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VOLUME 3

BIOLOGY

EXPLORING THE DIVERSITY OF LIFE



FIRST CANADIAN EDITION

RUSSELL • WOLFE • HERTZ • STARR
FENTON • ADDY • MAXWELL • HAFFIE • DAVEY

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Exploring the Diversity of Life

First Canadian Edition

Volume Three

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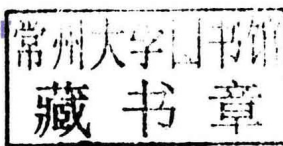
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E D U C A T I O N

Biology: Exploring the Diversity of Life, First Canadian Edition, Volume Three

by Peter J. Russell, Stephen L. Wolfe, Paul E. Hertz, Cecie Starr, M. Brock Fenton,
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About the Cover: A flying little brown bat frozen in mid-wing stroke moves through the blackness of an underground passage. Echolocation allows the bat to collect information about its surroundings or to locate flying insects. In the background is the elegantly sinuous double helix of DNA, a widely recognized vernacular icon for life itself. The blurred DNA connotes the generative activity inherent in the molecule that carries the genetic code of all life into the future.





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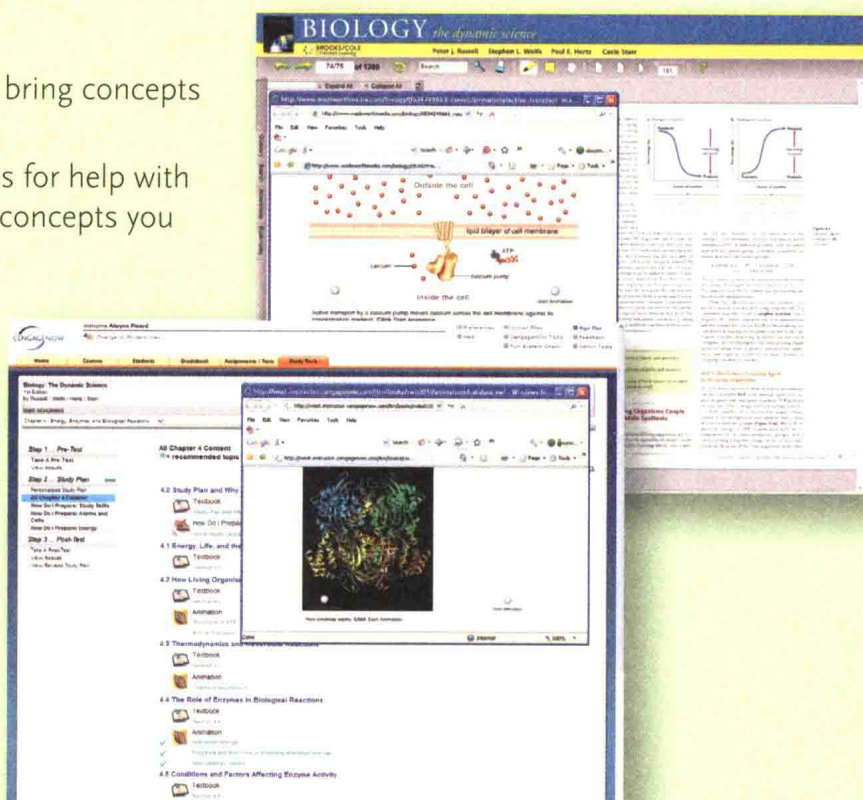
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About the Canadian Authors

M.B. (BROCK) FENTON received his Ph.D. from the University of Toronto in 1969. Since then, he has been a faculty member in biology at Carleton University, then at York University, and then at The University of Western Ontario. In addition to teaching parts of first-year biology, he has also taught vertebrate biology, animal biology, and conservation biology, as well as field courses in the biology and behaviour of bats. He has received awards for his teaching (Carleton University Faculty of Science Teaching Award, Ontario Confederation of University Faculty Associations Teaching Award, and a 3M Teaching Fellowship, Society for Teaching and Learning in Higher Education) in addition to recognition of his work on public awareness of science (Gordin Kaplan Award from the Canadian Federation of Biological Societies; Honourary Life Membership, Science North, Sudbury, Ontario; Canadian Council of University Biology Chairs Distinguished Canadian Biologist Award; The McNeil Medal for the Public Awareness of Science of the Royal Society of Canada; and the Sir Sanford Fleming Medal for public awareness of Science, the Royal Canadian Institute). He also received the C. Hart Merriam Award from the American Society of Mammalogists for excellence in scientific research. Bats and their biology, behaviour, evolution, and echolocation are the topic of his research, which has been funded by the Natural Sciences and Engineering Research Council of Canada (NSERC).

HEATHER ADDY is a graduate of the University of Alberta and received her Ph.D. in plant–soil relationships from the University of Guelph in 1995. During this training and in a subsequent postdoctoral fellowship focusing on mycorrhizas and other plant–fungus symbioses at the University of Alberta, she discovered a love of teaching. In 1998, she joined the Department of Biological Sciences at the University of Calgary in a faculty position that places emphasis on teaching and teaching-related scholarship. In addition to teaching introductory biology classes and an upper-level mycology class, she has led the development of investigative labs for introductory biology courses and the introduction of peer-assisted learning groups in large biology and chemistry classes. She received the Faculty of Science Award for Excellence in Teaching in 2005 and an Honourable Mention for the Student's Union Teaching Excellence Award in 2008.

