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Sixth Canadian Edition

Biology

Exploring the Diversity of Life

Fenton · Maxwell · Haffie · Milsom · Ellis · Riskin
Russell · Hertz · McMillan · Benington

Biology

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Exploring the Diversity of Life

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Biology: Exploring the Diversity of Life, **Sixth Canadian Edition**

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For, and because of,
our generations of students.

About the Canadian Authors

M. B. Fenton

M. B. (Brock) Fenton received his PhD 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 Western University. 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. Brock 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; Honorary 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 Sandford 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 topics of his research, which has been funded by the Natural Sciences and Engineering Research Council of Canada (NSERC). In November 2014, Brock was inducted as a Fellow of the Royal Society of Canada.

Denis Maxwell

Denis Maxwell received his PhD from the University of Western Ontario in 1995. His thesis focused on photosynthetic acclimation in green algae. Following his doctorate, 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, Denis moved in 2003 to the Department of Biology at Western University. Currently, he is Assistant Dean for the Faculty of Science, with a portfolio that includes Recruitment and First-Year Studies and outreach. Passionate about teaching in first-year, Denis has taught biology to over 40 000 students over the past 20 years.

Mitch Zimmer

Tom Haffie is a graduate of the University of Guelph and the University of Saskatchewan in the study of microbial genetics. Now retired, he devoted his 33-year career at Western University 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; he was an early adopter of computer animation in lectures; and, most recently, he led a deep blended redevelopment of introductory biology informed by a students-as-partners approach to collaborative course design. Tom was a founding force in the Western Biology Undergraduate Society (BUGS), the Open Consortium for Undergraduate Biology Educators (oCUBE), and the Western Conference on Science Education (WCSE). Tom's educational practice was honoured with several awards, including a Western University Students' Council Award for Excellence in Teaching, a Western University Edward G. Pleva Award for Excellence in Teaching, a Western University Fellowship in Teaching Innovation, a Western University Teaching Fellowship for Science, a Province of Ontario Award for Leadership in Faculty Teaching (LIFT), and a 3M National Teaching Fellowship for excellence in teaching.

Bridget Milsom

Bill Milsom received his PhD from the University of British Columbia and is a professor in UBC's Department of Zoology, where he has taught a variety of courses, including first-year biology, for over 40 years. His research interests include the evolutionary origins of respiratory processes and the adaptive changes in these processes that allow animals to exploit diverse environments. He examines respiratory and cardiovascular adaptations in vertebrate animals in rest, sleep, exercise, altitude, dormancy, hibernation, diving, and so on. Bill's research has been funded by NSERC, and he has received several academic awards and distinctions, including the Fry Medal of the Canadian Society of Zoologists, the August Krogh Distinguished Lectureship Award of the American Physiological Society, the Bidder Lecture of the Society for Experimental Biology, and the Izaak Walton Killam Award for Excellence in Mentoring. He received the Distinguished Service Award from the Canadian Society of Zoologists in recognition of contributions to the well-being of zoology in Canada beyond the call of duty. He has served as President of the Canadian Society of Zoologists and as President of the International Congress of Comparative Physiology and Biochemistry. His research contributes to our understanding of the mechanistic basis of biodiversity and the physiological costs of habitat selection.

Leoné Bellingan

Shona Ellis holds an MSc from the University of British Columbia and is an emeritus professor of teaching in the Botany Department. Raised on the central coast of British Columbia in Heiltsuk Territory, she developed a deep interest in forests and oceans. Shona's MSc research focused on tissue culture, phytochemistry, and plant anatomy, and she joined UBC's Department of Botany in 1998 as teaching faculty. During her time at UBC, Shona served as Director of the Combined Major in Science program and as Associate Head of Biology. She has taught a wide range of botany courses, including vascular plants, bryology, and plant systematics. She currently teaches through the Haida Gwaii Institute, where students engage directly with the natural environment of Haida Territory. Shona integrates Indigenous knowledge into her teaching, highlighting sustainable practices and diverse ways of knowing. Her approach attempts to encourage cultural competence and deepen students' understanding of their natural surroundings. An advocate of outdoor learning and an early adopter of online education, Shona has received two Killam Teaching Awards, a Dean of Science Service Award (UBC), UBC's Margaret Fulton Award for student development, and the Charles Edwin Bessey Teaching Award from the Botanical Society of America.

Dan Riskin

Shelby Riskin received her BA from Grinnell College in Iowa, where she was first exposed to the wonderful world of biological research, and her PhD from Brown University in a joint program with the Marine Biological Laboratory in Woods Hole, Massachusetts. Her dissertation focused on ecosystem-level biogeochemical consequences of conversion to agriculture in the Brazilian Amazon, the region of the world where deforestation and conversion to large-scale farming are happening most rapidly. Shelby, Associate Professor in the teaching stream at the University of Toronto, teaches a variety of undergraduate courses exploring ecology and conservation biology in the Ecology and Evolutionary Biology Department. She has won the Cheryl Regehr Early Career Teaching Award (U of T) and the Faculty of Arts & Science Outstanding Teaching Award–Early Career (U of T). Shelby is passionate about mentoring undergraduates through independent research projects and about teaching biology and ecology to students outside the Life Sciences—understanding the diversity of life is for everyone.

About the US Authors

Courtesy of Peter J. Russell

Peter J. Russell received his BSc in biology from the University of Sussex, England, in 1968 and his PhD in genetics from Cornell University in 1972. He has been a member of the Biology faculty of Reed College since 1972 and is currently Professor of Biology, Emeritus. Peter taught a section of the introductory biology course, a 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; the current edition is *iGenetics: A Molecular Approach.* Peter's research was in the area of molecular genetics, with a specific interest in characterizing the role of host genes in the replication of the RNA genome of a pathogenic plant virus and the expression of the genes of the virus; yeast was used as the model host. His research has been funded by agencies such as the National Institutes of Health, the National Science Foundation, the American Cancer Society, the Department of Defense, the Medical Research Foundation of Oregon, and the Murdoch Foundation. He has published his research in a variety of journals, including *Genetics, Journal of Bacteriology, Molecular and General Genetics, Nucleic Acids Research, Plasmid,* and *Molecular and Cellular Biology.* Peter has a long history of encouraging faculty research involving undergraduates, including cofounding the biology division of the Council on Undergraduate Research in 1985. He was Principal Investigator/Program Director of a National Science Foundation Award for the Integration of Research and Education (NSF–AIRE) to Reed College, 1998 to 2002.

Courtesy of Aaron Kinard

Paul E. Hertz was born and raised in New York City. He received a BA in biology from Stanford University in 1972, a master's degree in biology from Harvard University in 1973, and a PhD in biology from Harvard University in 1977. While completing field research for his doctorate, he served on the Biology faculty of the University of Puerto Rico at Rio Piedras. After spending two years as an Izaac Walton Killam Postdoctoral Fellow at Dalhousie University, Paul 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 the Claire Tow Professor of Biology in 2016. He received The Barnard Award for Excellence in Teaching in 2007. In addition to serving on numerous college committees, Paul chaired Barnard's Biology Department for eight years and served as Acting Provost and Dean of the Faculty from 2011 to 2012. He was also the founding Program Director of the Hughes Science Pipeline Project at Barnard, an undergraduate curriculum and research program funded continuously by the Howard Hughes Medical Institute, from 1992 to 2016. The Pipeline Project included the Intercollegiate Partnership, a program for local community-college students that facilitated their transfer to four-year colleges and universities. Since 2016, he has served as Director of the Science Pathways Scholars Program, which provides support and research opportunities to first-generation college students and students of colour at Barnard. He teaches one semester of the introductory sequence for biology majors and pre-professional students, lecture and laboratory courses in vertebrate zoology and ecology, and seminars that introduce first-year students to scientific research. Paul 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 and Puerto Rico. 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, Oecologia,* and *The Proceedings of the Royal Society*.

Courtesy of Beverly McMillan

Beverly McMillan holds undergraduate and graduate degrees from the University of California, Berkeley. She has worked extensively in educational and commercial publishing as an author, science writer, project manager, and multimedia content developer. In addition to her contributions to college textbooks, Beverly has written or coauthored multiple popular books on topics in natural history and human health and biology, as well as field guides to the flora and fauna of more than 20 US states. She has also created Web and print content for such clients as the US National Park Service, the Science Museum of Virginia, The Mariners' Museum, the San Francisco Exploratorium, the University of California system, and the Virginia Institute of Marine Science/College of William and Mary.

Courtesy of Joel H. Benington

Joel H. Benington received his BA from St. John's College in Annapolis, Maryland, in 1985 and his PhD in biology from Stanford University in 1992. He performed postdoctoral research at the UCLA and Stanford University until 1996. Since then, he has been a member of the Biology faculty of St. Bonaventure University, where he is currently Professor of Biology and Director of the Bioinformatics and Health and Society programs. He has twice served as Chair of the Department of Biology. During his entire time at St. Bonaventure University, he has taught one or both semesters of the general biology sequence for first-year life science majors. He also teaches upper-level Neurobiology, Genomics, and Evolution courses and has led a variety of seminar courses in the university's Honors Program. He has published his research in journals such as *Progress in Neurobiology, Brain Research, The American Journal of Physiology*, and *The Scientist.* In addition to laboratory research, he has published hypotheses concerning the role of sleep in brain energy metabolism, the functional relationship between REM sleep and non-REM sleep, and connections between sleep and learning. Joel's research has been funded by the National Institutes of Health, and he has served as Principal Investigator of a National Grid grant to support K–12 STEM education in Cattaraugus County, New York.

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Appendix A: Answers to Self-Test Questions A-1

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Get the most from your readings

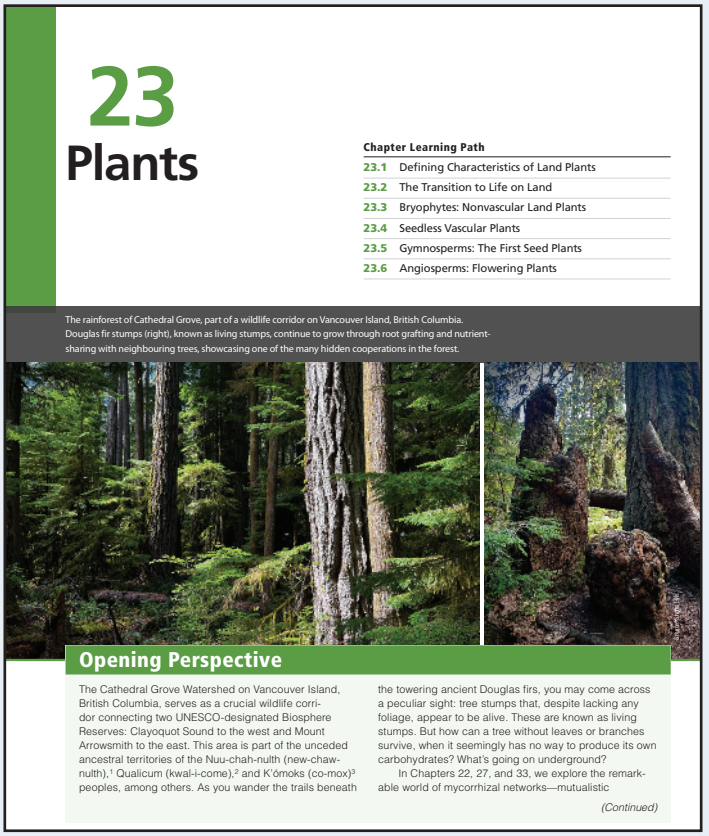
This textbook is a toolbox…

Although it's typical to think of this textbook as a resource to be read cover-to-cover, you will make the most of your learning experience by imagining it as a toolbox. Each of the features in the book are important learning tools that have been designed to work together to help you succeed. To optimize your learning experience, approach each learning tool with an awareness of its purpose and how it works with the others to make your learning more durable.

