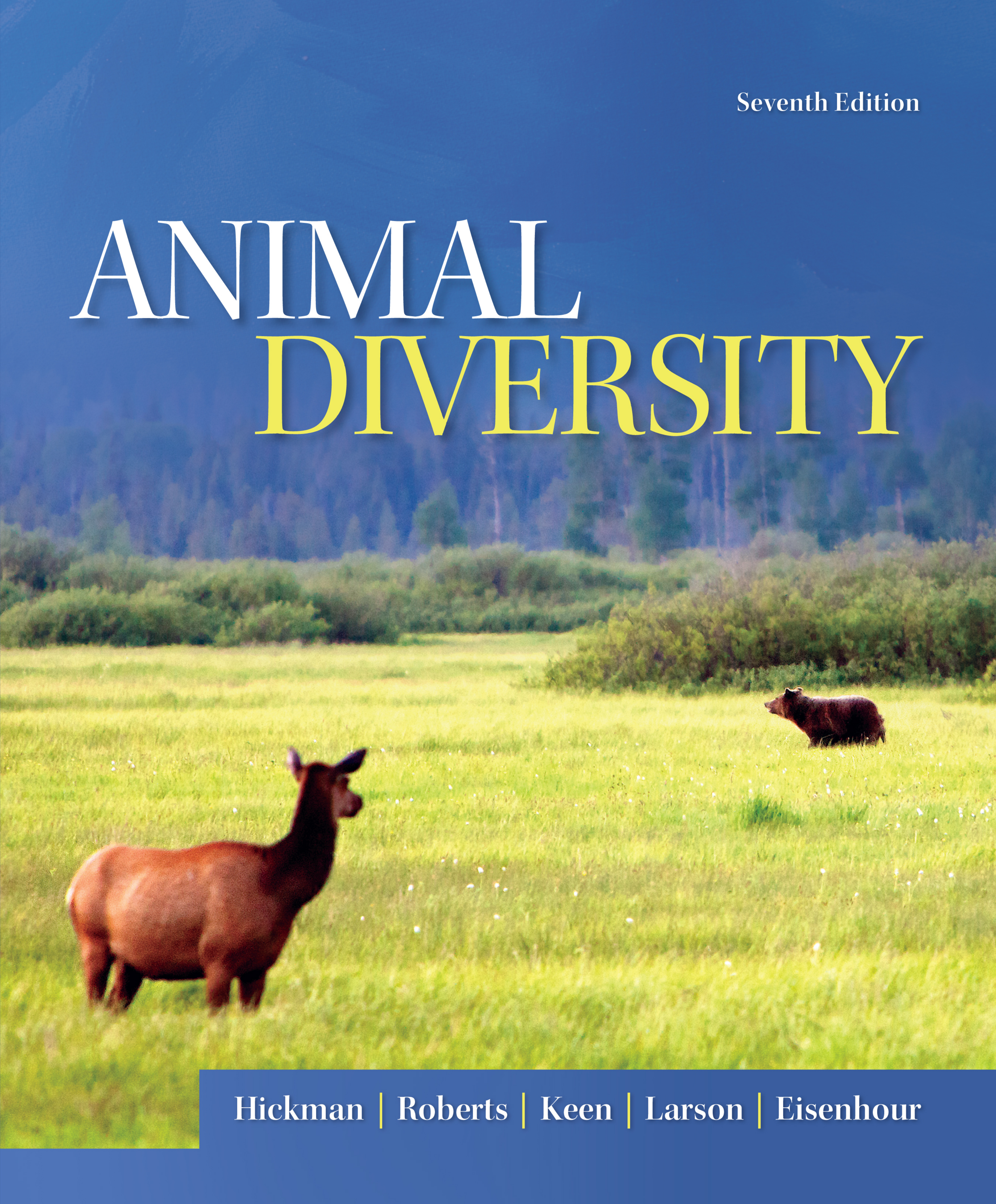
Seventh Edition

ANIMAL DIVERSITY



Hickman | Roberts | Keen | Larson | Eisenhour

Animal Diversity

SEVENTH EDITION

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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 three field guides in the Galápagos Marine Life Series for the identification of echinoderms, marine molluscs, and marine crustaceans. (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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Larry S. Roberts, Professor Emeritus of Biology at Texas Tech University and an adjunct professor at Florida International University, has extensive experience teaching invertebrate zoology, marine biology, parasitology, and developmental biology. He received his Sc.D. in parasitology at the Johns Hopkins University and is the lead author of Schmidt and Roberts' *Foundations of Parasitology.* Dr. Roberts is also co-author of *Integrated Principles of Zoology, Biology of Animals, and Animal Diversity*, and is author of *The Underwater World of Sport Diving*.

Dr. Roberts has published many research articles and reviews. He has served as president of the American Society of Parasitologists, Southwestern Association of Parasitologists, and Southeastern Society of Parasitologists, and is a member of numerous other professional societies. Dr. Roberts also serves on the Editorial Board of the journal *Parasitology Research*. His hobbies include scuba diving, underwater photography, and tropical horticulture.

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Susan Keen is Associate Dean for Undergraduate Academic Programs, College of Biological Sciences, at the University of California at Davis. She received her Ph.D. in zoology from the University of California at Davis, following a M.Sc. from the University of Michigan at Ann Arbor. She is a native of Canada and obtained her undergraduate education at the University of British Columbia in Vancouver.

Dr. Keen is an invertebrate zoologist fascinated with jellyfish life histories. She has a particular interest in life cycles where both asexual and sexual phases of organisms are present, as they are in most jellyfishes. Her other research has included work on sessile marine invertebrate communities, spider populations, and Andean potato evolution.

Dr. Keen has been teaching evolution and animal diversity within the Introductory Biology series for 15 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 for the Davis Honors Challenge program and works with an animator to depict aspects of animal development. She was given an Excellence in Education Award from the Associated Students group at Davis in 2004. She attended the National Academies Summer Institute on Undergraduate Education in Biology in 2005, and was a National Academies Education Fellow in the Life

