binds to other genes, thereby altering their expression. For example, evolution of the paired limbs of terrestrial vertebrates occurred by activating a caudal “tool kit” of homeobox genes at

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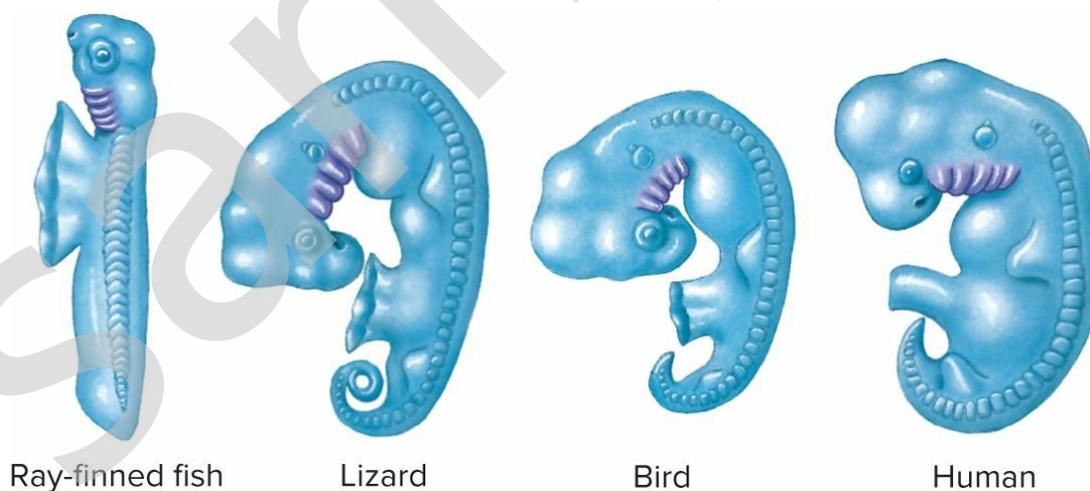
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the paired pectoral and pelvic regions of the body where limbs develop. Genetic and developmental tools evolved for constructing a tail were thus available for the new role of constructing paired limbs.

The German zoologist Ernst Haeckel, a contemporary of Darwin, proposed the influential hypothesis that each successive stage in an organism’s development represented an adult form present in its evolutionary history. For example, a human embryo with gill-like depressions in its neck was considered to signify a fishlike ancestor. On this basis, Haeckel gave his generalization: *ontogeny (individual development) recapitulates (repeats) phylogeny (evolutionary descent)*. This notion later was simply called **recapitulation**, or the **biogenetic law**. Haeckel based his biogenetic law on the premise that evolutionary change often occurs by successively adding stages onto the end of an unaltered ancestral ontogeny, condensing the ancestral ontogeny into earlier developmental stages. This notion was based on Lamarck’s concept of inheritance of acquired characteristics (see p. 7).

A nineteenth-century embryologist, K. E. von Baer, gave an alternative explanation of the relationship between ontogeny and

phylogeny. He argued that early developmental features were simply more widely shared among different animal groups than were later ones. For example, figure 1.20 shows early embryological similarities between organisms whose adult forms are very different. Adults of animals with relatively short and simple ontogenies often resemble the pre-adult stages of other animals whose ontogeny is more elaborate, but the embryos of descendants do not necessarily resemble the adults of their ancestors. However, even early development undergoes evolutionary divergence among groups, and it is not as stable as von Baer thought.



**figure 1.20**

Comparison of gill arches (purple) of different embryos. All are shown separated from the yolk sac. Note the remarkable similarity of these four embryos at this early stage in development.

We now know many parallels between ontogeny and phylogeny, but features of an ancestral ontogeny can be shifted to either earlier or later stages in descendant ontogenies. Evolutionary change in the timing of development is called **heterochrony**, a term initially used by Haeckel to denote exceptions to recapitulation. Because the lengthening or shortening of ontogeny can change different parts of an organism independently, we often see a mosaic of different kinds of developmental evolutionary change in a single lineage. Therefore, cases in which an entire ontogeny recapitulates phylogeny are rare.