Content and Perspective

Read the **Opening Perspectives** to spark your interest with an engaging story that shows you how the contents of the chapter are relevant to biology and the world beyond. Opening Perspectives help you see the relevance of the material and allow you to make some personal connections to the concepts. This is often where Indigenous words are introduced.

Pronunciation is provided for **words in Indigenous languages** wherever possible, along with a footnote including the source of that pronunciation and additional context, if required. ▶



23
Plants

Chapter Learning Path

23.1 Defining Characteristics of Land Plants
23.2 The Transition to Life on Land
23.3 Bryophytes: Nonvascular Land Plants
23.4 Seedless Vascular Plants
23.5 Gymnosperms: The First Seed Plants
23.6 Angiosperms: Flowering Plants

The rainforest of Cathedral Grove, part of a wildlife corridor on Vancouver Island, British Columbia. Douglas fir stumps (right), known as living stumps, continue to grow through root grafting and nutrient-sharing with neighbouring trees, showcasing one of the many hidden cooperations in the forest.

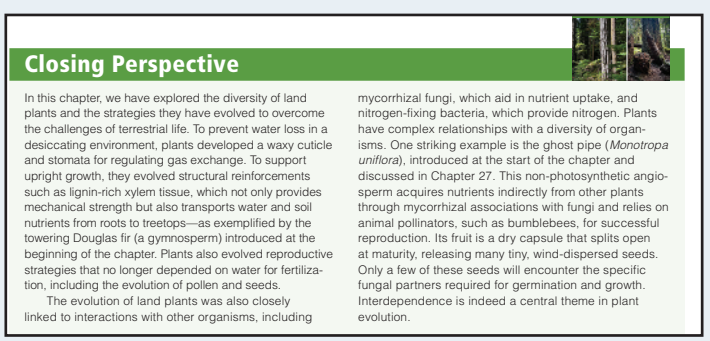
Opening Perspective

The Cathedral Grove Watershed on Vancouver Island, British Columbia, serves as a crucial wildlife corridor connecting two UNESCO-designated Biosphere Reserves: Clayoquot Sound to the west and Mount Arrowsmith to the east. This area is part of the unceded ancestral territories of the Nuu-chah-nulth (new-chaw-nulth),[1] Qualicum (kwal-i-come),[2] and K'ómoks (co-mox)[3] peoples, among others. As you wander the trails beneath the towering ancient Douglas firs, you may come across a peculiar sight: tree stumps that, despite lacking any foliage, appear to be alive. These are known as living stumps. But how can a tree without leaves or branches survive, when it seemingly has no way to produce its own carbohydrates? What's going on underground?

In Chapters 22, 27, and 33, we explore the remarkable world of mycorrhizal networks—mutualistic

(Continued)

The story in the Opening Perspective is revisited in the **Closing Perspective** at the end of each chapter.



Closing Perspective

In this chapter, we have explored the diversity of land plants and the strategies they have evolved to overcome the challenges of terrestrial life. To prevent water loss in a desiccating environment, plants developed a waxy cuticle and stomata for regulating gas exchange. To support upright growth, they evolved structural reinforcements such as lignin-rich xylem tissue, which not only provides mechanical strength but also transports water and soil nutrients from roots to treetops—as exemplified by the towering Douglas fir (a gymnosperm) introduced at the beginning of the chapter. Plants also evolved reproductive strategies that no longer depended on water for fertilization, including the evolution of pollen and seeds.

The evolution of land plants was also closely linked to interactions with other organisms, including mycorrhizal fungi, which aid in nutrient uptake, and nitrogen-fixing bacteria, which provide nitrogen. Plants have complex relationships with a diversity of organisms. One striking example is the ghost pipe (*Monotropa uniflora*), introduced at the start of the chapter and discussed in Chapter 27. This non-photosynthetic angiosperm acquires nutrients indirectly from other plants through mycorrhizal associations with fungi and relies on animal pollinators, such as bumblebees, for successful reproduction. Its fruit is a dry capsule that splits open at maturity, releasing many tiny, wind-dispersed seeds. Only a few of these seeds will encounter the specific fungal partners required for germination and growth. Interdependence is indeed a central theme in plant evolution.

Science in Real-Life Scenarios

Reinforce and expand your understanding of the scientific method and see how it is applied in real-life research scenarios with three types of research figures:

Observational Research figures show you actual research where biologists have tested hypotheses by comparing systems under varying natural circumstances. ▶

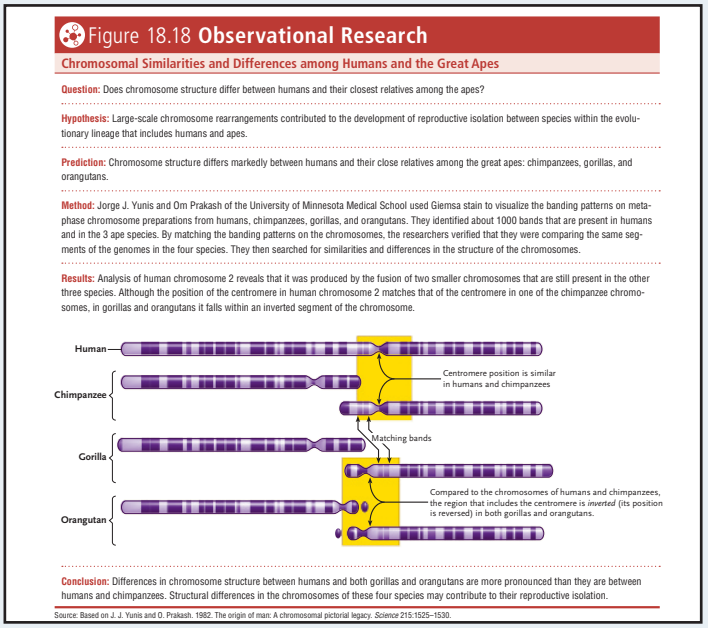


Figure 18.18 **Observational Research**

Chromosomal Similarities and Differences among Humans and the Great Apes

Question: Does chromosome structure differ between humans and their closest relatives among the apes?

Hypothesis: Large-scale chromosome rearrangements contributed to the development of reproductive isolation between species within the evolutionary lineage that includes humans and apes.

Prediction: Chromosome structure differs markedly between humans and their close relatives among the great apes: chimpanzees, gorillas, and orangutans.

Method: Jorge J. Yunis and Om Prakash of the University of Minnesota Medical School used Giemsa stain to visualize the banding patterns on metaphase chromosome preparations from humans, chimpanzees, gorillas, and orangutans. They identified about 1000 bands that are present in humans and in the 3 ape species. By matching the banding patterns on the chromosomes, the researchers verified that they were comparing the same segments of the genomes in the four species. They then searched for similarities and differences in the structure of the chromosomes.

Results: Analysis of human chromosome 2 reveals that it was produced by the fusion of two smaller chromosomes that are still present in the other three species. Although the position of the centromere in human chromosome 2 matches that of the centromere in one of the chimpanzee chromosomes, in gorillas and orangutans it falls within an inverted segment of the chromosome.

Conclusion: Differences in chromosome structure between humans and both gorillas and orangutans are more pronounced than they are between humans and chimpanzees. Structural differences in the chromosomes of these four species may contribute to their reproductive isolation.

Source: Based on J. J. Yunis and O. Prakash. 1982. The origin of man: A chromosomal pictorial legacy. *Science* 215:1525–1530.

Experimental Research figures show you studies where research used both experimental and control treatments—either in the laboratory or in the field—to test hypotheses or answer research questions by manipulating the system they studied. ▶

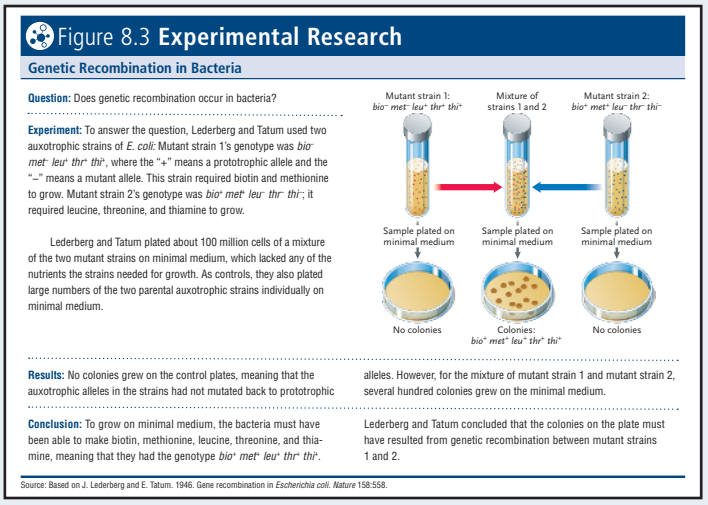


Figure 8.3 **Experimental Research**

Genetic Recombination in Bacteria

Question: Does genetic recombination occur in bacteria?

Experiment: To answer the question, Lederberg and Tatum used two auxotrophic strains of *E. coli:* Mutant strain 1's genotype was *bio⁻ met⁻ leu⁺ thr⁺ thi⁺*, where the "+" means a prototrophic allele and the "–" means a mutant allele. This strain required biotin and methionine to grow. Mutant strain 2's genotype was *bio⁺ met⁺ leu⁻ thr⁻ thi⁻*; it required leucine, threonine, and thiamine to grow.

Lederberg and Tatum plated about 100 million cells of a mixture of the two mutant strains on minimal medium, which lacked any of the nutrients the strains needed for growth. As controls, they also plated large numbers of the two parental auxotrophic strains individually on minimal medium.

Results: No colonies grew on the control plates, meaning that the auxotrophic alleles in the strains had not mutated back to prototrophic alleles. However, for the mixture of mutant strain 1 and mutant strain 2, several hundred colonies grew on the minimal medium.

Conclusion: To grow on minimal medium, the bacteria must have been able to make biotin, methionine, leucine, threonine, and thiamine, meaning that they had the genotype *bio⁺ met⁺ leu⁺ thr⁺ thi⁺*. Lederberg and Tatum concluded that the colonies on the plate must have resulted from genetic recombination between mutant strains 1 and 2.

Source: Based on J. Lederberg and E. Tatum. 1946. Gene recombination in *Escherichia coli*. *Nature* 158:558.

Research Method figures will show you examples of important techniques and lead you through the purpose of the techniques and lead you through the purpose of the technique and protocol, describing how scientists interpret the data generated. ▶

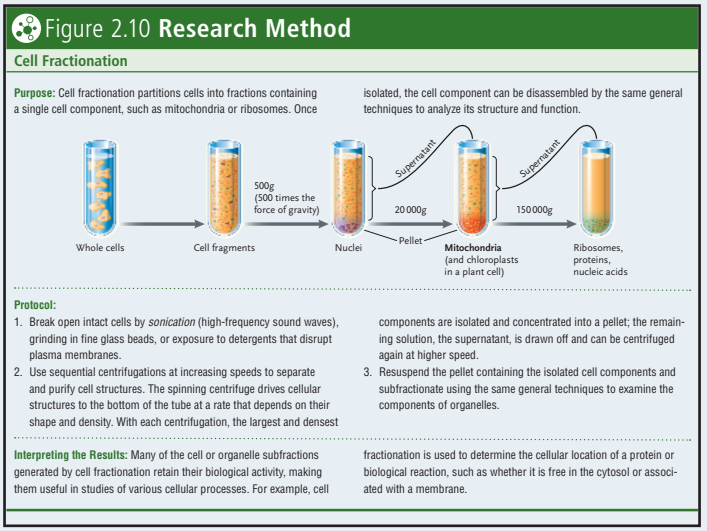


Figure 2.10 **Research Method**

Cell Fractionation

Purpose: Cell fractionation partitions cells into fractions containing a single cell component, such as mitochondria or ribosomes. Once isolated, the cell component can be disassembled by the same general techniques to analyze its structure and function.