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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 evolutionary relationships among vertebrate species, especially salamanders and lizards. The students in Dr. Larson's laboratory have participated in zoological field studies around the world, including in Africa, Asia, Australia, Madagascar, North America, South America, and the Caribbean Islands. Dr. Larson has authored numerous scientific publications, and has edited for the journals *The American Naturalist, Evolution, Journal of Experimental Zoology, Molecular Phylogenetics and Evolution*, and *Systematic Biology*. Dr. Larson serves as an academic advisor to undergraduate students and supervises the undergraduate biology curriculum at Washington University.

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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 graduate students have authored several publications. David serves as an academic advisor to prepharmacy students.

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

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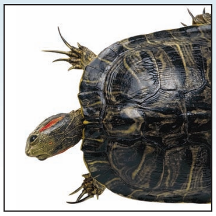
Preface



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 seventh 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

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

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. 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 Seventh Edition

We continue in updated form the major new structural feature of the previous edition: 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.

The seventh edition includes an unusually large overhaul of our photographic illustrations to maintain consistently high quality in our depiction of animal diversity. Recent revision of the standard geological timescale has required many updates in our coverage of the historical ages of animal taxa and the timing of major evolutionary events. We have updated throughout the book the major taxa recognized within animal phyla and the numbers of species recognized within them. In many cases, newly recognized taxa do not carry the formerly mandatory Linnean ranks. We retain Linnean ranks wherever possible, but our readers must become accustomed to more widespread usage of a rank-free taxonomy. Also added throughout the book are references to new primary literature and to updated textbooks.

The process of scientific inquiry (Chapter 1) is more fully illustrated with zoological examples. We introduce the contrast between ultimate versus proximate causes as the primary distinction between comparative methodologies and experimental ones. Our revised coverage of Lamarck's evolutionary theory illustrates why inheritance of acquired characters seemed to be the simplest explanation of adaptation, and how refutation of its conjectures led scientists to better evolutionary hypotheses. We expand coverage of industrial melanism in moths to illustrate fundamental principles of scientific inquiry, and to show how Darwin's theories of gradualism and natural selection are logically and empirically separable.