Despite many changes in scientific thinking about the relationships between ontogeny and phylogeny, one important fact remains clear. Darwin's theory of common descent is strengthened enormously by

the many homologies found among developmental stages of organisms belonging to different species.

## Multiplication of Species

Multiplication of species through time is a logical corollary to Darwin's theory of common descent. A branch point on a phylogenetic tree means that an ancestral species has split into two different ones. Darwin's theory postulates that variation present within a species, especially variation between geographically separated populations, provides material from which new species are produced. Because evolution is a branching process, the total number of species produced by evolution increases through time, although most of these species eventually go extinct without leaving descendant species. A major challenge for evolutionists is to discover the processes by which an ancestral species "branches" to form two or more descendant species.

Before we explore multiplication of species, we must decide what we mean by "species." No consensus exists regarding the definition of species (see Chapter 4). Most biologists would agree, however, on three important criteria for recognizing a species:

1. Individuals of the same species descend from a common ancestral population and form an unbranched lineage of ancestral-descendant populations.
2. Individuals of the same species exhibit reproductive compatibility (ability to interbreed) among individuals and reproductive incompatibility between species (for sexually reproducing organisms).
3. Individuals within the same species maintain genotypic and phenotypic cohesion (lack of abrupt differences among populations in allelic frequencies [see p. 29] and in organismal appearance).

The criterion of reproductive compatibility has received the greatest attention in studies of species formation, also called **speciation**.

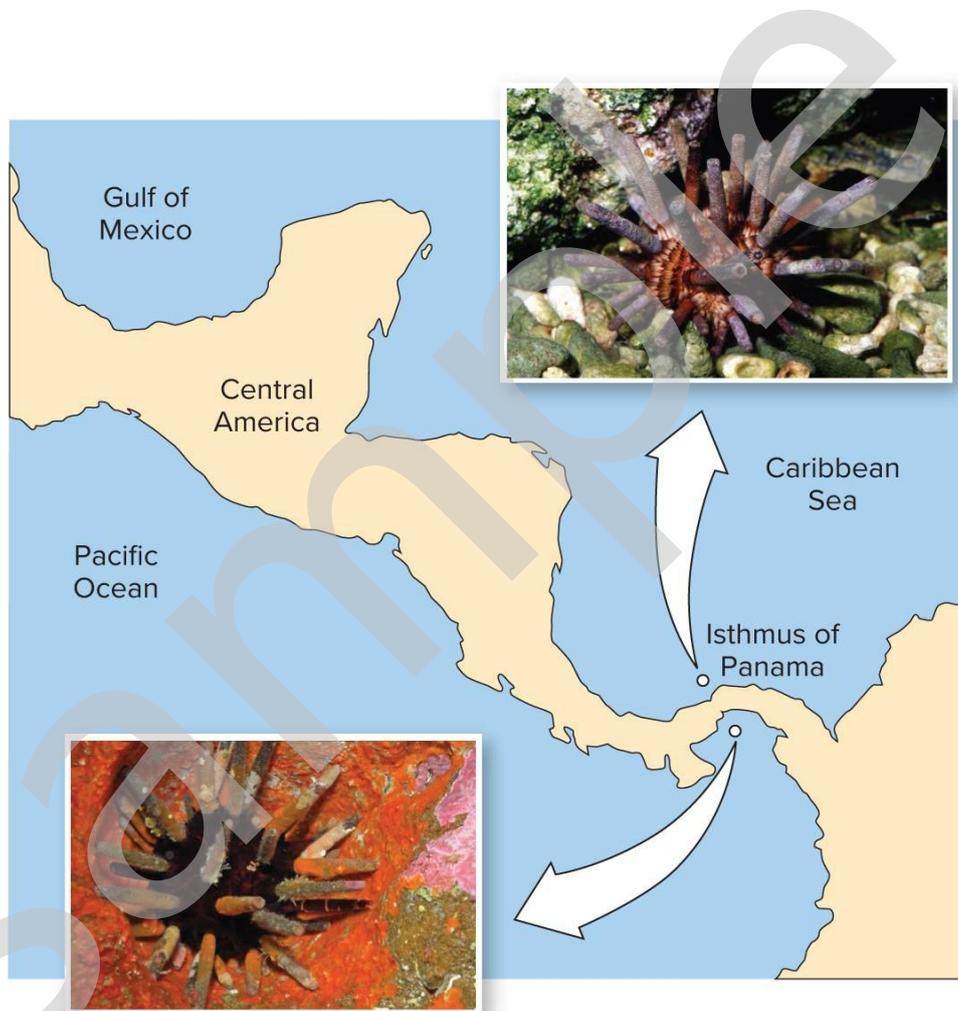
Biological factors that prevent different species from interbreeding are called **reproductive barriers**. A primary problem of speciation is to discover how two initially compatible populations evolve reproductive barriers that cause them to become distinct, separately evolving lineages. How do populations diverge from each other in their reproductive properties while maintaining complete reproductive