Protocol:

1. Break open intact cells by *sonication* (high-frequency sound waves), grinding in fine glass beads, or exposure to detergents that disrupt plasma membranes.
2. Use sequential centrifugations at increasing speeds to separate and purify cell structures. The spinning centrifuge drives cellular structures to the bottom of the tube at a rate that depends on their shape and density. With each centrifugation, the largest and densest components are isolated and concentrated into a pellet; the remaining solution, the supernatant, is drawn off and can be centrifuged again at higher speed.
3. Resuspend the pellet containing the isolated cell components and subfractionate using the same general techniques to examine the components of organelles.

Interpreting the Results: Many of the cell or organelle subfractions generated by cell fractionation retain their biological activity, making them useful in studies of various cellular processes. For example, cell fractionation is used to determine the cellular location of a protein or biological reaction, such as whether it is free in the cytosol or associated with a membrane.

Refine, Review, Connect, and Correct

Pay careful attention to **Concept Fix** sections because they will help you identify and correct common misconceptions and misunderstandings. ▶

> **Concept Fix:** You may think that LUCA was the first form of life to exist on Earth, but that is not the case. Calling something the *last* common ancestor is like saying the *last* team to win the Stanley Cup; what we mean is the *most recent*. LUCA is the most recent ancestor that gave rise to all the organisms we see on Earth today. Given that LUCA was quite complex in both structure and function, it was likely to have been preceded by other, simpler forms of life (**Figure 1.20**). Also, as shown in Figure 1.20, it is likely that life arose more than once on the early Earth; each form perhaps having only some of the seven attributes we see in all forms of life today. For example, perhaps a form of life arose that did not use ATP as a common source of chemical energy, or perhaps never developed DNA as the repository of genetic information. The similarities across all domains of life present today indicate, however, that only one of these primitive life forms has descendants that survive today.

Use the **Pause and Review** questions as a checkpoint at the end of each major section to ensure that you have identified and understood the main ideas before moving on to the next section. If you have trouble answering these questions, go back to the reading to find the answer. These questions and answers are also available on the MindTap. ▶

Pause and Review

1. What is the *plasma membrane*, and what are its main functions?
2. Compare a golf ball with a basketball. Which has a higher surface area-to-volume ratio? Explain.
3. What is the difference between the word *prokaryote* and the term *prokaryotic cell*?
4. In what way is scanning electron microscopy different than transmission electron microscopy?

Organize your study time for each chapter using the **Chapter Summary** table. Review the chapter contents, see how key concepts connect to other chapters in the book, and test your understanding of the contents of each section with references to the relevant **Self-Test Questions**, organized by Bloom's Taxonomy. ▶

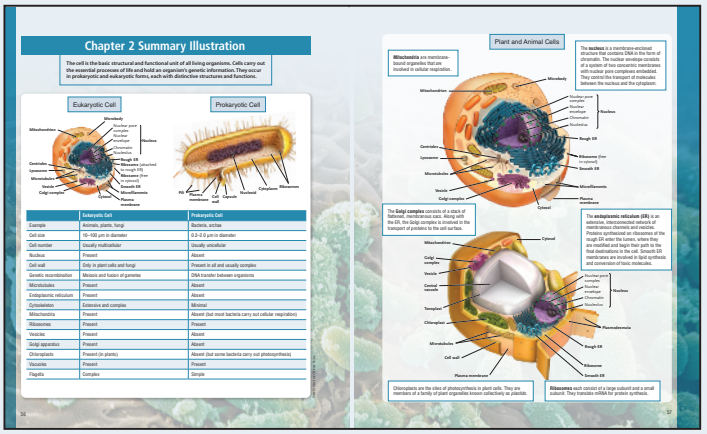
Chapter 2 Summary

The Cell

The cell is the fundamental unit of life.

Section Overview	Make a Connection	Self-Test Questions
2.1 Basic Features of Cell Structure and Function All cells contain DNA and a range of organelles and are surrounded by a lipid membrane. What Is Life?		1, 8, 11, 12, 13, 14
2.2 Prokaryotic Cells Bacteria and Archaea have distinct prokaryotic cell structure that includes DNA that is free in the cell.	See Chapter 20, *Bacteria and Archaea.*	2, 3
2.3 Eukaryotic Cells Eukaryotic cells are typically larger than prokaryotic cells, with DNA found within the nucleus and energy-transducing organelles.	See Chapter 2, *The Cell,* and Chapter 3, *Energy and Enzymes.*	4, 5, 7, 15
2.4 Specialized Structures of Plant Cells In addition to mitochondria, plant cells contain chloroplasts, vacuoles, and cell walls.	See chapters of Unit 7: *Systems and Processes—Plants.*	13
2.5 The Animal Cell Surface Animal cells have specialized structures that help hold them together, produce avenues of communication between cells, and organize body structures.	See chapters of Unit 8: *Systems and Processes—Animals.*	6, 13, 16
2.6 Evolution of the Eukaryotic Cell Eukaryotic cells have structural and functional complexity not found in prokaryotic cells. In addition to the nucleus, this includes mitochondria and chloroplasts that are descended from bacteria.		9, 10

Visualize the main concepts in the chapter with the **Summary Illustration.** ▶



Core Concepts at Your Fingertips

Need a refresher? The Purple Pages cover all the important background information about ways of knowing in biology, including foundational material in biology and chemistry in a handy reference section in the middle of the book. ▶

The Purple Pages

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- The Scientific Method R-2
- Testing a Hypothesis Is Central to the Scientific Method R-3
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- A Theory Is a Model of Reality R-5
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Ways of Knowing Biology

The knowledge that is made available in this textbook—the observations, theories, experimental results, analyses, generalizations, relationships and applications—represents the culmination of thousands of years of investigative activity carried out by countless curious people who questioned their place in the universe, constantly revising how they defined, understood, and related to the living world. We're going to take some time and summarize various investigative approaches used to improve our understanding of the world around us.

We'll look at how knowledge is gathered and ideas are tested, and then work our way through the hierarchy of complexity, starting from atoms and ending with the evolutionary and geologic timescales. Note that the different levels of complexity are human constructions; nature doesn't automatically fall into the categories we scientists create. Levels of complexity below atoms and above geologic timescales definitely exist, and there are tiers of complexity that can be found between the ones we highlight here.

Science

Experimental Versus Observational Science

When you think about doing science the first idea that probably comes to mind is carrying out an experiment. You carefully set up a control condition and then change one or more variables to determine how they affect what is being studied. By doing experiments you can establish a causal relationship between one or more specific variables and what you are studying (e.g., cause and effect). Although you may think that "science" and "experiment" are nearly synonymous, in some situations, the system under scientific study may be too large or too complex to conduct actual experiments. In astronomy, for example, one cannot manipulate stars and galaxies as if they were potted plants. Astronomy is considered an observational science, as are many research themes in ecology and evolutionary biology. Observational science starts by having a theoretical framework of understanding and, through the collection and analysis of data, refining that framework. Because observational scientists cannot manipulate specific variables and study their effects, they rely on sophisticated statistical tools to provide a method to infer pattern and probable cause from the collected data.

The Scientific Method

By the 19th century, researchers around the world were using the scientific method (see **Fig. R1**)—an investigative approach to acquiring knowledge in which scientists make observations about the natural world, develop working explanations about what they observe, and then test those explanations by collecting more information.

It can be hard today to realize today how revolutionary this approach to understanding the natural world was. The scientific method came up out of the more broad Age of Enlightenment during the 17th and 18th centuries which saw huge cultural and intellectual shifts. Instead of a general fear of the natural world and reliance on religious text, superstition, reason, and logic were embraced. The shift towards science and empirical evidence coincided with development of improved scientific tools (e.g. telescope and microscopes) and techniques that allowed one to more effectively study the natural world.

Application of the scientific method requires both curiosity and skepticism: successful scientists question the current state of our knowledge and challenge old concepts with new ideas and new observations. Explanations of natural phenomena must be backed up by objective evidence rooted in observation and measurement. Most importantly, scientists share their ideas and results by publishing their work.

The Chemical and Physical Foundations of Biology

Biology can be complex—incredibly complex! As a biology student there is so much to know and understand. This section is designed to help you with this complexity and understanding by going over some foundational topics that apply to many different areas of biology. Sure, biology is a stand-alone discipline, but as you will see in this section, it is built on fundamentals of chemistry and physics that are universal. For example, the formation and breakage of chemical bonds obey the same rules whether they are inside living cells or inside a rock. Understanding these fundamentals will provide you with a tool kit to help you on your journey through this textbook.

Emergent Properties

One very interesting aspect of biology relates to the term **emergent properties**: new functions arise through increasing complexity. In our physical world we all have the sense that combining things together leads to more elaborate structure with increased complexity in a kind of hierarchy. If we start with simple atoms that make up all matter, there are only a few properties and they exert their effect in a very small, localized way (e.g., electronegativity). Moving up the hierarchy, the interaction of atoms leads to the formation of chemical bonds. These different bonds are new properties that emerge when atoms combine to form compounds. Molecules are a form of a compound in which atoms are joined using fairly fixed bonds. As the hierarchy progresses we have macromolecules such as DNA and proteins. An emergent property of DNA is that it carries information in the way the A, G, C, and Ts are ordered. From macromolecules we move up through organelles, cells, tissues, organs, and, finally, organisms. Then moving even further to organisms interacting with one another and the physical world in ecosystems and the biosphere as a whole. The key feature of emergent properties is that this property of a system is something that the individual components that define the system do not possess. Here are some examples: the cell, which is the foundation of all life has the property of being alive, which is something its constituent components (DNA, protein, organelles) do not by themselves possess. The brain is another example. The traits of consciousness, cognition, behavior emerge from the collective organization of neural networks that individual brain cells (e.g. neuron's) do not possess.

The Organization of Matter

Any substance in the universe that has mass and occupies space is defined as **matter**. The fundamental scientific concepts that explain how matter is organized in biological systems are no different from those for non-living forms of matter. Living organisms are built from the same chemical building blocks as non-living systems and abide by the same fundamental laws of chemistry and physics. Hence, a basic understanding of how all matter is organized is important for a complete picture of the structure and function of organisms.

Elements and Compounds

All matter is composed of elements. An **element** is a pure substance composed of only one type of atom. Ninety-two different elements occur naturally on Earth. Living organisms are composed of about 25 elements, with only four elements—carbon, hydrogen, oxygen, and nitrogen—accounting for more than 96% of the mass of an organism. Seven other elements—calcium, phosphorus, potassium, sulfur, sodium, chlorine, and magnesium—contribute most of the remaining 4%. The proportions by mass of different elements differ markedly in ocean water, the human body, Earth's crust, and grains as shown in **Fig. R4**.

Preface

Welcome to the exploration of the diversity of life! The main goal of this textbook is to guide students on a journey of discovery about life's diversity across interconnected levels of organization, ranging from molecules to genes, from cells to organs, and from species to ecosystems. Along the way, we will explore many questions about the mechanisms underlying diversity as well as the importance of maintaining diversity for all species, including our own.

Diverse Perspectives…

With this edition of *Biology: Exploring the Diversity of Life*, we continue our deliberate and ongoing process of opening this resource to a wider range of sources, voices, and perspectives devoted to a more fulsome understanding of the interconnected biological world. We offer this edition as part of our continuing effort to respond to the Truth and Reconciliation Commission of Canada's (TRC) Calls to Action and to the United Nations Declaration on the Rights of Indigenous Peoples (UNDRIP). The truth of the relationship between science and Indigenous Peoples in Canada has often, unfortunately, been one of oppression and exploitation. The racism that fuelled the colonization of the land that is now Canada influenced all aspects of social life, including the delivery of education and the conduct of science. The residential school system used education as a tool of cultural assimilation, with tragic effects on Indigenous communities that continue to play out today. Science education was rarely provided in these schools, thus limiting the capacity for Indigenous Peoples to effectively interact with scientists representing government, industry, or academia. A significant underrepresentation of Indigenous Peoples in Canadian science- and technology-related careers continues to this day.