The latter part of Chapter 1 now includes brief conceptual coverage of gene expression to enable better understanding of evolutionary developmental topics in Chapter 3. We consolidate here related material on Mendelian genetics and population genetics, using protein polymorphism to illustrate measurement of allelic frequencies in populations. Our aim is to provide access to new discoveries in evolutionary developmental biology, conservation biology, and molecular phylogenetic analysis without burdening the introductory treatment with excessive detail. We clarify, for example, the use of inbreeding of captive animals to eliminate deleterious recessive traits from endangered species.

In Chapter 2, we revise our diagram and explanation of contrasting survivorship curves and their ecological interpretations. We expand our coverage of demographic changes that typically occur as human populations become industrialized. Updated information appears on human population growth and the earth's carrying capacity for humans. We systematically add Latin names for animal species used in ecological experiments and examples. Comments from an expert reviewer have helped us to make more precise our discussion of ecological resource partitioning, and the relationship between food chains and food webs. We continue from Chapter 1 our emphasis on process of science by updating our coverage of mimicry; new data have revised our interpretations of some hypotheses of Batesian versus Müllerian mimicry. We expand our coverage of biodiversity and extinction at the end of the chapter, and include in Chapter 18 a new essay on the ecological consequences of introduced pythons in southern Florida.

Animal architecture, development and biomechanics (Chapter 3) receive extended treatment through various additions to the chapters on individual taxa. A new opening essay for Chapter 6 discusses the similarities between sponge cell layers and the tissues of other animals. We add the astonishingly complex harp sponge, *Chondrocladia lyra*, to our discussion of Porifera. This deep-sea sponge is surprising in its morphology, mode of feeding, and reproductive biology. We also add a figure of the morphology of a hexactinellid sponge. Chapter 7 includes new discussion of muscle evolution and the nature of true muscles in cnidarians and ctenophores. Chapters 15–16 present new information on hagfish reproduction and embryology, including the discovery that some hagfishes do have vertebrae. Substantial changes to the section on bird flight include better explanations of how a bird's wing generates lift and how thrust is produced by flapping flight. Classification of wing types now follows the scheme from the Cornell bird laboratory.

Chapter 4 features expanded coverage of the contrasting concepts of species, including their partial unification by the increasingly popular "general lineage concept" of species. A new boxed essay illustrates common sources of difficulty in testing the hypothesis that two or more populations observed in nature constitute the same versus different species. Material formerly presented in Chapter 4 on the contrast between protostomes and deuterostomes is now consolidated with coverage of evolutionary developmental biology in Chapter 3.

Many systematic updates appear in the detailed coverage of Chapters 5–20. The unicellular eukaryotes described in Chapter 5 are no longer called protozoans, and a new cladogram describes hypothesized relationships among these taxa. We present here a new life-cycle diagram of *Volvox carteri* to illustrate one of the 25 hypothesized origins of multicellularity. We discontinue use of "Radiata" given phylogenetic evidence that phyla Cnidaria and Ctenophora do not form a monophyletic group.

Many cladistic changes are evident within lophotrochozoan protostomes. Evolutionary relationships and taxonomy within phylum Annelida (Chapter 11) are completely revised, discontinuing the traditional, but now clearly paraphyletic taxa Polychaeta and Oligochaeta. The terms "polychaete" and "oligochaete" continue to denote particular morphologies but not formal taxa. The basal phylogenetic split within annelids shows chaetopterid worms forming the sister taxon to the archiannelids. Many years ago, zoologists taxonomically separated errant polychaetes from sedentary polychaetes, but modern biologists rejected this dichotomy. New phylogenies resurrect this distinction, but place sedentary polychaetes in a clade with members of Clitellata. We include members of former phylum Echiura, the spoon worms, as a branch within the sedentary polychaetes and discuss the loss of metamerism implied by this position. We continue to place phylum Sipuncula outside Annelida despite some conflicting phylogenetic evidence. The revised molluscan cladogram in Chapter 16 now places Aculifera (Solenogastres, Caudofoveata, and Polyplacophora) as the sister taxon to Conchifera (shellbearers).