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Geographical barriers between populations are not equivalent to reproductive barriers. Geographical barriers refer to spatial separation of two populations. They prevent gene exchange and are usually a precondition for speciation. Reproductive barriers are various morphological, physiological, ecological, and behavioral factors that prevent interbreeding between different species. Geographical barriers do not guarantee that reproductive barriers will evolve. Reproductive barriers are most likely to evolve under conditions that include a generation of small population size, a favorable combination of selective factors, and long periods of geographical isolation. One or both of a pair of geographically isolated populations may become extinct prior to evolution of reproductive barriers between them. Over the vast span of geological time, however, conditions sufficient for speciation have occurred many millions of times.

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Reproductive barriers between populations usually evolve gradually. Evolution of reproductive barriers requires that diverging populations be kept physically separate (“isolated”) for long periods of time. If the diverging populations were reunited before reproductive barriers were completely formed, interbreeding would occur between the populations and they would merge. Speciation by gradual divergence in animals usually requires perhaps 10,000–100,000 years or more. Geographical isolation followed by gradual divergence is the most effective way for reproductive barriers to evolve, and many evolutionists consider geographical separation a prerequisite for branching speciation. Speciation that results from evolution of reproductive barriers between geographically separated populations is called **allopatric speciation**, or geographical speciation. For example, geological formation of the Isthmus of Panama fragmented an ancestral population of *Eucidaris* sea urchins into separate Caribbean and Pacific Ocean isolates, leading to formation of the pair of species shown in figure 1.21.



**figure 1.21**

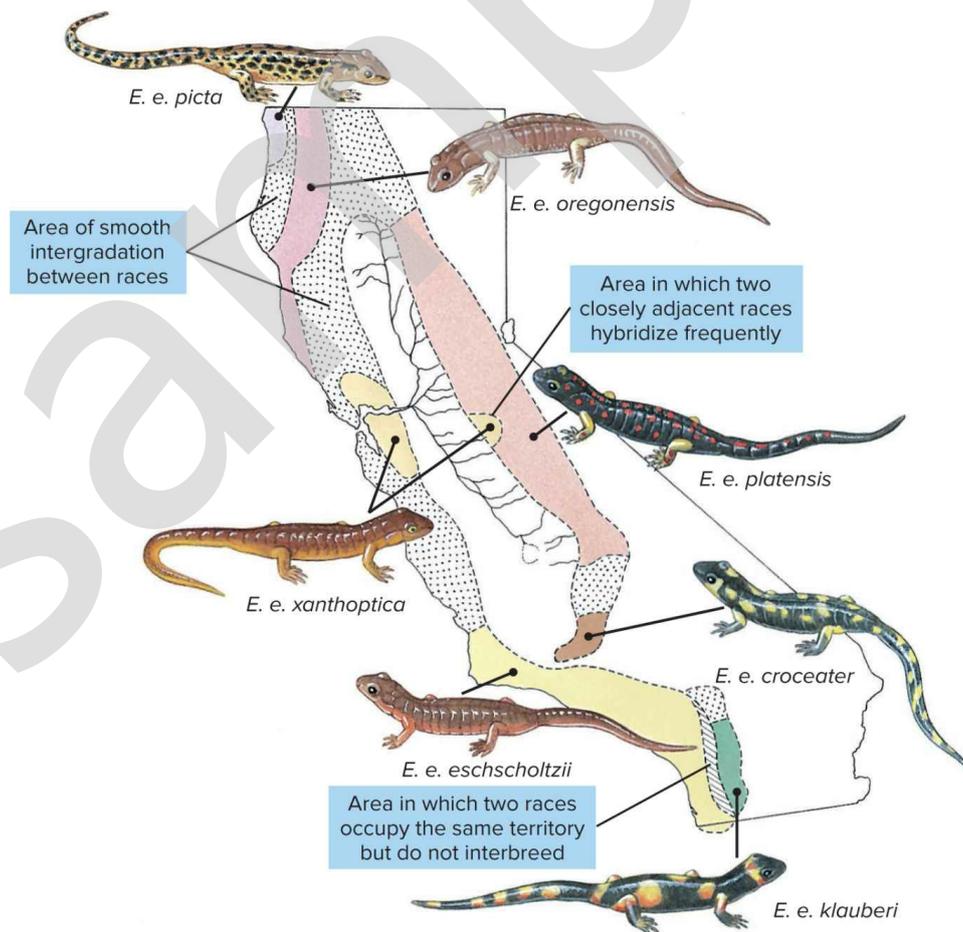
Geographic formation of species in the sea urchin (*Eucidaris*). Formation of the Isthmus of Panama separated an ancestral population, leading to evolution of separate Caribbean (*E. tribuloides*) and Pacific (*E. thouarsi*) species.