DENIS MAXWELL received his Ph.D. from the University of Western Ontario in 1995. His thesis under the

supervision of Norm Hüner focused on the role of the redox state of photosynthetic electron transport in photoacclimation in green algae. Following his doctorate, he was awarded an NSERC postdoctoral fellowship. He undertook postdoctoral training at the Department of Energy Plant Research Laboratory at Michigan State University, where he studied the function of the mitochondrial alternative oxidase. After taking up a faculty position at the University of New Brunswick in 2000, he moved in 2003 to the Department of Biology at The University of Western Ontario. His research program, which is supported by NSERC, is focused on understanding the role of the mitochondrion in intracellular stress sensing and signalling. In addition to research, he is passionate about teaching biology and science to first-year university students.

TOM HAFFIE is a graduate of the University of Guelph and the University of Saskatchewan in the area of microbial genetics. Currently the learning development coordinator for the Faculty of Science at the University of Western Ontario, Tom has devoted his 20-year career to teaching large biology classes in lecture, laboratory, and tutorial settings. He led the development of the innovative core laboratory course in the biology program, was an early adopter of computer animation in lectures and, most recently, has coordinated the implementation of personal response technology across campus. He holds a UWO Pleva Award for Excellence in Teaching, a UWO Fellowship in Teaching Innovation, a Province of Ontario Award for Leadership in Faculty Teaching (LIFT), and a national 3M Fellowship for Excellence in Teaching.

KEN DAVEY is a graduate of the University of Western Ontario and received his Ph.D. from Cambridge University. He is an emeritus professor of biology at York University and has by preference taught elementary courses in zoology at McGill and York and more advanced courses in invertebrate physiology, parasitology, and endocrinology. He has held a number of academic administrative positions at York. His research interests include invertebrate physiology and the endocrinology of insects and parasitic worms, supported by NSERC. Ken has accumulated a number of academic awards, including the Canadian Council of University Biology Chairs Distinguished Canadian Biologist Award and the Wigglesworth Award for Service to Entomology of the Royal Entomological Society. He is a Fellow of the Royal Society of Canada and an Officer of the Order of Canada.

About the U.S. Authors

PETER J. RUSSELL received a B.Sc. in Biology from the University of Sussex, England, in 1968 and a Ph.D. in Genetics from Cornell University in 1972. He has been a member of the Biology faculty of Reed College since 1972; he is currently a Professor of Biology. He teaches a section of the introductory biology course, a genetics course, an advanced molecular genetics course, and a research literature course on molecular virology. In 1987 he received the Burlington Northern Faculty Achievement Award from Reed College in recognition of his excellence in teaching. Since 1986, he has been the author of a successful genetics textbook; current editions are *iGenetics: A Mendelian Approach*, *iGenetics: A Molecular Approach*, and *Essential iGenetics*. He wrote nine of the BioCoach Activities for The Biology Place. Peter Russell's research is in the area of molecular genetics, with a specific interest in characterizing the role of host genes in pathogenic RNA plant virus gene expression; yeast is used as the model host. His research has been funded by agencies including the National Institutes of Health, the National Science Foundation, and the American Cancer Society. He has published his research results in a variety of journals, including *Genetics*, *Journal of Bacteriology*, *Molecular and General Genetics*, *Nucleic Acids Research*, *Plasmid*, and *Molecular and Cellular Biology*. He has a long history of encouraging faculty research involving undergraduates, including cofounding the biology division of the Council on Undergraduate Research (CUR) in 1985. He was Principal Investigator/Program Director of an NSF Award for the Integration of Research and Education (AIRE) to Reed College, 1998–2002.

STEPHEN L. WOLFE received his Ph.D. from Johns Hopkins University and taught general biology and cell biology for many years at the University of California, Davis. He has a remarkable list of successful textbooks, including multiple editions of *Biology of the Cell*, *Biology: The Foundations*, *Cell Ultrastructure*, *Molecular and Cellular Biology*, and *Introduction to Cell and Molecular Biology*.

PAUL E. HERTZ was born and raised in New York City. He received a bachelor's degree in Biology at Stanford University in 1972, a master's degree in Biology at Harvard University in 1973, and a doctorate in Biology at Harvard University in 1977. While completing field research for the doctorate, he served on the Biology faculty of the University of Puerto Rico at Rio Piedras. After spending 2 years as an Isaac Walton Killam Postdoctoral Fellow at Dalhousie University, Hertz accepted a teaching position at Barnard College, where he has taught since 1979. He was named Ann

Whitney Olin Professor of Biology in 2000, and he received The Barnard Award for Excellence in Teaching in 2007. In addition to his service on numerous college committees, Professor Hertz was Chair of Barnard's Biology Department for 8 years. He has also been the Program Director of the Hughes Science Pipeline Project at Barnard, an undergraduate curriculum and research program funded by the Howard Hughes Medical Institute, since its inception in 1992. The Pipeline Project includes the Intercollegiate Partnership, a program for local community college students that facilitates their transfer to 4-year colleges and universities. He teaches one semester of the introductory sequence for Biology majors and preprofessional students as well as lecture and laboratory courses in vertebrate zoology and ecology. Professor Hertz is an animal physiological ecologist with a specific research interest in the thermal biology of lizards. He has conducted fieldwork in the West Indies since the mid-1970s, most recently focusing on the lizards of Cuba. His work has been funded by the National Science Foundation, and he has published his research in such prestigious journals as *The American Naturalist*, *Ecology*, *Nature*, and *Oecologia*.