Within Ecdysozoa (Chapter 12), recent work places Onychophora and Tardigrada as sister taxa, with this pair being the sister taxon to Arthropoda. The arthropod cladogram in Chapter 13 now depicts relationships supported under the mandibulate hypothesis: all taxa sharing mandibles are united and this group is distinct phylogenetically from the chelicerate taxa.

Evolutionary relationships among the crustacean arthropods are revised, and terminology for crustacean limbs has been standardized across all diagrams and text. Some major groupings within Crustacea have not been assigned traditional Linnaean ranks (classes and orders) and are thus presented as rank-free taxa.

Chapter 14 includes new information about a possible phylogenetic grouping of Xenoturbella with acoelomorph worms and on phylogenetic placement of bilaterally symmetrical fossil echinoderms. Chapters 15–16 include a new rank-free cladistic taxonomy of chordates. Following numerous studies (mainly incorporating molecular phylogenetic studies, but also a few evolutionary developmental ones), hagfishes and lampreys are once again united in the clade Cyclostomata. Chapter 17 features updated coverage of early tetrapod evolution to reflect new fossil discoveries and interpretations. In Chapter 19, the order-level taxonomy of birds is substantially revised. Chapter 20 updates human evolution to include new molecular studies and fossil finds.

Teaching and Learning Aids

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.

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.

Web Pages

At the end of each survey chapter is a selection of related Internet links. These related links can be found in the instructor resources on Connect. For more information on Connect, go to: *http://connect.mheducation.com*.

Supplements

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 through the Instructor Resources on Connect. You can find more information on Connect at: *http://connect.mheducation.com*.

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Animal Diversity Laboratory Manual

The laboratory manual by Cleveland P. Hickman, Jr., Lee B. Kats, and Susan L. Keen *Laboratory Studies in Animal Diversity*, is designed specifically for a survey course in zoology.

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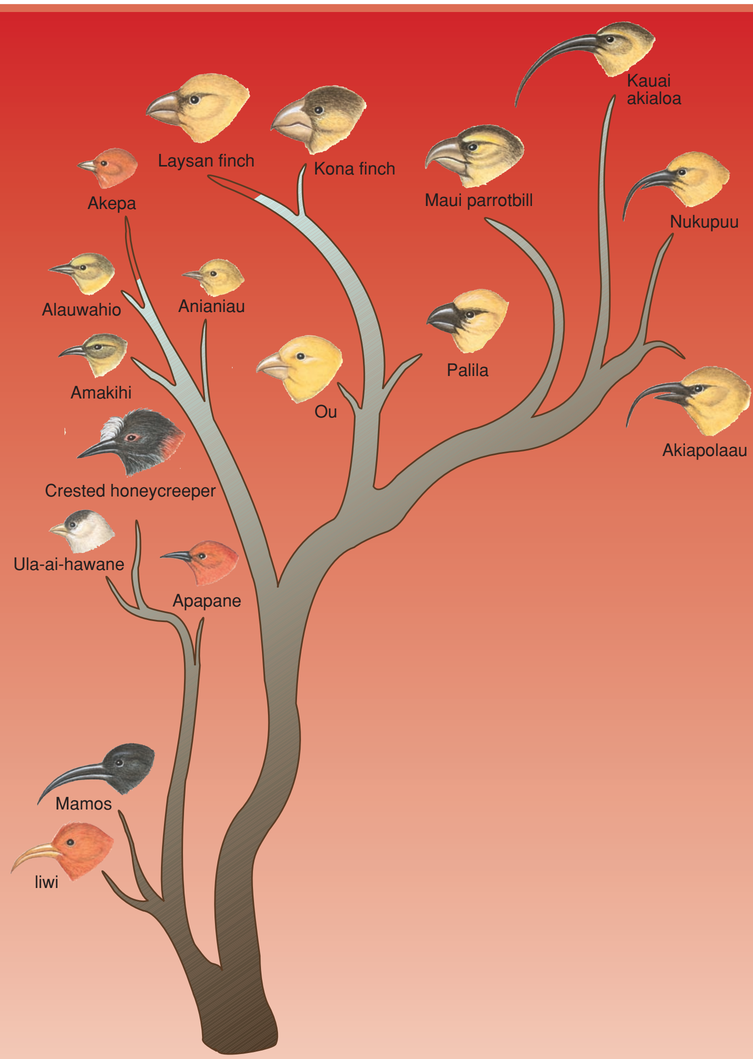
Science of Zoology and Evolution of Animal Diversity