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Evidence for allopatric (“in another land”) speciation occurs in many forms, but perhaps most convincing is an occurrence of geographically separated but adjoining, closely related populations that illustrate the gradual origin of reproductive barriers. Populations of a salamander, *Ensatina eschscholtzii*, in California are a particularly clear example (figure 1.22). These populations show evolutionary divergence in color pattern and collectively form a geographical ring around California’s central valley. Genetic exchange between differentiated, geographically adjoining populations is evident through the formation of hybrids and occasionally regions of extensive genetic exchange

(called zones of introgression). Two populations at the southern tip of the geographical range (called *E. e. eschscholtzii* and *E. e. klauberi*) make contact but do not interbreed. A gradual accumulation of reproductive differences among contiguous populations around the ring is visible, with the two southernmost populations separated by strong reproductive barriers.



**figure 1.22**

Speciation in progress: geographic variation of color patterns in the salamander genus *Ensatina*. Populations of *Ensatina eschscholtzii* form a geographic ring around the Central Valley of California. Adjacent, differentiated populations throughout the ring can exchange genes except at the bottom of the ring where the subspecies *E. e. eschscholtzii* and *E. e. klauberi* overlap without interbreeding. These two subspecies would be recognized as distinct species if intermediate populations linking them across the ring were extinct. This example demonstrates that reproductive barriers between populations can evolve gradually.

Additional evidence for allopatric speciation comes from

observations of animal diversification on islands. Oceanic islands formed by volcanoes are initially devoid of life. Plants and animals from a continent or from other islands occasionally colonize new islands in separate invasions. Invaders often encounter situations ideal for evolutionary diversification, because environmental resources that were exploited heavily by other species on the mainland are free for colonization on a sparsely populated island. Because colonization of oceanic islands is rare, populations established on islands are effectively isolated geographically from their parental populations and can undergo divergent evolution, leading to reproductive barriers and speciation. Archipelagoes, such as the Galápagos Islands, greatly increase opportunities for speciation in this manner.

Evolutionists have often wondered whether the isolation of populational gene pools needed for reproductive barriers to evolve might sometimes occur without geographical isolation. Populations that are reproductively active at different seasons or on different substrates could, in theory, achieve gene-pool isolation without geographic isolation. The term *sympatric speciation* is used to denote species formation not involving geographical isolation. Intermediate between allopatric and sympatric speciation is a condition in which the diverging populations are geographically separate but make contact along a borderline; speciation arising in this manner is called *parapatric speciation*. Many zoologists doubt that sympatric and parapatric speciation have been important in animal evolution.