CECIE STARR is the author of best-selling biology textbooks. Her books include multiple editions of *Unity and Diversity of Life*, *Biology: Concepts and Applications*, and *Biology Today and Tomorrow*. Her original dream was to be an architect. She may not be building houses, but with the same care and attention to detail, she builds incredible books: "I invite students into a chapter through an intriguing story. Once inside, they get the great windows that biologists construct on the world of life. Biology is not just another house. It is a conceptual mansion. I hope to do it justice."

BEVERLY McMILLAN has been a science writer for more than 20 years and is coauthor of a college text in human biology, now in its seventh edition. She has worked extensively in educational and commercial publishing, including 8 years in editorial management positions in the college divisions of Random House and McGraw-Hill. In a multifaceted freelance career, Bev also has written or coauthored six trade books and numerous magazine and newspaper articles, as well as story panels for exhibitions at the Science Museum of Virginia and the San Francisco Exploratorium. She has worked as a radio producer and speechwriter for the University of California system and as a media relations advisor for the College of William and Mary. She holds undergraduate and graduate degrees from the University of California, Berkeley.

Preface

Welcome to an exploration of the diversity of life. The main goal of this text is to guide you on a journey of discovery about life's diversity across levels ranging from molecules to genes, cells to organs, and species to ecosystems. Along the way, we will explore many questions about the mechanisms underlying diversity as well as the consequences of diversity for our own species and for others.

At first glance, the riot of life that animates the biosphere overwhelms the minds of many who try to understand it. One way to begin to make sense of this diversity is to divide it into manageable sections on the basis of differences. In this book, we highlight the divisions between plants and animals, prokaryotes and eukaryotes, protostomes and deuterostomes, but we also consider features found in all life forms. We examine how different organisms solve the common problems of finding nutrients, energy, and mates on the third rock from our Sun. What basic evolutionary principles inform the relationships among life forms regardless of their different body plans, habitats, or life histories? Unlike many other first-year biology texts, this book has chapters integrating basic concepts such as genetic recombination, the effects of light, nutrition, and domestication across the breadth of life from microbes to mistletoe to moose. As you read this book, you will be referred frequently to other chapters for linked information that expands the ideas further.

Evolution provides a powerful conceptual lens for viewing and understanding the roots and history of diversity. We will demonstrate how knowledge of evolution helps us appreciate the changes we observe in organisms. Whether the focus is the conversion of free-living prokaryotes into mitochondria and chloroplasts or the steps involved in the domestication of rice, selection for particular traits over time can explain the current condition.

We hope that Canadian students will find the subject of biology as it is presented here accessible and engaging because it is presented in familiar contexts. We have highlighted the work of Canadian scientists, used examples of Canadian species, and referred to Canadian regulations and institutions, as well as discoveries made by Canadians.

Although many textbooks use the first few chapters to introduce and/or review background information, we have used the first chapters to convey the excitement and interest of biology itself. Within the centre of the book, we have placed important background information about biology and chemistry in the reference section entitled *The Chemical and Physical Foundations of Biology*. These pages are distinct and easy to find with their purple edges and have become

affectionately known as the “Purple Pages.” These pages enable information to be readily identifiable and accessible to students as they move through the textbook rather than information that is tied to a particular chapter. The purple background makes the pages easy to find when you need to check a topic. This section keeps background information out of the mainstream of the text, allowing you to focus on bigger pictures.

The Organization of Matter

Any substance in the universe that has mass and occupies space is defined as **matter**. The basic scientific concepts that explain how matter is organized in biological systems are no different from those for nonliving forms of matter. Living organisms are built

from the same chemistry building blocks as nonliving systems and abide by the same laws of chemistry. Because of this, a basic understanding of these chemistry principles is important for our understanding of how biological systems operate.

Elements and Compounds


All matter in the universe—anything that occupies space and has mass—is composed of elements. An element is a pure substance that cannot be broken down into simpler substances by ordinary chemical or physical techniques. Ninety-two different elements occur naturally on Earth, and more than 15 artificial elements have been synthesized in the laboratory.

Living organisms are composed of about 25 elements, with only 4—carbon, hydrogen, oxygen, and nitrogen—accounting for more than 96% of the weight of living organisms. Seven other elements—calcium, phosphorus, potassium, sulphur, sodium, chlorine, and magnesium—contribute most of the remaining 4%. Nine additional elements occur in organisms in quantities so small (<0.01%) that they are known as trace elements. The proportions by mass of different elements differ markedly in seawater, the human body, a fruit, and Earth's crust.