Evolutionary diversification of Hawaiian honeycreepers.

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.

Zoology (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.

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,

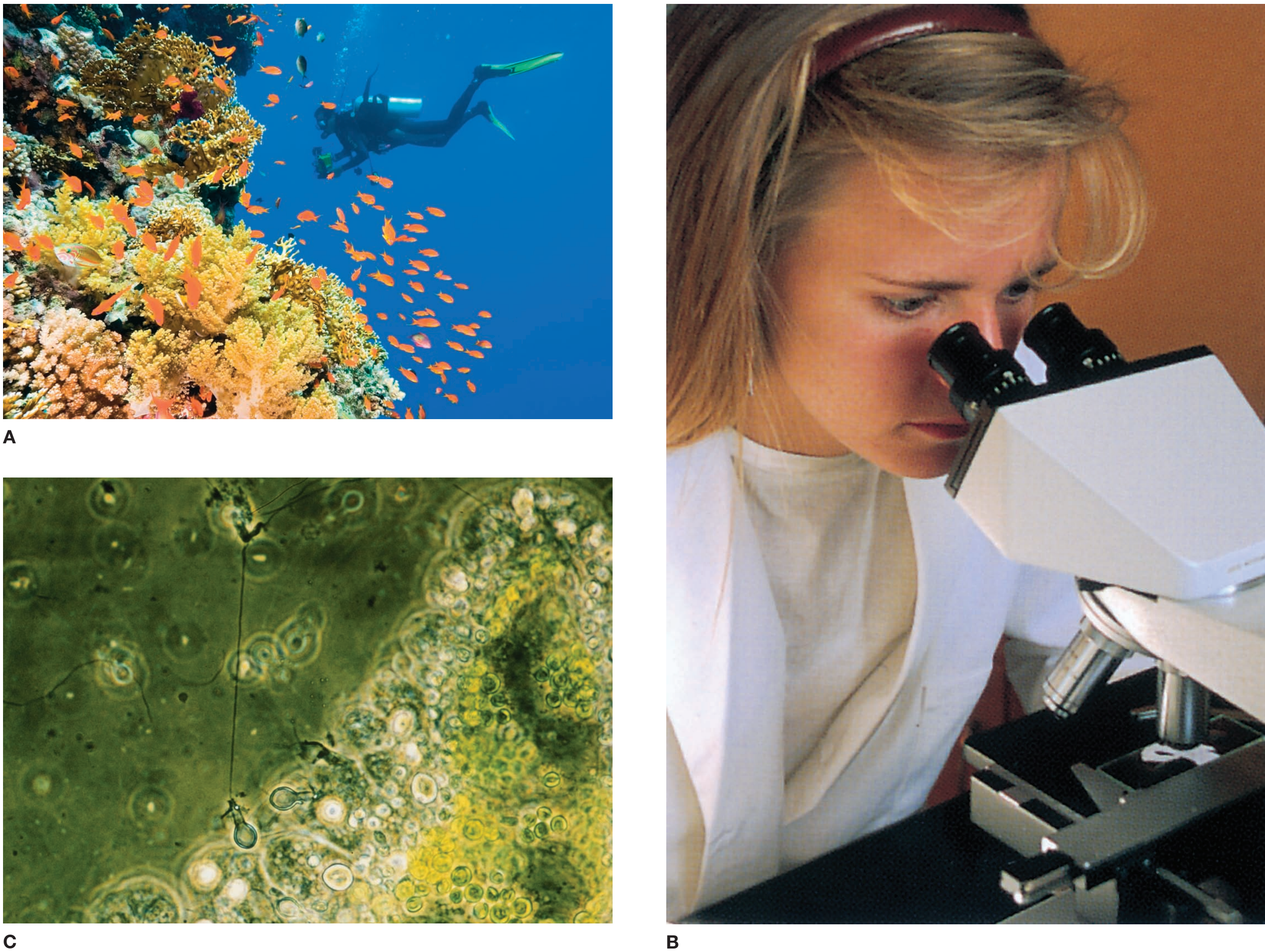


figure 1.1

Examples of observation in zoological research. **A,** Observing a coral reef. **B,** Observing nematocyst discharge, **C,** from cnidarian tentacles (see p. 142).

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

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).

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.

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.

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

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.