In many Indigenous communities, science and research have been viewed fearfully as tools of oppression. Some scientists have engaged in unethical practices in Indigenous communities that have resulted in deliberate harm to people and/or their environment. Traditional Ecological Knowledge (TEK) and technologies have been taken, and sometimes commercialized, without consent from or benefit to the original Knowledge-Keeping Elders and their communities.

Part of the work of reconciliation in this edition is a contribution to the ongoing shift in perspectives of science from those of Eurocentrism (i.e., science as emanating from, and largely exclusive to, European nations and their current or former colonies) to a more open, decolonized, "multi-science" perspective that acknowledges all Indigenous Peoples as having scientific knowledge of the natural world, albeit through their own cultural lenses. This perspective is rooted in the accumulated empirical knowledge that has been generated by thriving and prosperous Indigenous Peoples through their observations of and relationships with natural phenomena over millennia.

This book is one result of deepening relationships among the primary authors and their professional colleagues, the editorial and production teams at Cengage Canada, students of biology, Indigenous Elders, scholars, and advisors. At the outset of this journey, the author team participated in Ceremony with Indigenous advisors, experiencing first-hand Indigenous cultural practices. Our purpose was to acknowledge the collective desire for the success of this project as an example of and inspiration for reconciliatory learning. With open minds and hearts, we reaffirm our commitment to creating a meeting place where scientists of all backgrounds can tell their stories.

As an author, advisory, and production team including both settlers and Indigenous People, we want our work to contribute to reconciliation and improved relations among settlers and First Nations, Inuit, and Métis Peoples. As educators, we want our classes to be widely accessible. We understand that this means making efforts to increase the level of safety felt by Indigenous students and others who have been excluded in our science education system. As authors of educational resources, we want to promote innovative, holistic, effective teaching and learning approaches that support teaching and learning by all students and instructors. As global citizens, we want to promote collaboration in harnessing the creative power of a wide variety of perspectives in the face of global challenges.

An emphasis on the diversity of life…

At first glance, the riot of life that animates the biosphere is overwhelming. One way to begin to make sense of this diversity in a textbook is to divide it into manageable sections on the basis of similarities or differences. We examine how different organisms solve the common problems of finding nutrients, energy, and mates on the third rock from our Sun.

Evolution provides a powerful conceptual lens for viewing and understanding the roots and history of the diversity of living things. What basic evolutionary principles inform the relationships among life forms regardless of their different body plans, habitats, or life histories?

We will demonstrate how an understanding of evolution deepens our appreciation of the changes and variation we observe in organisms. Whether the focus is the conversion of free-living prokaryotic organisms into mitochondria and chloroplasts inside

our cells or the lack of eyes in cave fish, evolutionary mechanisms such as natural selection can explain the extraordinary biodiversity of our planet.

Examining how biological systems function is another theme pervading this text and underlying the concept of diversity. We have intentionally tried to include examples that will stretch the imagination, from sea slugs that steal chloroplasts for use as solar panels, to the molecular basis of high-altitude adaptations in deer mice, to adaptive radiation of viruses. In each case, we examine how biologists have explored and assessed the inner workings of organisms, spanning topics from gene regulation to the complexities of digesting cellulose.

Problem-solving is another key theme that runs throughout the book. Whether the topic is gene therapy to treat a disease in people, preventing harmful algal blooms, or reducing the incidence of human cancer, both the challenges and solutions are grounded in biology. We will explore large problems facing planet Earth, some of the social implications that arise from them, and the biological activity underlying them.

Emphasizing the big picture…

While many biology textbooks use the first few chapters to review fundamentals of chemistry and biochemistry as well as information on the scientific method, this book immediately engages in some of the excitement, mystery, and controversy that is modern biology right up front in Chapter 1. Important background information appears in the centre of the book as a distinct reference section entitled ***The Purple Pages***. With their purple borders, these pages are distinct, easy to find, and enable foundational information to be readily identifiable and accessible. *The Purple Pages* begin with a look at Ways of Knowing Biology, including both science and Indigenous Ways of Knowing. The Chemical and Physical Foundations of Biology explores the concepts of how atoms, molecules, and macromolecules are connected through the theme of "emergent properties." By considering how the "stuff of life" interrelates as a function of increasing complexity rather than just memorizing the attributes of individual items, the student can better grasp *why* biology works the way it does rather than be awed by how much information we know about it. In the MindTap, *The Purple Pages* are placed at top of the learning path for easy navigation.

Throughout this book, we have highlighted the work of Indigenous and non-Indigenous scientists in Canada and elsewhere, and we present many examples and biological concepts in Canadian contexts.

Focusing on research to engage the living world through a scientific lens…

A primary goal of this book is to evoke and sustain the student's curiosity about biology, rather than dulling it with a mountain of disconnected facts. We help the student develop the mental habits of scientists and a fascination with the living world by conveying our passion for biological research. We explore *what biologists know* about the living world as well as *how they know it* and *what they still need to learn*. In doing so, we hope to encourage students to accept the challenge and become biologists, posing and answering important new questions through their own innovative research. For those who pursue other careers, we hope that they will leave their introductory—and perhaps only—biology course armed with intellectual skills that will enable them to evaluate future knowledge with a critical eye.

In this book, we introduce students to a biologist's "way of learning." Research biologists constantly integrate new observations, hypotheses, questions, experiments, and insights with existing knowledge and ideas. To help students engage with the world as biologists do, we must not simply introduce them to the current state of knowledge, we must also foster an appreciation of the historical context within which those ideas developed and identify the future directions that biological research is likely to take.

Because advances in science occur against a background of research, we also give students a feel for how biologists of the past formulated basic knowledge in the field. By fostering an appreciation of such discoveries, given the information and theories available to scientists in their own time, we can help students understand the successes and limitations of what we consider cutting-edge today. This historical perspective also encourages them to view biology as a dynamic intellectual enterprise, not just a collection of facts and generalities to be memorized.

We have endeavoured to make the science of biology come alive by describing how biologists formulate hypotheses and evaluate them using hard-won data can sometimes reveal only part of the story, and how scientific findings often raise more questions than they answer. Our exploration of Patrick Keeling's research is a case in point. His team has conducted groundbreaking work uncovering the hidden diversity and ecological significance of microbial eukaryotes in marine environments, as highlighted in Chapter 21 in the discussion of diplonemids. Through the use of advanced molecular and genomic techniques, this research has reshaped our understanding of ocean food webs and eukaryotic evolution.

Although students might prefer simply to learn the right answer to a question, we encourage them to embrace the unknown—those gaps in knowledge that create opportunities for further research. An appreciation of what biologists do *not* yet know may draw them into the field. And by defining *why* scientists do not understand interesting phenomena, we encourage them to think critically about possible solutions and to follow paths dictated by your own curiosity. We hope that this approach will encourage students to make biology a part of their

daily life by having informal discussions and debates about new scientific discoveries with members of their personal and academic communities.

In summary, we have applied our collective experience as teachers, researchers, and writers to create a text that provides accessible explanations of fundamental concepts from an evolutionary perspective that binds all the biological sciences. We hope that students are as captivated by the biological world as we are and are drawn from one chapter to another. We also hope students will use MindTap and other resources to broaden their search for understanding and, most importantly, observe and enjoy the diversity of life around them.

M. Brock Fenton
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London, Toronto, and Vancouver
January 2026

New to This Edition

This section highlights the changes we made to enhance the effectiveness of *Biology: Exploring the Diversity of Life,* sixth Canadian edition. The most obvious change to the new edition is our fresh new interior design. Created with the student experience in mind, the interior design of the sixth Canadian edition boasts some important pedagogical enhancements:

- New **Unit Openers** situate students and list the chapters in each unit.
- The **Chapter Learning Path** provides a mini table of contents at the beginning of each chapter.
- **Opening Perspectives** contextualize the content of each chapter and are revisited in the **Closing Perspectives** at the end of the chapter.
- Figures are now presented in boxes so that it is clear where they begin and end.
- Study Break questions are now **Pause and Review** questions, intended to help students pause after each major section of the book and ensure they understand what they have read.
- The new **Chapter Summary** section is designed to help students review and test their understanding of the chapter contents:
  - The **Summary Table** provides an overview of each section in the chapter, connects the concepts in that section with other sections and chapters in the book, and provides a correlation between each section of the book and the Self-Test Questions at the end of each chapter.
  - The **Summary Illustration** helps students visualize the important concepts in each chapter.
  - **Self-Test Questions** help students review the chapter material in a sequence that moves from basic knowledge of factual material to more challenging and sophisticated applications of that knowledge to novel situations.
- Over 100 new and revised figures and over 200 new photos.

Inspiring Students

We begin the sixth Canadian edition with the question "What is *life*?" Chapter 1: Defining Life and Its Origins starts with the recognition that the origin and definition of *life* are widely considered to be one of the great mysteries and challenges in science.

The chapter explores why it is so difficult to arrive at a simple definition of life. In this edition we expand on the discussion from the previous edition by providing a broad Indigenous view of what it means to be living, and framing that within narrower scientific definitions of life that are often discipline specific. After providing a less contentious list of the characteristics of life, the chapter explores what we know about how life developed some 4 billion years ago. This opening chapter situates biology as a method of inquiry that has at its core curiosity and a sense of awe.

Diversity in Ways of Knowing and Learning

The sixth Canadian edition is part of our contribution to the ongoing shift in perspectives of science from Eurocentrism to a more open, decolonized, "multi-science" perspective that acknowledges all Indigenous Peoples as having scientific knowledge of the natural world through their own cultural lenses. Throughout the book, we have made connections to Indigenous Ways of Knowing and Learning in the Opening Perspectives. We have included specific examples from First Nations, Inuit, and Métis communities, using the traditional names of Indigenous Nations and the traditional languages of Indigenous groups. Where Indigenous words appear in each chapter we have endeavored to include a pronunciation guide and a footnote indicating the context and provenance of that word, along with a link to an audio recording of the word wherever possible.

We have attempted to cite research from Indigenous researchers; research where Indigenous communities have partnered with the researchers; and research where Indigenous knowledge has informed, enhanced, or changed our understanding of a particular phenomenon. To authentically represent concepts and stories that we have been given permission to share, we have committed to ensuring that any associated artwork is created by an Indigenous artist.

The Purple Pages: Your Ultimate Reference for the Foundations of Biology

The Purple Pages are now divided into two distinct sections. Ways of Knowing Biology outlines the fundamentals of the scientific method, and Indigenous Ways of Knowing, including new sections on communicating scientific findings and applications of Indigenous ecological knowledge. The Chemical and Physical Foundations of Biology contains foundational material in biology and chemistry so that students can refresh their memory and brush up on the concepts that underpin this course. This handy reference has been redesigned with its own table of contents and numbered figures so that students and instructors can navigate this material with ease.

Points of Interest in Each Chapter

Every chapter has been updated to ensure currency of information and key chapters have been extensively revised to provide a full treatment of the subject matter that reflects new developments in these specialized fields.

Chapter 1: Defining Life and Its Origins

- Discussion of defining life now includes an Indigenous perspective.