Molecules whose component atoms are different (such as carbon dioxide) are called compounds. The chemical and physical properties of compounds are typically distinct from those of their atoms or elements. For example, we all know that water is a liquid at room temperature. We also know that water does not burn. However, the properties of the individual elements of water—hydrogen and oxygen—are quite different. Hydrogen and oxygen are gases at room temperature, and both are highly reactive.

Atoms combined chemically in fixed numbers and ratios form the molecules of living and nonliving matter. For example, the oxygen we breathe is a molecule formed from the chemical combination of two oxygen atoms; a molecule of the carbon dioxide that we exhale contains one carbon atom and two oxygen atoms. Because carbon dioxide is a molecule consisting of different elements, it is referred to as a compound.

Percentage Composition			
Seawater	Human	Pumpkin	Earth's crust
Oxygen 88.3	Oxygen 65.0	Oxygen 85.0	Oxygen 46.6
Hydrogen 11.0	Carbon 18.5	Hydrogen 10.7	Silicon 27.7
Chlorine 1.9	Hydrogen 9.5	Carbon 3.3	Aluminum 8.1
Sodium 1.1	Nitrogen 3.3	Potassium 0.34	Iron 5.0
Magnesium 0.1	Calcium 2.0	Nitrogen 0.16	Calcium 3.6
Sulphur 0.09	Phosphorus 1.1	Phosphorus 0.05	Sodium 2.8
Potassium 0.04	Potassium 0.35	Calcium 0.02	Potassium 2.6
Calcium 0.04	Sulphur 0.25	Magnesium 0.01	Magnesium 2.1
Carbon 0.001	Sodium 0.15	Iron 0.008	Other elements 1.5
Silicon 0.0019	Chlorine 0.15	Iron 0.001	
Nitrogen 0.0015	Magnesium 0.05	Zinc 0.0002	
Strontium 0.0008	Iron 0.004	Copper 0.0001	
	Iodine 0.0004		



In addition to presenting material about biology, this book also makes a point of highlighting particular people, important molecules, interesting contexts, and examples of life in extreme conditions. Science that appears in textbooks is the product of people who have made careful and systematic observations, which led them to formulate hypotheses about these observations and, where appropriate, design and execute experiments to test these hypotheses. We illustrate this in each chapter with boxed stories about how particular people have used their ingenuity and creativity to expand our knowledge of biology. We have endeavoured to show not just the science itself but also the process behind the science.

Although biology is not simply chemistry, specific chemicals and their interactions can have dramatic effects on biological systems. From water to progesterone, amanitin, and DDT, each chapter features the activity of a relevant chemical.



MINICASE BIOLOGY

Relaxin

The hormone relaxin (Figure 1) is a polypeptide produced by the ovaries during pregnancy in humans, relaxin occurs at higher levels earlier in pregnancy than closer to parturition. Relaxin promotes angiogenesis, the growth of new blood vessels, and influences the interface between the uterus and the placenta. Relaxin might relax the contractions of the uterus that could terminate pregnancy and stimulate



Figure 1 Relaxin

the growth of glands that produce milk in breast tissue.
New parturition relaxin causes relaxation of the pelvic ligaments and softens and enlarges the cervical opening.

of intervertebral ligaments at the time of parturition (see Minicase: Infant Biology)

39.1 Housing and Feeding Developing Young

Some animal parents invest significant energy in housing and feeding their developing young. This is one aspect of the generally selfish drive to ensure that their genes are represented in future generations.

39.1a Housing: Providing a Place in Which the Embryo Can Develop

There is a recurring tendency across phyla for parents to put eggs and developing young in situations that minimize their exposure to predators and parasites while maximizing favorable conditions for growth and development. Many species of birds use nests to house their eggs and unborn young. Parents of other species, such as some species of scorpions (see Figure 1.22a), frogs, and snakes, carry their young with them, often on their backs. This allows the parent (parents) to avoid or actively deter would-be predators.

An evolution in parental investment in moving eggs and young inside the parent's body (ovovivipary and viviparity; see Chapter 18). This approach to parental care has several different stages (see Chapter 18, "On the Road to Viviparity"). Although we associate viviparity with mammals, many species of fish are mouthbrooders, keeping eggs and, for a time, developing young in their mouths. Other fish, such as sea hares and pipefish, female seahorses (see Figure 1.22b), keep eggs and developing young in specialized anatomical areas, called brood pouches, located on the tail or head of the male. "Pregnancy" in male sea hares represents an increase in parental investment. It also allows males to be confident about the paternity of the young they raise.

Some amphibians also show high levels of parental care. In Australia, female frogs, *Rheobatrachus* spp., use their stomachs as brood pouches. While the young are developing, they secrete prostaglandin E_2 , which inhibits the secretion of gastric acid in the stomach and slows the developing young from being digested. On Mount Nimba in west Africa, female trade *Archipophis* spp. also use their stomachs as brood pouches. In their stomachs, where the young feed on uterine secretions in the absence of a placenta, the gestation period for these trade is nine months, and newborns are 7 to 8 cm long and weigh 40 to 60 mg. Retention of developing embryos in the stomachs has evolved independently in each of the three living groups of Amphibia: Anura, Urodela, and Gymnophiona (see Chapter 22).