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 Power of a Theory

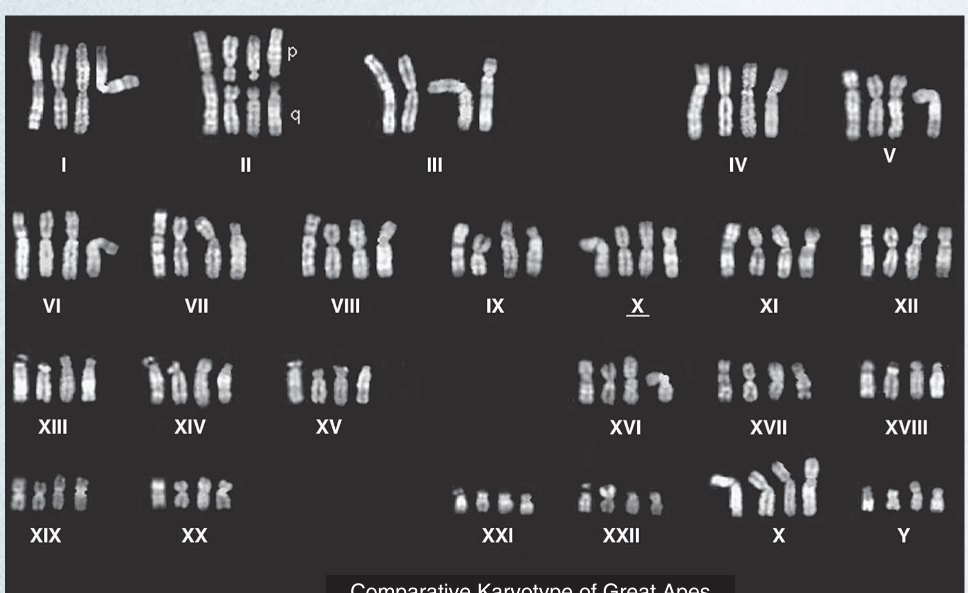
Darwin's theory of common **descent** (p. 11) illustrates the scientific importance of general theories that give unified explanations to diverse kinds of data. Darwin proposed his theory of descent with modification of all living forms because it explained the patterns of similarity and dissimilarity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

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 (p. 406, 436). 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.

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.

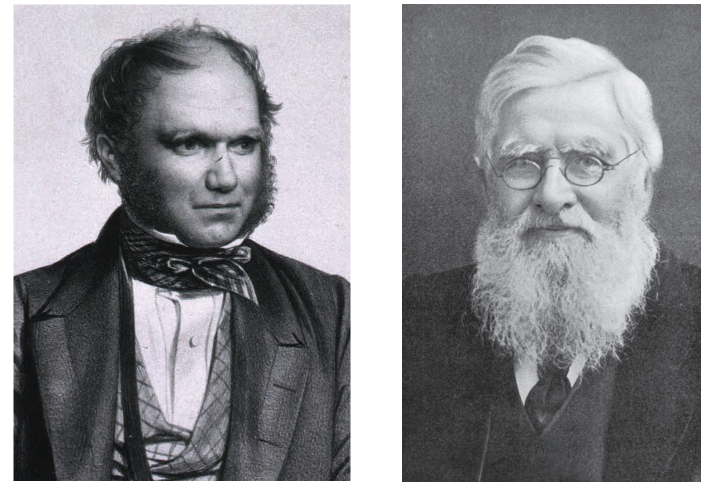


figure 1.3

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.