- Expanded and deepened the discussion and model of LUCA
- Moved content related to endosymbiosis to Chapter 2

Chapter 2: The Cell

- New Opening Perspective related to the discovery of HIV-AIDS
- New section (with figures) providing a historical context on Cell Theory
- New sections related to endosymbiosis and the rise of the eukaryotic cell
- Improved discussion of major eukaryotic features

Chapter 3: Energy and Enzymes

- Revised and improved discussion of the basics of thermodynamics

Chapter 4: Cell Membranes and Signalling

- Revised and improved discussion of integral membrane proteins and membrane transport more generally.

Chapter 5: Cellular Respiration

- Revised and reworked section on chemical basis of respiration

Chapter 6: Photosynthesis

- Revised to provide a stronger linkage between photosynthesis and respiration

Chapter 7: Cell Cycles

- Revised Opening Perspective

Chapter 9: The Chromosomal Basis of Inheritance

- Revised chapter to improve overall clarity, including clarification of a gene defined as the unit of inheritance

Chapter 11: DNA Structure, Replication, and Repair

- Revised and improved discussion on the historical perspective related to the elucidation of DNA as the hereditary molecule

Chapter 12: Gene Structure and Expression

- Important new section that provides a molecular definition of "gene"
- Refined discussion of the three major classes of genes (rRNA, tRNA, and mRNA genes).

Chapter 13: Regulation of Gene Expression

- Revised Opening Perspective to emphasize the importance of changes in gene expression over gene content in phenotype

Chapter 14: DNA Technologies

- Updates made to the usage of a range of DNA technologies in diagnostics

Chapter 15: Genomes

- Clarified description of the basics of DNA sequencing
- Improved linkage between evolution and genome changes

Chapter 16: Evolution: The Development of the Theory

- Clarified and expanded discussion of natural selection
- Enhanced discussion of common misconceptions about natural selection and evolution
- New figures added to increase understanding of evolutionary concepts

Chapter 17: Microevolution: Changes within Populations

- New Opening Perspective featuring *Moksgm'ol* (mach-kmo)[1] or Spirit Bear, to frame the chapter
- Clarified the discussion of ring species and outbreeding
- Revised and replaced a suite of figures to increase interpretability and understanding

Chapter 18: Speciation and Macroevolution

- Moved the discussion of binomial nomenclature to the beginning of this chapter (from Chapter 19) to improve the flow and the order in which information is presented
- Incorporated new Canadian examples, such as caribou as the example of a species with many subspecies
- Revised figures to improve the visual contribution to learning in this chapter

Chapter 19: Systematics and Phylogenetics: Revealing the Tree of Life

- Reordered information to improve the walk through the concepts
- Streamlined and reorganized information on naming conventions
- Added and revised figures for increased visual learning

Chapter 20: Bacteria and Archaea

- Expanded emphasis on the metabolic diversity, ecological significance, and environmental adaptability of bacteria and archaea to better contextualize their symbiotic relationships with eukaryotes
- New summary illustration providing an integrative comparison between bacteria and archaea

Chapter 21: Protists

- Closing Perspective updated and revised to include both Indigenous and ecological perspectives, such as the role of diatoms in biofilms important to migratory bird habitats
- Added new insights into protist classification within the eukaryotic supergroups, based on an interview with Dr. Patrick Keeling
- Revised Summary Illustration to incorporate figures by Keeling and Eglit, supplemented with additional information on photosynthetic, heterotrophic, mixotrophic, and endosymbiotic protists

[1]Pronunciation guide provided by Jenn Ashton of Sḵwx̱wú7mesh First Nation, March 2025. Recording of the spoken word can be found on FirstVoices, a website of The First Peoples' Cultural Council. Sgüüx̱s (Kitasoo – Xai'xai Stewardship Authority) https://www.firstvoices.com/

Chapter 22: Fungi
- Updated to reflect current fungal taxonomy
- New Summary Illustration provides an overview of fungal nutrition, supported by relevant images

Chapter 23: Plants
- Expanded on the concept of the underground network, including mycorrhizae and root grafting
- Added information on Sphagnum moss as an ecosystem engineer and its ecological significance
- New discussion on the monophyly of leafy and thalloid liverworts
- Integrated recent archaeological and botanical findings from SGang Gwaay Llnagaay (Haida Gwaii), including the ecological impact of deer introduction by settlers on native plant communities

Chapter 24: Animals
- New Pause and Review and Self-Test Questions

Chapter 25: Viruses, Viroids, and Prions: Infectious Biological Particles
- Recognition of Canadian Nobel Laureate Dr. Michael Houghton's contribution to the discovery of the hepatitis C virus
- New information on the monkeypox (mpox) virus, a pathogen responsible for multiple pandemics over the past two millennia
- Updated content on COVID-19
- New discussion about global scientific collaboration post-COVID-19 to monitor and prepare for future pandemic threats

Chapter 26: Population Ecology
- Revised Opening Perspective
- Revised discussion of human population growth

Chapter 27: Species Interactions and Community Ecology
- New Opening Perspective about ghost plant and species interactions
- Revised the introduction to energy flows for clarity and to remove any redundancy with the Ecosystems chapter

Chapter 28: Ecosystems
- Revised the definitions and first discussion of primary producers and photosynthesis
- Updated the discussions of nutrient cycles and climate change
- Updated climate change data throughout

Chapter 29: Conservation of Biodiversity
- Simplified the Opening Perspective about the extinct passenger pigeon and revised to review and define extinctions and mass extinctions
- Revised and updated the discussion of acid rain, lifting it up as an example of conservation action and success

Chapter 30: Organization of the Plant Body
- New discussion on the cultural and historical importance of Western red cedar and monument poles to the Haida Nation, with a focus on SG̲ang Gwaay Llnagaay (a UNESCO World Heritage Site)
- New discussion of the 2024 Haida Title Lands Agreement, recognizing Haida sovereignty over Haida Gwaii and advancing reconciliation and conservation efforts
- Updated Summary Illustration with additional detail

Chapter 31: Transport in Plants
- Enhanced discussion of CAM photosynthesis
- Revised and improved the Summary Illustration

Chapter 32: Reproduction and Development in Flowering Plants
- Updated Opening Perspective now includes a section on the "Three Sisters" and the role of angiosperms in Indigenous agricultural practices.
- Example from the Fabaceae (pea family) now used to illustrate plant and floral structure as well as seed germination.

Chapter 33: Plant Nutrition
- Expanded coverage of mycorrhizal associations, detailing different types and the benefits to symbionts beyond nutrient exchange
- Enhanced section on mycoheterotrophy
- Added plants now included to Figure 33.4 (soil horizons) to illustrate interactions
- Summary Illustration updated to reflect mycorrhizal interactions, nitrogen-fixing bacteria, and decomposition processes
- New chapter summary illustration offering an overview of various types of symbioses and alternative nutrient acquisition strategies

Chapter 34: Plant Signals and Responses to the Environment
- Explanation added on the role of salicylic acid in triggering a systemic immune response in plants, providing long-term protection against a wide range of pathogens.

Chapter 35: Introduction to Animal Organization and Physiology
- Revised Opening and Closing Perspectives dealing with seasonal changes and presence and abundance of species followed by Indigenous Peoples for generations
- Added new Self-Test Questions.

Chapter 36: Animal Nutrition
- Revised Opening Perspective dealing with diet changes as humans evolved and migrated. Includes how Indigenous communities developed a knowledge of malnutrition and how to cure scurvy
- New section on human diets
- Expanded the conclusion of the Experimental Research figure

Chapter 37: Gas Exchange: The Respiratory System

- Revised Opening Perspective dealing with how the space between inhalation and exhalation is sacred to some Indigenous communities

Chapter 38: Internal Transport: The Circulatory System

- Revised Opening Perspective about importance of references to the heart in Unangan culture of the Indigenous people of the Aleutian Islands, Alaska
- New Experimental Research Figure: Demonstration That the Heart Is Myogenic
- New material on comparison of cardiovascular risk profiles among ethnic groups
- New material on cardiovascular risk profiles in Indigenous groups and how traditional Indigenous cultural activities have a reduced risk of cardiometabolic disease

Chapter 39: Regulation of the Internal Environment: Water, Solutes, and Temperature

- New Experimental Research Figure: Demonstration That Avian Salt Glands Vary as a Function of Diet
- New discussion of differences in cold and heat tolerance across different populations

Chapter 40: Control of Animal Processes: Endocrine Control

- Expanded discussion of diabetes to include semaglutides (Ozempic and Wegovy)

Chapter 41: Animal Reproduction and Development

- Expanded on the Concept Fix on twins
- Expanded section on controlling reproduction
- NEW section discussing sex versus gender

Chapter 42: Control of Animal Processes: Neural Control

- Revised Closing Perspective that includes a discussion of colour change in cephalopods and arctic foxes as examples of neural control
- New Pause and Review questions added
- New Self-Test Questions added

Chapter 44: Animal Behaviour and Responses to the Environment

- Revised Opening Perspective related to hunting societies relying on knowledge of behaviour of animals for survival
- New discussion of the role of Traditional Ecological Knowledge (TEK) in partnership with researchers enriching knowledge of animal behaviour

Chapter 45: Defences against Disease

- Clarified key concepts, including inflammatory response, variolation, chronic inflammation, and plant immunity
- Enhanced emphasis on how the inflammatory response primes the adaptive immune system
- Updated content on COVID-19 and vaccines
- New section on emerging disease threats and considerations for future pandemics

A Note Regarding Inclusion, Equity, and Diversity

Cengage Canada has a critical role to play in providing quality, inclusive learning materials that empower progress. We believe in the importance of inclusion, equity, and diversity to advance the way students learn inside and outside the classroom. Research demonstrates that students who experience a sense of belonging in class are more successful in making meaning out of, and finding relevance in, the learning content they encounter. To improve both the learning process and outcomes, our materials seek to affirm the fullness of human diversity that students bring to the classroom, including Indigenous and other racialized groups, and identities across spectrums of linguistic, age, ability, sexual, and gender diversity. We also actively strive for equity and inclusivity in content through the solicitation, promotion, recruitment, valuation, and incorporation of different views and experiences. Our efforts centre on recognizing and reducing implicit biases, being intentional in our learning design, and including diverse sources of scholarship and authorship.

Student and Instructor Resources

Cengage MindTap

MindTap

MindTap is the online learning platform that gives you complete control to craft a personalized, engaging learning experience that challenges your students, builds their confidence, and elevates their performance. *MindTap* delivers access to an eTextbook, study tools, a variety of auto-graded assessment options, and student performance reporting.

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Instructor Resources

CCTA

The **Cengage Canada Teaching Advantage** program delivers research-based instructor resources that promote student engagement and higher-order thinking to enable the success of Canadian students and educators. With a focus on quality, all of our resources are copyedited, and questions are reviewed to ensure the content is accurate and relevant to the new edition.

The following instructor resources have been created for *Biology: Exploring the Diversity of Life*, Sixth Canadian Edition. Access these tools for customizing lectures and presentations at https://faculty.cengage.com/.

cognero® Full-Circle Assessment®

Test Bank

The test bank is available on a cloud-based platform. **Testing Powered by Cognero®** is a secure online testing system that allows instructors to author, edit, and manage test-bank content from anywhere Internet access is available. No special installations or downloads are needed, and the desktop-inspired interface, with its drop-down menus and familiar, intuitive tools, allows instructors to create and manage tests with ease. Multiple test versions can be created in an instant, and content can be imported from or exported into other systems. Tests can be delivered from a learning management system, the classroom, or wherever an instructor chooses.

This resource was revised and updated by Jessica Li, University of British Columbia. It includes over 2,600 multiple-choice questions written according to Cengage Canada Teaching Advantage for Authors guidelines for effective construction and development of higher-order questions. Also included are over 250 true or false questions, over 100 matching questions, and over 150 short-answer questions.