39.1b Feeding: Aiding and Assisting Developing Young

Almost everyone has seen pictures of parent birds feeding their young (see Figures 80.2 and 80.4). In many species, both males and females deliver food to the nestlings. Some fruit-eating adult birds feed insects to their young.



Figure 39.1 A male sea hare gives birth.

To help frame the material with an engaging context, we begin each chapter with a section called "Why It Matters." In addition, several chapters include boxed accounts of organisms thriving "on the edge" at unusual temperatures, pressures, radiation dosages, salt concentrations, etc. These brief articles explain how our understanding of "normal" can be increased through study of the "extreme."

Examining how biological systems work is another theme pervading this text and underlying the idea of diversity. We have intentionally tried to include examples that will tax your imagination, from sea slugs that steal chloroplasts for use as solar panels, to hummingbirds fuelling their hovering flight, to adaptive radiation of viruses. In each situation, we examine how biologists have explored and assessed the inner workings of organisms from gene regulation to the challenges of digesting cellulose.



PEOPLE BEHIND BIOLOGY

Dr. Aurora Nedelcu, University of New Brunswick

Whereas the octopus and lamprey are members of the phylum Chordata, they are members of the phylum Cephalopoda and the phylum Agnatha, respectively. The octopus and lamprey are members of the phylum Cephalopoda and the phylum Agnatha, respectively. The octopus and lamprey are members of the phylum Cephalopoda and the phylum Agnatha, respectively.

Multiple autopolyploidization events have led to the same (A) the homologous chromosome pair, they are held together tightly by a protein framework called the synaptonemal complex (Figure 10.15, p. 228). Supported by this framework, regions of homologous chromosomes exchange segments, producing new combinations of alleles (see Figure 10.16, step 2). Recall that the exchange process is very precise and involves the breakage and rejoining of DNA molecules by enzymes (Figure 10.11). When the exchange is complete toward the end of prophase I, the synaptonemal complex dissolves, and chromosomes disappear. If you now follow one of the four resulting nuclei, you will find that each of the four resulting nuclei receives one of these four chromatids (see Figure 10.16, step 3). Two new recombinant chromatids, and two new recombinant nuclei have been produced, and two new recombinant nuclei have been produced, and two new recombinant nuclei have been produced.

Note that illustrations of recombination usually show chromosomes "paired" side by side with only one chromosome participating in recombination (see Figure 10.14). However, chromosomes actually pair one on top of the other, such that one of the four chromatids can participate in a gene recombination event. Recombination takes place largely at random, at almost any position along the chromosome arms.

recombination is usually leading with sister chromatids. A variety of recombination events can occur, including nonreciprocal exchange of segments (unequal crossing over), which can lead to the formation of gametes with missing or extra chromosomes. In the case of the octopus and lamprey, the exchange process is very precise and involves the breakage and rejoining of DNA molecules by enzymes (Figure 10.11). When the exchange is complete toward the end of prophase I, the synaptonemal complex dissolves, and chromosomes disappear. If you now follow one of the four resulting nuclei, you will find that each of the four resulting nuclei receives one of these four chromatids (see Figure 10.16, step 3). Two new recombinant chromatids, and two new recombinant nuclei have been produced, and two new recombinant nuclei have been produced.

Several events likely occur at various locations along all chromosomes. Since in Figure 10.14 that a recombination event does not "cut" "break" the ability of a gene given in a localized area. All of the DNA sequence stretching from the site of recombination to the end of the chromosome is exchanged.

Random segregation. Random segregation of chromosomes at meiosis is a key feature of genetic variability in meiosis. Recall that the maternal and paternal chromosomes of each homologous pair are different in that they typically carry different alleles of many of the genes on that chromosome. During meiosis, random segregation of chromosomes leads to the formation of four haploid daughter cells, each containing one of the two chromosomes of each homologous pair. Since chromosomes make specific connections leading to one pair and the other chromosome connects to the opposite pole. In making these connections, all the maternal chromosomes mix, connect to one pole, and all the paternal chromosomes mix, connect to the opposite pole. (In a most likely, a random combination of maternal and paternal chromosomes may be segregated to a given spindle pole (Figure 10.16, p. 223).)

The number of possible combinations depends on the number of chromosomes pairs on a species. For example, the 39 chromosome pairs in dogs allow 2^{39} different combinations of maternal and paternal chromosomes to be delivered to the poles, producing potentially 540 billion genetically different gametes from this source of variability alone. Note that this random partitioning of maternal and paternal chromosomes is responsible for the independent assortment of the alleles of two genes in Mendel's experiments with garden peas described in Chapter 11.

Solving problems is another theme that runs through the book. Whether the topic is gene therapy to treat a disease in people, increasing crop production, or conserving endangered species, both the problem and the solution lie in biology. We will explore large problems facing planet Earth and the social implications that arise from them.

Science is by its nature a progressive enterprise in which answers to questions open new questions for consideration. Each chapter presents unanswered questions as well as questions for discussion to emphasize that biologists still have a lot to learn—topics for you to tackle should you decide to pursue a career in research.