Production of many ecologically diverse species from a common ancestral species is called **adaptive radiation**, especially when these species arise within a short interval of geological time (a few million years). Some of our best examples of adaptive radiation occur in lakes or on young islands, which provide new evolutionary opportunities for aquatic and terrestrial organisms, respectively. Oceanic islands formed by volcanoes are initially devoid of life. They are gradually colonized

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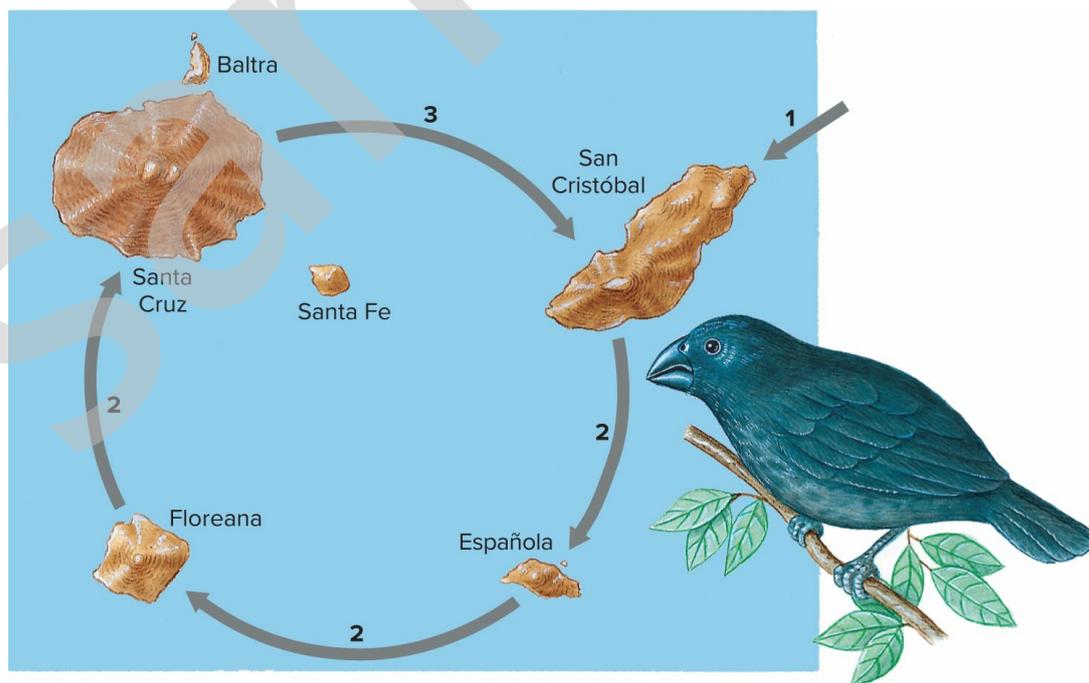
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by plants and animals from a continent or from other islands in separate founder events. These colonizations involve floating of seeds across an expanse of ocean followed by germination on the island. Birds or insects might be carried by wind from a continent to the island, or animals might be carried by flotation in sea-swept debris. The probability that a particular species will make a successful colonization is low, but given large numbers of continental species and

millions of years of evolutionary time, such colonizations occur and eventually establish an oceanic island biota. Archipelagoes, such as the Galápagos Islands, greatly increase opportunities for both founder events and ecological diversification. The entire archipelago is isolated from the continent, and each island is geographically isolated from the others by sea; moreover, each