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.

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

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.

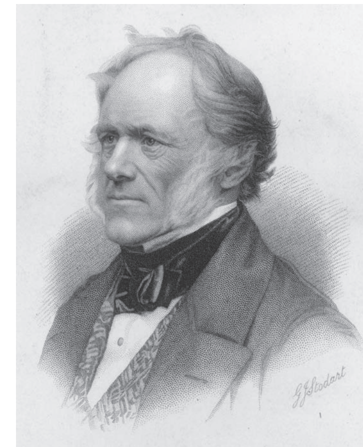


figure 1.5

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

their necks by stretching to obtain food and then passed the lengthened neck to their offspring. Lamarck proposed that over many generations, these changes accumulated to produce the long necks of modern giraffes.

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. 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. Lyell's geological studies convinced him that earth's age must be many millions of years. 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.

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.

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 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

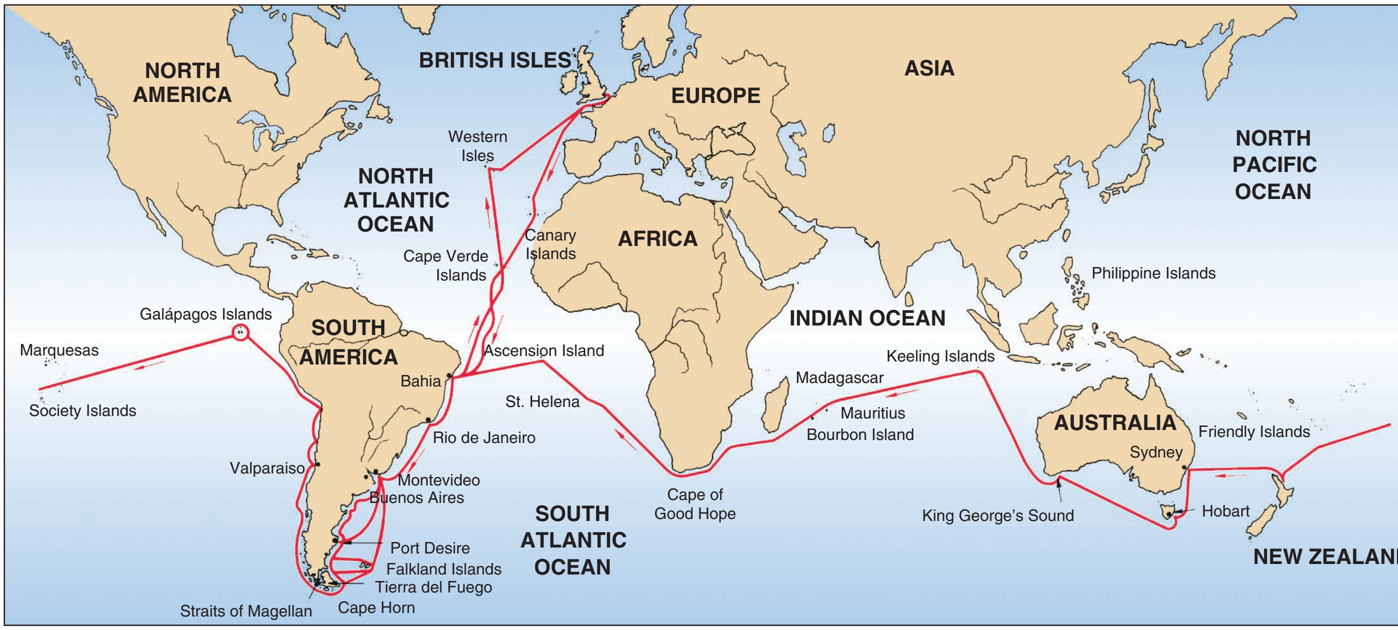


figure 1.6

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*.

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.

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."