"Study Breaks" occur after each section in the chapters. They contain questions written by students to identify some of the important features of the section. The answers are embedded in the "Review" section at the end of each chapter. Also included at the end of each chapter is a group of multiple-choice self-test questions, the answers to which can be found at the end of the book. "Questions for Discussion" at the end of each chapter challenge you to think more broadly about biology. You are encouraged to use these in discussions with other students and to explore potential answers by using the resources of the electronic library.

To maximize the chances of producing a useful text that draws in students (and instructors), we sought the advice of colleagues who teach biology (members of the Editorial Advisory Board). We also asked students (members of the Student Advisory Boards) for their advice and comments. Both groups read draft chapters and provided valuable feedback, but any mistakes are ours. The members of the Student Advisory Boards also wrote the Study Break questions found throughout the text.

We hope that you are as captivated by the biological world as we are and are drawn from one chapter to another. But don't stop there—use electronic resources to broaden your search for understanding.



LIFE ON THE EDGE Rate of Evolutionary Change

How quickly can evolution occur? The rate of the local record in our knowledge and understanding of evolution can be measured by the rate at which evolution occurs over millions of years, or at least millions of generations. But this is not always true. In 1971, five adult pairs of lizards from the island of Pohnpei were introduced to the island of Pohnpei. In 1971, five adult pairs of lizards from the island of Pohnpei were introduced to the island of Pohnpei. In 1971, five adult pairs of lizards from the island of Pohnpei were introduced to the island of Pohnpei.

experiment measuring a short generation time and high rates of R, the intrinsic rate of population increase (see Chapter 46). In 36 years, a stable established population on both sides was genetically indistinguishable from the mainland source population. However, the proportions had changed by morphology. Specifically, introduced lizards differed both from source populations and from one another in head morphology, hind limb length, and digestive tract. On Pohnpei, *P. tigris* have longer snouts and taller heads than those on Pohnpei, coexisting with a different *P. tigris* on Pohnpei.

are more plastic material than those on Pohnpei. The changes in morphology and performance of *P. tigris* after introduction to the island are similar to those documented among other species and families of lizards. Lizards with heads on small islands demonstrate adaptability, a foundation for evolutionary change. Lizards with heads on small islands demonstrate adaptability, a foundation for evolutionary change. Lizards with heads on small islands demonstrate adaptability, a foundation for evolutionary change.

But some *F₂* hybrids are healthy, vigorous, and fully fertile and can breed with other hybrids and with both parental species. Sometimes the *F₂* generation, produced by matings between *F₁* hybrids, or between *F₁* hybrids and either parental species, may exhibit reduced survival or fertility, a phenomenon known as hybrid breakdown. Experimental crosses between fruit fly (*Drosophila*) species may produce functional interspecific hybrids, but their offspring experience a high rate of chromosomal abnormalities and harmful types of genetic recombination. Thus, reproductive isolation is maintained between the species because there is little long-term mixing of their gene pools.

STUDY BREAK

1. What is a reproductive isolating mechanism? Distinguish between two major types of reproductive isolating mechanisms.
2. Define five types of postzygotic isolating mechanisms that can prevent intergeneric mating.
3. Prezygotic isolating mechanisms prevent gene pools of two species from mating, so why do postzygotic isolating mechanisms exist? Distinguish between three types of postzygotic isolating mechanisms.

18.8 Geography of Speciation

Geography has a huge impact on whether gene pools have the opportunity to mix. Biologists define three modes of speciation based on the geographic relationship of populations as they become reproductively isolated: allopatric speciation (also = divergent speciation), sympatric speciation (also = divergent speciation), and sympatric speciation (also = divergent speciation).

18.8a Allopatric Speciation: New Species Develop from Isolated Populations

Allopatric speciation can occur when a physical barrier subdivides a large population or when a small population becomes separated from a species' main geographic distribution. Allopatric speciation probably the most common mode of speciation in large animals, occurs in two stages. First, two populations become geographically separated, preventing gene flow between them. Then, as the populations experience distinct mutations as well as different patterns of natural selection and genetic drift, they may accumulate genetic differences that isolate them reproductively. Geographic separation sometimes occurs when a barrier divides a large population into two or more

Supplementary Materials

An extensive array of supplemental materials is available to accompany this text. These supplements are designed to make teaching and learning more effective. For more information on any of these resources, please contact your local Nelson Education sales representative or call Nelson Education Limited Customer Support at 1-800-268-2222.

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The *Instructor's Resource Manual* for this First Canadian Edition has been dramatically revised by Tanya Noel, Tamara Kelly, and Julie Clark from York University to include tips on teaching using cases as well as suggestions on how to present material and use technology and other resources effectively, integrating the other supplements available to both students and instructors. This manual doesn't simply reinvent what's currently in the text; it helps the instructor make the material relevant and engaging to students.

ExamView® Computerized Test Bank

Create, deliver, and customize tests (both print and online) in minutes with this easy-to-use assessment and tutorial system. ExamView® offers both a Quick Test Wizard and an Online Test Wizard that guide you step-by-step through the process of creating tests, while its "what you see is what you get" capability allows you to see the test you are creating on the screen exactly as it will print or display online. You can build tests of up to 250 questions using up to 12 question types. Using *ExamView's* complete word-processing capabilities, you can enter an unlimited number of new questions or edit existing questions.