PowerPoint

Microsoft® PowerPoint® lecture slides were revised and updated by Lyndsay Fraser. There is an average of 45 slides per chapter, many featuring key figures, tables, and photographs from Biology: Exploring the Diversity of Life, 6th Canadian Edition. CCTA principles of clear design and engaging content have been incorporated throughout, making it simple for instructors to customize the deck for their courses.

Instructor Guide

This resource was revised and updated by Sobia Iqbal of Wilfrid Laurier University, and includes a preface/introduction written by Heidi Swanson of Wilfrid Laurier University, and Gùdia (Mary Jane) Johnson of Lhu'ààn Mân Keyí, Kluane First Nation, Burwash Landing, YT, Canada, with contributions by Roy Golsteyn of the University of Lethbridge. This guide offers instructors advice on how to create positive classroom environments that foster student-centred, deep, and active learning. Drawing on their extensive experience as instructors, the authors offer advice on how to increase student motivation, overcome barriers to learning, develop engagement strategies, and tailor assessment tools to your pedagogical goals.

Image Library

This resource consists of digital copies of figures, tables, and photographs used in the book. Instructors may use the images in these PowerPoint slides to create their own presentations.

Acknowledgments

As we publish the 6th edition, we acknowledge that the author team has seen a few changes over the years. We appreciate the tremendous contribution of Tom Haffie, whose authorship of the chapters comprising Unit 2 (Genes) and Unit 3 (DNA and Gene Expression) over the first five editions of the book have undergone light updates for this edition. With heavy hearts, we remember Todd Nickle (1967–2021) for his contributions to earlier editions. Todd's work included chapters on respiration, photosynthesis, and the cell cycle, as well as The Purple Pages. We also thank Richard Walker at the University of Calgary and Ken Davey at York University, who began this journey with us but were unable to continue. And we are very grateful to Heather Addy of the University of Calgary for her significant contributions to the first three editions.

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When we started on the journey of adding Indigenous Ways of Knowing to the book, we benefited greatly from the assistance of Jonathan Ferrier, Assistant Professor in the Department of Biology of Dalhousie University, Jeff Baker, Indigenous Engagement and Education Specialist at the Resilience Institute, and Erin Hodson, Educational Developer in the Teaching Excellence and Innovation Team at Wilfrid Laurier University. The three of you have been a source of inspiration, guidance, and encouragement.

With great appreciation we acknowledge the contributions of Chester Lawson and Elroy White of the Haíłzaqv (pronunciation guide)[2] (Heiltsuk) Territory, Central Coast, British Columbia. Chester (Q'vúmkviá)[3] is Yím'ás[4] (Haíłzaqv hereditary chief). He is a community artist and retired teacher. Chester has been creating art for over 70 years in several traditional and western art forms. Elroy (Q'íxitasu)[5] is Yímás[6] a potlatch historian, and an archaeologist (Central Coast Archeology). We are grateful for the cultural knowledge he generously shared about seaweed harvest and processing and his work on assessing culturally modified trees (CMTs). As an archaeologist, Elroy approaches his research in a way that combines academia and oral history; he calls this approach *Mnuxvit*[7] (to unite/become one).

We are deeply grateful for the leadership and guidance of the late Linda Isaac, of the Alderville First Nation. Linda's steady and insightful counsel played an essential role in both the planning and development of the 5th Canadian edition.

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[1]Pronunciation guide provided by Jenn Ashton Skwxwú7mesh (December 2025).

[2,3,4,5,6,7]For more information on the Haíłzaqv language, see https://www.firstvoices.com/, and select "Explore Languages"

work on endosymbiosis, horizontal gene transfer, and plastid diversity has reshaped our understanding of the tree of life and earned him major honours, including his recent election to the U.S. National Academy of Sciences—one of the highest honours in the scientific community.

We were very fortunate to have the assistance of some extraordinary instructors of biology and Indigenous advisors from across Canada who provided us with feedback that helped shape this textbook into what you see before you. As such, we would like to say a very special thank you to our Editorial Advisory Board:

Jennifer Ashton of the Sḵwx̱wú7mesh (Squamish Nation)
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Paul Fam was a warm friend and a truly fearless leader through previous editions of this text. The direction and emphasis of previous editions of this book was sparked by his energy and enthusiasm and carries his vision forward.

It is never easy to be the family of an academic scientist. We are especially grateful to our families for their sustained support over the course of our careers, particularly during those times when our attentions were fully captivated by bacteria, algae, fungi, parasites, snakes, geese, or bats. Saying "yes" to a textbook project means saying "no" to a variety of other pursuits. We appreciate the patience and understanding of those closest to us that enabled the temporary reallocation of considerable time from other endeavours and relationships.

Many of our colleagues have contributed to our development as teachers and scholars by acting as mentors, collaborators, and, on occasion, "worthy opponents." Like all teachers, we owe particular gratitude to our students. They have gathered with us around the discipline of biology, sharing their potent blend of enthusiasm and curiosity, and leaving us energized and optimistic for the future.

1

Defining Life and Its Origins

Chapter Learning Path

1.1	What Is Life?
1.2	The Chemical Origins of Life
1.3	The First Life
1.4	The Tree of Life
1.5	The Fossil Record

Perseverance landed on Mars in February 2021 to search for signs of life.

Triff/Shutterstock.com

Opening Perspective

Finding evidence of life somewhere beyond Earth would be the most profound discovery in human history. In February 2021, the NASA rover *Perseverance* landed on Mars and, along with characterizing the Martian climate and geology, it is looking for signs of life. The landing site of *Perseverance* is the 45-km-wide Jezero Crater

(Continued)

that a few billion years ago was the site of a large lake. As the rover slowly roams over the Jezero lakebed, it employs an instrument with the acronym SHERLOC that uses laser light to detect within the sediments the presence of organic molecules that, on Earth, we know are produced only through biological activity. Detailed analysis of samples that *Perseverance* collects will have to wait until they are sent back to Earth as part of a Mars Sample Return mission that will take place in the 2030s.

A hope of many astrobiologists is that *Perseverance* comes across a geological feature that can only be attributed to the activity of ancient microbial life. On Earth, a good example of that is *stromatolites*, which are sediment formations generated by the action of photosynthetic bacteria. But therein lies one of the problems with searching for life elsewhere: we only know about life on Earth, and maybe life on other planets is very different. And then, of course, what is *life* anyway? It is actually really hard to come up with a simple and widely accepted definition. As we continue to search for life elsewhere, our understanding of how life developed on Earth is getting better through both a better understanding of ancient geology and laboratory experiments.

1.1 What Is Life?

Picture a frog sitting in a pond, slowly shifting its head to follow the movements of an insect flying nearby (**Figure 1.1**). We instinctively know that the frog is alive and the water is not. But why don't we consider water alive? The atoms found in living and non-living entities are the same. The oxygen and hydrogen atoms, for example, aren't any different within cells than they are in a pool of water or a rock. As well, living cells may be extraordinary things but they abide by the same fundamental laws of chemistry and physics as the non-living world. Before we embark on a discussion of the characteristics of life and how life may have started billions of years ago, it would be helpful if we had a clear notion of what distinguishes something that is living from something that is not living.

1.1a Why Life Is Hard to Define

Biology is the study of life, and the purpose of *Biology: Exploring the Diversity of Life* is to provide you with an introduction to many aspects of living things: from the unique features of biological molecules like DNA and proteins, reaching outward to different cell types, the huge diversity of organisms, to the interconnectedness between organisms that define ecosystems.

Figure 1.1 **Northern leopard frog resting in a pond**

Alexander Sviridov/Shutterstock.com

While we can describe in considerable detail the features that one organism has compared to another, and certainly we can think about the things that living things can do that non-living things can't do—you might find it surprising that we struggle to come up with a clear definition of what life actually is and what it is not. Doesn't that seem a little odd? If you think about the other core disciplines taught in first year, chemistry and physics, most of the fundamental concepts in those disciplines are well defined, even if they may not necessarily be easy to learn.

A major hurdle in defining life is the pursuit of a concept that is universal. Ideally, such a definition should resonate with both scientists and non-scientists and be applicable across disciplines. However, definitions of life are deeply influenced by the perspectives and values of those creating them. Indigenous worldviews, for example, emphasize the interconnectedness and reciprocity of all living things, often extending the notion of life beyond what science considers living—acknowledging relationships with plants, animals, water, and even rocks as vital and meaningful. This perspective encourages us to explore questions about what it means to exist in balance with the natural world, challenging the boundaries between living and non-living.

Looking more closely at the scientific view of life, one of the first people to take a crack at defining *life* was Aristotle, who mentioned that it is something that "grows, is self-sustaining and reproduces." This seems like a pretty solid start; the ability to make more of itself seems a central feature of all forms of life. Another central feature of all known life is the cell. Peering into primitive microscopes in the mid-1600s, Robert Hooke and his contemporaries noticed that plant and animal tissues are made up of cells. As we will discuss in the next chapter, the cell is the smallest unit of life and new cells are formed only when other cells divide. So, for a long time, if we couldn't strictly define life, at least everyone could agree that the cell is a universally accepted characteristic of

life. Both of these early ideas have problems. Fire is also something that grows and is self-sustaining and reproduces but scientists do not consider it living. As well, the cell is a feature of all life on Earth, but couldn't we envision life elsewhere in the galaxy that is not based on the cell? I think we could.

The growing field of artificial life (Alife) is leading to important insights that may help with defining life. Alife areas of study include computer software (e.g., computer viruses) and hardware (e.g., robotics) as well as the subdiscipline of synthetic biology, which is focused on building artificial cells or rudimentary biochemical pathways in the laboratory. Instead of tackling the huge complexity of a living cell, Alife researchers are addressing key questions about what it means to be living by understanding simpler systems that each possess some of the characteristics of living systems, but not all. For example, computer viruses can replicate as well as change (e.g., evolve) over time as they infect and move across computer systems. Biochemists have developed DNA molecules that can replicate in artificial cells and actually accumulate mutations over time. Recently it has been shown that energy from light can be used to drive life-like, self-organizing behaviours in particles that the scientists referred to as "living crystals."

In 1992, a committee of NASA scientists put forward a definition of *life* as: "a self-sustaining chemical system capable of Darwinian evolution." By "self-sustaining chemical system" the committee was making reference to the ability of all forms of life to bring in molecules from the surroundings and use energy to transform those molecules into different forms necessary for life. The term, "Darwinian evolution" means that life undergoes the process of natural selection—variation in hereditary material arises randomly, resulting in having beneficial traits certain individuals that increase their reproductive success.

As shown in **Figure 1.2**, a difficulty with defining life comes from differences in perspective. An Alife researcher, for example, thinks about life in some ways that are different from the NASA scientist trying to detect signs of life on a distant planet. Furthermore, incorporating Indigenous knowledge alongside these scientific perspectives (Figure 1.2) challenges us to think even more broadly about what it means to be alive—recognizing life not just as a set of traits but as a system shaped by relationships, interdependence, and adaptation.

1.1b Viruses Complicate Our Idea of Life

Whether or not viruses should be considered life has been an argument that goes back to when they were first visualized early in the 20th century after the electron microscope was invented. Viruses, which we will discuss in detail in Chapter 25, lack their own metabolism, and thus by the NASA definition are not self-sustaining systems. For example, they don't undergo cellular respiration or synthesize their own proteins. But, like traditional forms of cellular life, they do contain nucleic acid and replicate—and they can evolve by natural selection. But the issue with viruses is that they can't complete their lifecycle without invading living cells, whether that be a bacterium or a human (**Figure 1.3**). Taking up residence within living cells is required for a virus because it does not have its own protein-making factories—ribosomes and key enzymes required for viral replication. Because of this last fact, many scientists put viruses clearly in the "not life" camp. If viruses are not considered life because they are parasitic and require a living host, what about *Rickettsia*? This genus of bacteria is considered to be alive despite the fact that, like viruses, it can only grow within host cells. Most bacteria can be cultured in the laboratory on artificial growth media, but so far this has not been possible for *Rickettsia*.