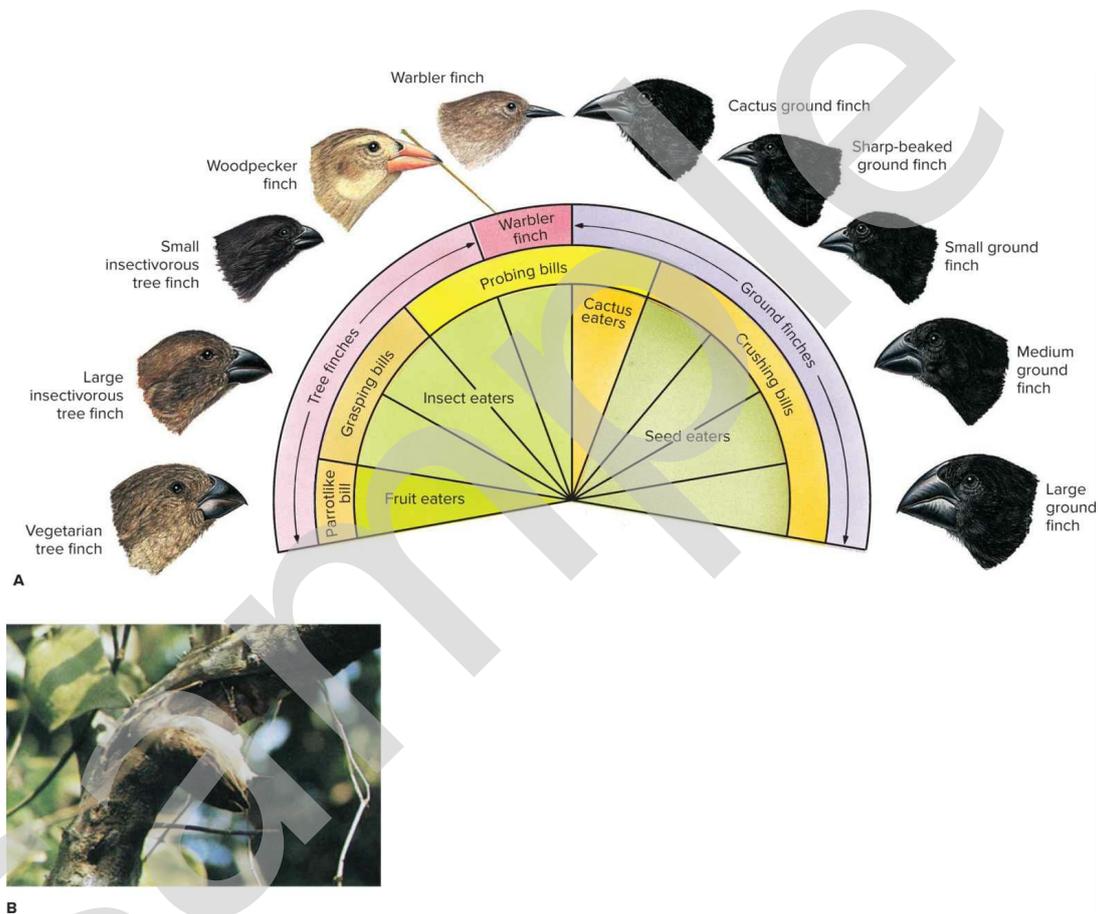
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island is different from every other one in its physical, climatic, and biotic features. Galápagos finches clearly illustrate adaptive radiation on an oceanic archipelago (figures 1.23 and 1.24).



**figure 1.23**

Tentative model for evolution of the 13 forms of Darwin's finches on the Galápagos Islands. This model postulates three steps: (1) Immigrant finches from South America reach the Galápagos and colonize an island; (2) after a population becomes established, finches disperse to other islands where they adapt to new conditions and change genetically; and (3) after a period of isolation, secondary contact is established between different populations. Different populations would be recognized as separate species if they cannot interbreed successfully, although reproductive isolation apparently is not strong among the different forms of Darwin's finches.



**figure 1.24**

**A**, Adaptive radiation in 10 contrasting forms of Darwin's finches from Santa Cruz, one of the Galápagos Islands. Differences in beaks and feeding habits are shown. All apparently descended from a single common ancestral finch from South America. **B**, Woodpecker finch, one of 13 forms of Galápagos Islands finches, using a slender twig as a tool for feeding. This finch worked for about 15 minutes before spearing and removing a wood roach from a break in the tree.

©Cleveland P. Hickman, Jr.

Galápagos finches (the name "Darwin's finches" was popularized in the 1940s by the British ornithologist David Lack) are close relatives, but each species differs from others in the size and shape of its beak and in its feeding habits. Darwin's finches descended from a single ancestral population that arrived from South America and subsequently colonized different islands of the Galápagos archipelago. These finches underwent adaptive radiation, occupying habitats that in South America were denied to them by other species better able to exploit those habitats. Galápagos finches thus acquired characteristics of mainland birds as diverse and unfinchlike as warblers and woodpeckers (figure 1.24B). The founding of new island populations

by a small number of migrants may have accelerated evolutionary divergence among these island finches (see p. 34). A fourteenth finch population, found on isolated Cocos Island far north of the Galápagos archipelago, resembles the Galápagos finches and almost certainly descends from the same ancestral founder. Despite their great adaptive diversification, the different forms of Galápagos finches do not form clearly distinct species lineages. Molecular genetic data indicate genetic compatibility and gene exchange among the adaptively diverse forms.