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Students and Instructors

Visit the website to accompany *Biology: Exploring the Diversity of Life*, First Canadian Edition, at <http://biologyedl.nelson.com>. This website contains quizzes, flashcards, weblinks, and more.

Using This Book

The following are things you will need to know in order to use this text and prosper in Biology.

Names

What's in a name? People are very attached to names—their own names, the names of other people, the names of flowers and food and cars, and so on. It is not surprising that biologists would also be concerned about names. Take, for example, our use of scientific names. Scientific names are always italicized and Latinized.

Castor canadensis Kuhl is the scientific name of the Canadian beaver. *Castor* is the genus name, *canadensis* is the species name, and Kuhl is the name of the person who described the species. “Beaver” by itself is not enough because there is a European beaver, *Castor fiber*, and an extinct giant beaver, *Castoides ohioensis*. Furthermore, common names can vary from place to place (*Myotis lucifugus* is sometimes known as the “little brown bat” or the “little brown myotis”).

Biologists prefer scientific names because the name (Latinized) tells you about the organism. There are strict rules about the derivation and use of scientific names. Common names are not so restricted, so they are not precise. For example, in *Myotis lucifugus*, *Myotis* means mouse-eared and *lucifugus* means flees the light; hence, this species is a mouse-eared bat that flees the light.

Birds can be an exception. There are accepted “standard” common names for birds. The American robin is *Turdus migratorius*. The common names for birds are usually capitalized because of the standardization. However, the common names of mammals are not capitalized, except for geographic names or patronyms (*geographic* = named

after a country; *patronym* = named after someone; e.g., Canadian beaver or Ord's kangaroo rat, respectively).

Although a few plants that have very broad distributions may have accepted standard common names (e.g., white spruce, *Picea glauca*), most plants have many common names. Furthermore, the same common name is often used for more than one species. Several species in the genus *Taraxacum* are referred to as “dandelion.” It is important to use the scientific names of plants to be sure that it is clear exactly which plant we mean. The scientific names of plants also tell us something about the plant. The scientific name for the weed quack grass, *Elymus repens*, tells us that this is a type of wild rye (*Elymus*) and that this particular species spreads or creeps (*repens* = creeping). Anyone who has tried to eliminate this plant from their garden or yard knows how it creeps! Unlike for animals, plant-naming rules forbid the use of the same word for both genus and species names for a plant; thus, although *Bison bison* is an acceptable scientific name for buffalo, such a name would never be accepted for a plant.

In this book, we present the scientific names of organisms when we mention them. We follow standard abbreviations; for example, although the full name of an organism is used the first time it is mentioned (e.g., *Castor canadensis*), subsequent references to that same organism abbreviate the genus name and provide the full species name (e.g., *C. canadensis*).

In some areas of biology, the standard representation is of the genus, for example, *Chlamydomonas*. In other cases, names are so commonly used that only the abbreviation may be used (e.g., *E. coli* for *Escherichia coli*).

Units

The units of measure used by biologists are standardized (metric or SI) units, used throughout the world in science.

Definitions

The science of biology is replete with specialized terms (sometimes referred to as “jargon”) used to communicate specific information. It follows that, as with scientific names, specialized terms increase the precision with which biologists communicate among themselves and with others. Be cautious about the use of terms because jargon can be a veneer of precision. When we encounter a “slippery” term (such as species or gene), we explain why one definition for all situations is not feasible.

Time

In this book, we use C.E. (Common Era) to refer to the years since year 1 and B.C.E. (Before the Common Era) to refer to years before that.

Geologists think of time over very long periods. A geologic time scale (see Table 1.1) shows that the age of Earth could be measured in years, but it's challenging to think of billions of years expressed in days (or hours, etc.). With the advent of using the decay rates of radioisotopes to measure the age of rocks, geologists adopted 1950 as the baseline, the “Present,” and the past is referred to as B.P. (“Before Present”). A notation of 30 000 years B.P. (^{14}C) indicates 30 000 years before 1950 using the ^{14}C method of dating.

Other dating systems are also used. Some archaeologists use PPNA (PrePottery Neolithic A, where A is the horizon or stratum). In deposits along the Euphrates River, 11 000 PPNA appears to be the same as 11 000

B.P. In this book, we use B.C.E. or B.P. as the time units, except when referring to events or species from more than 100 000 years ago. For those dates, we refer you to the geologic time scale (see Table 1.1 on page xiv).

Sources

Where does the information presented in a text or in class come from? What is the difference between what you read in a textbook or an encyclopedia and the material you see in a newspaper or tabloid? When the topic relates to science, the information should be based on material that has been published in a scholarly journal. In this context, “scholarly” refers to the process of review. Scholars submit their manuscripts reporting their research findings to the editor (or editorial board) of a journal. The editor, in turn, sends the manuscript out for

comment and review by recognized authorities in the field. The process is designed to ensure that what is published is as accurate and appropriate as possible. The review process sets the scholarly journal apart from the tabloid.

There are literally thousands of scholarly journals, which, together, publish millions of articles each year. Some journals are more influential than others, for example, *Science* and *Nature*. These two journals are published weekly and invariably contain new information of interest to biologists.