Things became more complicated on the virus front in 1992 with the discovery of a virus initially thought to be a bacterium. Named *mimivirus* for "mimicking microbe," no one had ever

Figure 1.2 Different perspectives of life

The Indigenous view of life is the broadest and includes relationships between all aspects of the natural world, including plants, animals, water, and rocks. The NASA definition of life is widely accepted across many branches of science. Some, but not all aspects of this definition are found in systems being studied by artificial life researchers.

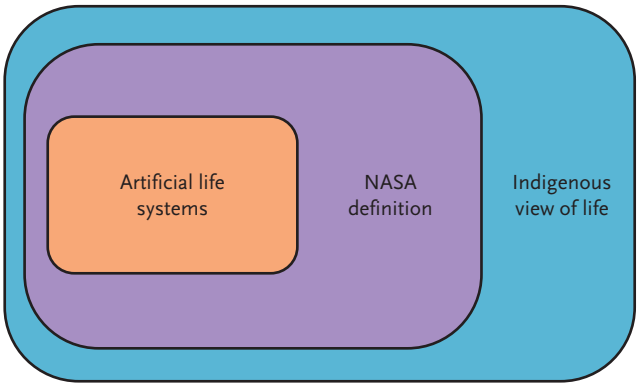
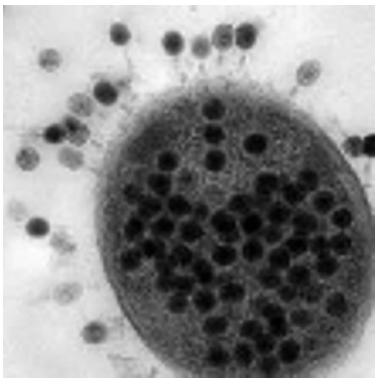


Figure 1.3 Bacteriophage infecting a bacterium

Notice the bacteriophages on the cell surface as well as inside the bacterium. A bacteriophage is a type of virus and has some characteristics of an organism but not others.



Courtesy of John Wertz, Yale University

observed a virus that was so large you could visualize it using conventional light microscopy. Its DNA genome, at 1.2 million base pairs, is 30 times larger than the genome found in a typical virus and larger than many bacterial genomes. The mimivirus genome codes for over 900 proteins, many of them associated with functions never before seen in a virus. This includes proteins central to protein synthesis and metabolism, two hallmarks of life. However, like other viruses, mimivirus is still dependent upon host cell ribosomes for protein synthesis. Clearly, if mimivirus is not allowed to be a member of the life "club," it stands right outside the door.

1.1c Five Characteristics Shared by All Life

Coming up with a universally accepted definition of life has proven to be very difficult. In fact, a growing number of researchers reject the need for a common definition of life but rather want a "theory of living systems" that can fully describe life (its origins and characteristics) without forcing a strict definition. Others argue that, since we have yet to discover life on another planet, trying to strictly define life is silly because we simply don't understand enough about it.

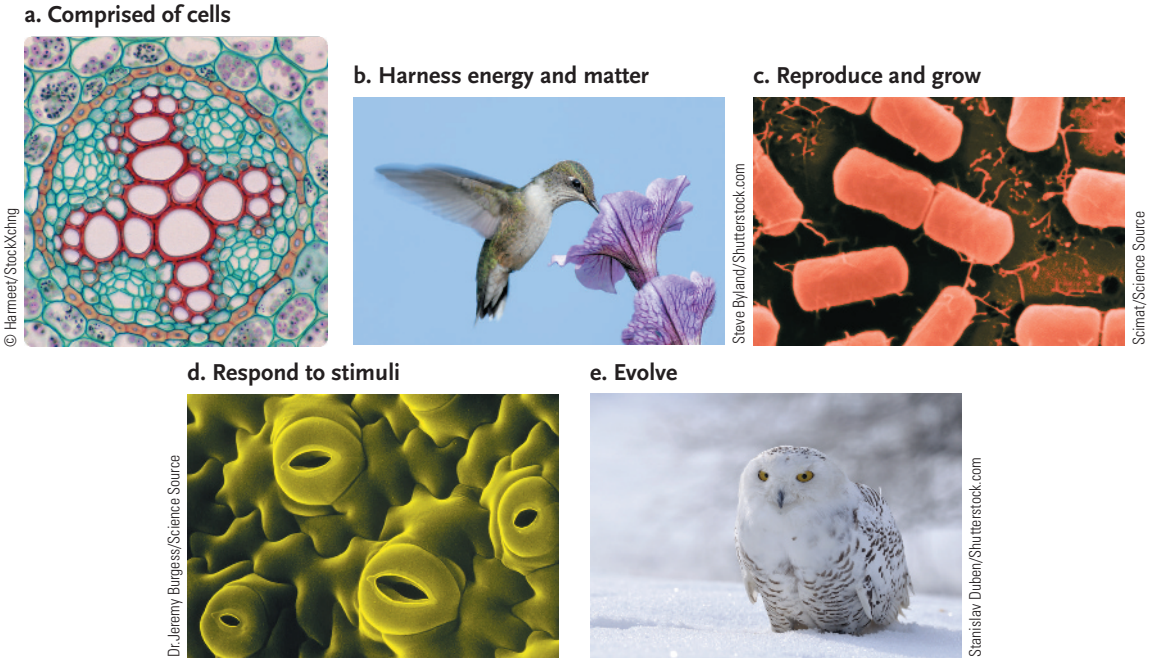
For now, we need to make a compromise. While we can use the word *entity* to include a wide range of self-replicating and evolving systems (e.g., viruses, computer programs), we are going to reserve the word *organism* for forms of life that possess the following five core characteristics and it is the structure, function, and interactions among organisms that will hold our attention through the next 44 chapters of this textbook (**Figure 1.4**).

Organisms Are Composed of Cells

The cell is the smallest unit of life. You can't have life without the cell and the only way you get a new cell is by an older cell dividing into two. While some organisms are comprised of billions of cells often organized into different tissues (e.g., muscles of animals, roots of plants), some organisms are comprised of only a single cell (e.g., many bacteria and protists). Cells can look wildly different; some have adapted over billions of years to specific environments or to specific roles (compare a long thin neuron to a chloroplast-packed leaf cell). Yet behind this diversity, all cells share some core unifying features. This includes the plasma membrane (often called the cell membrane). Inside the plasma membrane you will find an array of organelles, some of which are found universally across all life (e.g., the protein-making factories, ribosomes) while others (e.g., nuclei, chloroplasts, mitochondria) are found only in certain cells. Exploring the components of cells is the focus of the next chapter.

Figure 1.4 **Although it is hard to strictly define life, all organisms on Earth display these five fundamental characteristics.**

(a) *Comprised of cells.* The cell is the fundamental unit of life. Here is a cross-section through a plant root showing different cell types. **(b)** *Harness energy and matter.* Like this hummingbird, all forms of life acquire energy and matter from the environment and use them to maintain their highly ordered state. **(c)** *Reproduce and grow.* Organisms reproduce giving rise to offspring that grow and develop into adults. Here, some of the bacteria have just divided into progeny cells. **(d)** *Respond to stimuli.* Organisms can make adjustments to their structure, function, and behaviour in response to changes to the external environment. A plant can adjust the size of the pores (*stomata*) on the surface of its leaves to regulate CO_2 uptake and water by the leaf. **(e)** *Evolve.* Populations of living organisms change over the course of generations to become better adapted to their environment. The snowy owl illustrates this perfectly.



Organisms Exchange Energy and Matter with the Environment

In Chapter 3 we will discuss how organisms are thermodynamically open systems: they are constantly bringing in energy and matter from their surroundings and releasing other forms of energy and matter back into the environment. It seems obvious that organisms need to do this in order to do the work associated with growing bigger and moving around, for example. But, in fact, most of the energy and matter is needed simply to maintain the highly ordered state required to stay alive. Like everything else, biological molecules and structures (e.g., DNA, proteins, membranes) are constantly breaking down and new ones need to be made using the matter and energy cells bring in from outside.

Organisms Reproduce and Grow

All organisms are part of an unbroken chain of life that began billions of years ago. This chain continues today through reproduction, the process by which parental organisms produce offspring. Offspring resemble their parents because the parents pass copies of their DNA to their offspring. The transmission of DNA (that is, genetic information) from one generation to the next is called inheritance, which is discussed in detail in Chapters 9–15.

Reproduction is closely tied to growth. With multicellular organisms, an increase in organism size (e.g., growth) is the result of an increase in the size of individual cells along with an increase in the number of cells (e.g., the process of cell division). The coordination of these events is referred to as the cell cycle and is a focus of Chapter 7. In single-celled organisms such as a bacterium, growth and reproduction are synonymous. Reproduction occurs when the parental cell divides into two cells and as a result growth occurs. Another feature of multicellular organisms that is related to growth is the process of development, which is a series of programmed changes encoded in DNA, through which plants (see Chapter 32) and animals (see Chapter 41) move from an embryonic state to maturity.

Life Can Respond to Stimuli

Organisms are not static objects but rather they can make adjustments to their structure, function, and behaviour in response to changes to the external environment. These adjustments can happen over time scales of seconds to years. These changes require organisms to sense changes in the environment (e.g., plants can sense a change in light intensity and animals can sense sound). The goal of many of these adjustments is for the organism to maintain a relatively constant internal state to compensate for when external conditions change. We refer to this process as homeostasis, which is particularly well studied in animals, as discussed in Chapter 35.

Organisms Can Evolve

The four traits listed above are true of an individual organism. But the ability to evolve is not something one organism can do; it's a trait that is true only of a population of individuals of a particular species. Evolution is so central to biology that it takes four chapters (Chapters 16–19) to cover all the different aspects, from early thinking about how evolution occurred through to understanding the relationships between organisms. One common mechanism of evolution is natural selection. In natural selection, random mutations, or changes, to DNA result in offspring within a population being better able to survive and reproduce than others, leading a population expressing the favourable trait in a greater proportion with each passing generation. This results in the population as a whole being better able to grow and reproduce in a particular environment over many generations, leading to what we refer to as evolutionary adaptation. As we will discuss at length later in the textbook, evolution results in changes to gene structure and function and the development of novel traits, and can lead to the emergence of new species.

Pause and Review

1. Why is it difficult to arrive at a definition for *life*?
2. Why is a virus often considered not to be alive?

1.2 The Chemical Origins of Life

One of the principles of what is referred to as "cell theory" is that living cells arise only from the growth and division of other pre-existing living cells. This has been true for billions of years, yet there must have been a time when this was not the case. There must have been a time when no cells existed—when there was no life. It is thought that, over the course of millions of years, cells with the characteristics of life arose out of a mixture of molecules that existed on early Earth. In this section, we present hypotheses for how biologically important molecules could have been synthesized on early Earth before life developed.

1.2a Biologically Important Molecules Can Be Synthesized outside Living Cells

All organisms are composed of four classes of organic macromolecules: nucleic acids, proteins, lipids, and polysaccharides (see *The Purple Pages* for an overview of organic molecules). Today, different types of macromolecules are synthesized within cells by a

diversity of biochemical pathways. But if at least some macromolecules were essential for the development of the earliest forms of life, then they must have been made on Earth before there was life. The synthesis of organic molecules in the absence of life is referred to as *abiotic synthesis*. Scientists today have a good understanding of how this likely occurred.

The earliest forms of life developed about 4 billion years ago, which is 600 million years after Earth formed; at that time the planet was vastly different from what it is today. The atmosphere of 4 billion years ago probably contained an abundance of water vapour from the evaporation of water at the hot surface, as well as large quantities of hydrogen (H_2), carbon dioxide (CO_2), ammonia (NH_3), and methane (CH_4). You might be surprised to know there was almost no oxygen (O_2) in the early atmosphere. As we will learn in Chapter 6, the O_2 in the atmosphere is a byproduct of photosynthesis.