## Gradualism

Darwin's theory of gradualism opposed arguments for a sudden origin of species. Small differences, resembling those that we observe among organisms within populations today, are the raw material from which different major forms of life evolved. This theory shares with Lyell's uniformitarianism a notion that we must not explain past changes by invoking unusual catastrophic events that are not observable today. If new species originated in single, catastrophic events, we should be able to see these events happening today, and we do not. What we observe instead are small, continuous changes in phenotypes occurring in natural populations. Such continuous changes can produce major differences among species only by accumulating over many thousands to millions of years. A simple statement

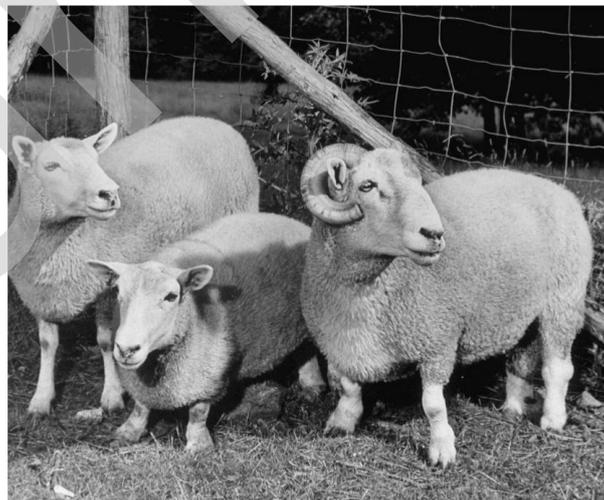
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of Darwin's theory of gradualism is that accumulation of quantitative changes leads to qualitative change.

Phenotypic gradualism was controversial when Darwin first proposed it, and it is still controversial. Not all phenotypic changes are small, incremental ones. For example, some mutations that appear during artificial breeding, traditionally called "sports," change a phenotype substantially in a single mutational step. Sports that produce dwarfing occur in many species, including humans, dogs, and sheep, and have been used by animal breeders to achieve desired results; for example, a sport that deforms limbs was used to produce ancon sheep, which cannot jump hedges and are therefore easily contained (figure 1.25). Many colleagues of Darwin who accepted his other theories considered phenotypic gradualism too extreme. If sports can be used in animal breeding, why must we exclude them from our

evolutionary theory? In favor of gradualism, some have replied that sports always have negative side effects that would prevent affected organisms from surviving in natural populations. Indeed, it is questionable whether the ancon sheep in figure 1.25, despite its attractiveness to farmers, would propagate successfully in the presence of its long-legged relatives without human intervention. Naturalists nonetheless report mutations of large effect that appear adaptive in natural populations; a mutation responsible for a large difference in beak size in the African finch species *Pyrenestes ostrinus* allows large-beaked birds to eat hard seeds, whereas small-beaked forms eat softer seeds.



**figure 1.25**

The ancon breed of sheep center arose from a “sport” mutation that caused dwarfing of their legs. Many of Darwin’s contemporaries criticized him for claiming that such large mutations are not important for evolution by natural selection.

©Herbert Gehr/The LIFE Picture Collection/Getty Images

When we view Darwinian gradualism on a geological timescale, we may expect to find in the fossil record a long series of intermediate forms bridging phenotypes of ancestral and descendant populations (figure 1.26). This predicted pattern is called **phyletic gradualism**. Darwin recognized that phyletic gradualism is not often revealed by the fossil record. Studies conducted since Darwin’s time likewise have failed to produce a continuous series of fossils as predicted by phyletic gradualism. Is the theory of gradualism therefore refuted by the fossil record? Darwin and others have claimed that it is not, because the