To collect information for this text, we have drawn on published works that have gone through the process of scholarly review. Specific references (citations) are provided, usually in the electronic resources designed to complement the book.

A citation is intended to make the information accessible. Although there are many different formats for citations, the important elements

include (in some order) the name(s) of the author(s), the date of publication, the title, and the publisher. When the source is published in a scholarly journal, the journal name, its volume number, and the pages are also provided. With the citation information, you can visit a library and locate the original source. This is true for both electronic (virtual) and real libraries.

Students of biology benefit by making it a habit to look at the most recent issues of their favourite scholarly journals and use them to keep abreast of new developments.

M. Brock Fenton
Heather Addy
Denis Maxwell
Tom Haffie
Ken Davey

London, Calgary and Toronto
February 2009

Table 1.1 The Geological Time Scale and Major Evolutionary Events

Eons (Duration drawn to scale)	Eon	Era	Period	Epoch	Millions of Years Ago	Major Evolutionary Events
Phanerozoic	Cenozoic			Holocene	0.01	
	Mesozoic		Quaternary	Pleistocene	1.7	Origin of humans; major glaciations
	Paleozoic			Pliocene	5.2	Origin of ape-like human ancestors
Proterozoic	Cenozoic			Miocene		Angiosperms and mammals further diversify and dominate terrestrial habitats
				Oligocene	23	Divergence of primates; origin of apes
				Eocene	33.4	Angiosperms and insects diversify; modern orders of mammals differentiate
				Paleocene	55	Grasslands and deciduous woodlands spread; modern birds and mammals diversify; continents approach current positions
					65	Many lineages diversify: angiosperms, insects, marine invertebrates, fishes, dinosaurs; asteroid impact causes mass extinction at end of period, eliminating dinosaurs and many other groups
	Mesozoic		Cretaceous		144	Gymnosperms abundant in terrestrial habitats; first angiosperms; modern fishes diversify; dinosaurs diversify and dominate terrestrial habitats; frogs, salamanders, lizards, and birds appear; continents continue to separate
			Jurassic		206	Predatory fishes and reptiles dominate oceans; gymnosperms dominate terrestrial habitats; radiation of dinosaurs; origin of mammals; Pangaea starts to break up; mass extinction at end of period
			Triassic		251	
	Phanerozoic					

Archaeon	Phanerozoic (continued)	Permian	290	Insects, amphibians, and reptiles abundant and diverse in swamp forests; some reptiles colonize oceans; fishes colonize freshwater habitats; continents coalesce into Pangaea, causing glaciation and decline in sea level; mass extinction at end of period eliminates 85% of species
		Carboniferous		Vascular plants form large swamp forests; first seed plants and flying insects; amphibians diversify; first reptiles appear
		Devonian	354	Terrestrial vascular plants diversify; fungi and invertebrates colonize land; first insects appear; first amphibians colonize land; major glaciation at end of period causes mass extinction, mostly of marine life
		Paleozoic	417	
		Silurian		Jawless fishes diversify; first jawed fishes; first vascular plants on land
		Ordovician	443	Major radiations of marine invertebrates and fishes; major glaciation at end of period causes mass extinction of marine life
			490	
		Cambrian		Diverse radiation of modern animal phyla (Cambrian explosion); simple marine communities
			543	
			2500	High concentration of oxygen in atmosphere; origin of aerobic metabolism; origin of eukaryotic cells; evolution and diversification of protists, fungi, soft-bodied animals
Archaeon				Evolution of prokaryotes, including anaerobic bacteria and photosynthetic bacteria; oxygen starts to accumulate in atmosphere
			3800	
Archaeon				Formation of Earth at start of era; Earth's crust, atmosphere, and oceans form; origin of life at end of era
			4600	

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It is never easy to be in the family of an academic scientist.

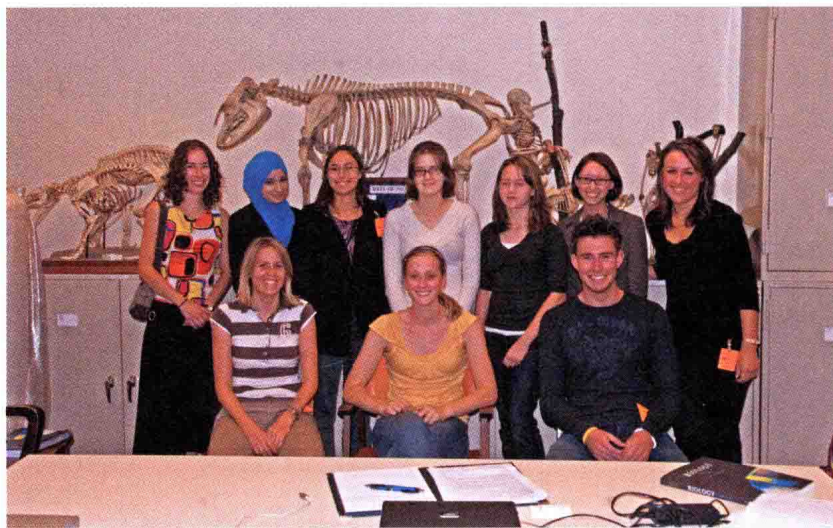
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