In the 1920s, two scientists, Aleksandr Oparin and John Haldane, independently proposed that organic molecules essential to the formation of life could have formed in the atmosphere of early Earth. A critical aspect of what is known as the *Oparin–Haldane hypothesis* is that the early atmosphere was a *reducing atmosphere* because of the presence of large concentrations of molecules such as hydrogen, methane, and ammonia and the absence of oxygen (O_2). In the presence of an energy source, these molecules would readily react with one another, producing larger, electron-rich molecules.

In comparison to the proposed reducing atmosphere of early Earth, today's atmosphere is classified as an *oxidizing atmosphere*. The presence of high levels of oxygen prevents complex, electron-rich molecules from being formed and persisting. Oxygen (O_2) is a particularly strong oxidizing molecule: it takes electrons from other molecules (oxidizes them) and those electrons along with hydrogen results in O_2 being chemically reduced to water (H_2O). In addition to allowing for the buildup of electron-rich molecules, the lack of oxygen in the young atmosphere also meant that there was no ozone (O_3) layer, a part of the upper atmosphere that today reflects ultraviolet (UV) radiation from the Sun back to space before it reaches Earth's surface. The ozone layer only developed after O_2 levels in the atmosphere began to increase. Both Oparin and Haldane hypothesized that, without the ozone layer, the energetic UV light was able to reach the lower atmosphere and, along with abundant lightning, provided the energy needed to drive the formation of biologically important organic molecules.

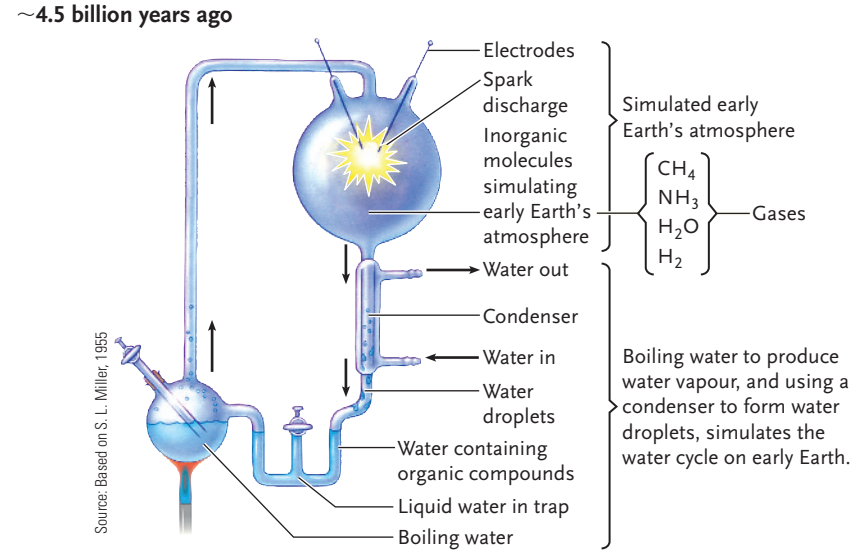
Experimental evidence in support of the Oparin–Haldane hypothesis came in 1952, when Stanley Miller (a graduate student in the laboratory of Harold Urey at the University of Chicago) created a laboratory simulation of a reducing atmosphere. Miller mixed the gasses hydrogen, methane, and ammonia in a closed apparatus and exposed the gases to an energy source in the form of continuously sparking electrodes (**Figure 1.5**). Water vapour was added to the "atmosphere" in one part of the apparatus and subsequently condensed back into water by cooling in another part. After running the experiment for one week, Miller found dissolved in the condensed water a large assortment of organic compounds, including urea, acetic acid, and an assortment of amino acids. In fact, as much as 15% of the carbon that was originally in the methane (CH_4) at the start of the experiment ended up in molecules that are common in living organisms.

Other chemicals have been tested as reactants in the Miller–Urey apparatus, including hydrogen cyanide (HCN) and formaldehyde (CH_2O), which are also considered to have been present in the primitive atmosphere. When cyanide and formaldehyde were added to the simulated atmosphere in the apparatus, all the building blocks of complex biological molecules were produced: amino acids (the building blocks of proteins); fatty acids (a component of lipids); **purine** and **pyrimidine** nucleotides (components of nucleic acids); and a range of sugars such as glyceraldehyde, ribose, glucose, and fructose.

In the decades since the first Miller–Urey experiment, considerable debate has developed in the scientific community over whether Earth's atmosphere held enough methane and ammonia for it to be considered a reducing atmosphere. Some geologists have suggested that, based on analysis of volcanic activity, the atmosphere of early Earth contained other gases that made it probably somewhat less reactive. Later in this chapter we will discuss

Figure 1.5 The Miller–Urey experiment

Using this apparatus, Stanley Miller, a graduate student, demonstrated that organic molecules can be synthesized under conditions simulating primordial Earth.



how the oceans may also be a likely place where abiotic synthesis took place. Regardless of the lingering debates, the significance of the Miller–Urey experiment cannot be overstated: It was the first experiment to demonstrate the abiotic formation of molecules critical to life, such as amino acids, nucleotides, and simple sugars, and it showed that they could be produced relatively easily. This remarkable finding laid the groundwork for further research into the origins of life.

1.2b Many Biological Molecules Come in Two Forms

Take a look at your left hand and compare it with your right one. The two hands seem to be identical—same number of fingers, in the same locations on each hand. Well, not so fast—they are in fact, different in a very fundamental way. You cannot lay one hand perfectly on top of the other (with both palms facing up). Your two hands represent a familiar example of a type of asymmetry called **chirality**. An item is chiral if it cannot be superimposed on its mirror image (Figure 1.6). Just like your hands, chiral molecules come in pairs. The two molecules have identical chemical properties (e.g., same chemical composition, molecular mass) but they differ in how the chemical groups are arranged.

It was the French chemist (and later microbiologist) Louis Pasteur who discovered chemical chirality and is now considered the father of the chemistry specialty called crystallography. While observing crystals of a pure compound under a microscope he noticed that each crystal has a tiny facet on one of its edges oriented sometimes to the right and sometimes to the left. Using tweezers, Pasteur painstakingly separated the crystals into two groups. He went on to discover that the two groups could be distinguished by how they interact with polarized light. Some molecules caused polarized light to rotate clockwise (denoted D for dextrorotatory) and others caused polarized light to rotate counterclockwise (denoted L for levorotatory).

One can readily synthesize a particular amino acid or simple sugar in a chemistry laboratory and what you get out is a perfect ratio of 50% of the D form of the molecule and 50% of the L form—what is referred to as a *racemic* mixture. In fact, that is what the Miller–Urey experiment produced, equal amounts of both. What is surprising is this is not what happens in living cells. The biosynthetic pathways within cells that produce amino acids only make L amino acids, and sugar biosynthetic pathways only make the D form. Furthermore, it is only these specific forms of the molecules that can be used for metabolic or biosynthetic reactions. For example, it is only the amino acid L-glycine that can be incorporated into a growing protein strand, and only D-ribose (a sugar) can be used in the synthesis of RNA.

So why is it that living cells only make and use one of the two chiral forms. The answer lies in the specificity of biological processes. The enzymes and receptors that need to bind precisely with specific molecules only accept one of the two chiral forms (Figure 1.7). You have experienced this specificity yourself when you've tried to put a left-hand glove on your right hand—it just doesn't fit. This tendency of living cells to only synthesize and use one chiral form of a molecule is termed *homochirality*. The answer to *how* homochirality evolved is still widely studied but *why* it evolved is easier to think about. Let's consider the two chiral forms of a molecule, each being a substrate of a specific enzyme. Because enzyme binding is very precise, the cell would need to synthesize two slightly differently shaped enzymes (see Figure 1.7), and since enzymes are proteins, that would mean the need for two different genes. Multiply this one example by the many thousands of enzymes, receptors, and substrate molecules within a cell and you quickly

Figure 1.6 Chirality

Just like your left and right hand, many biological molecules come in two forms that are not superimposable on each other. An example of a chiral molecule is the amino acid alanine, pictured here. The two forms differ in how the chemical groups are arranged around the central carbon atom.

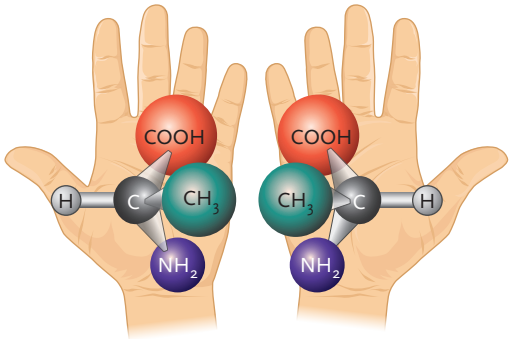
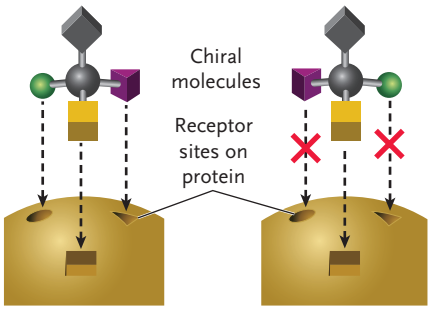


Figure 1.7 Homochirality

In biology, usually only one of the two chiral forms of a molecule are synthesized and functional. As shown here, this homochirality is because of the specificity that occurs between molecules and their binding sites on receptors or enzyme active sites.

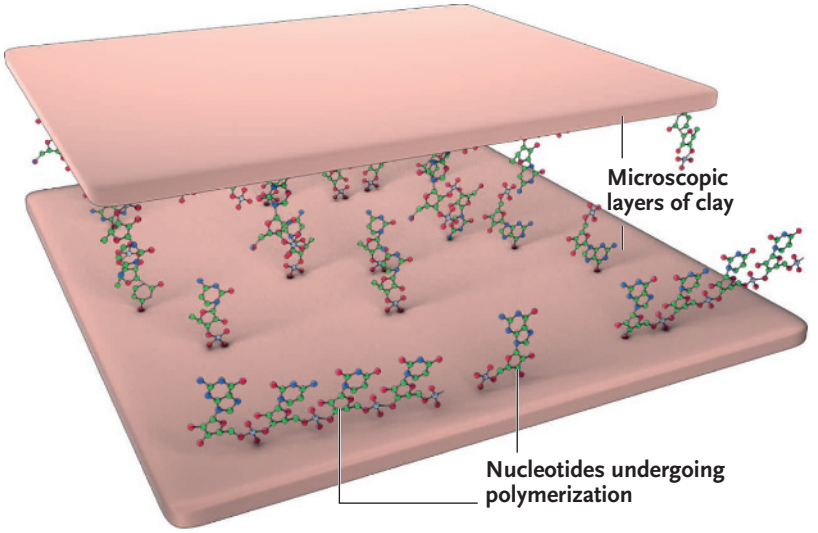


see how an already complex system of biochemistry would become unmanageable. From an evolutionary perspective, the increase in complexity would be disadvantageous and thus very early on in evolution, life must have favoured one chiral form over the other.

So why did biology decide on using specifically L amino acids and D sugars? It might simply have been chance. When life evolved there was a "flip of the coin," and early biochemistry was built around L forms of some molecules and D form of others. But another explanation comes from space. Each year more than 500 meteorites impact Earth, many of which are particularly rich in organic molecules. One of these, the Murchison meteorite has been found to contain over 70 different amino acids and close analysis shows a slightly higher abundance of the L form of these molecules (the ones found in living cells today). This finding suggests that unique conditions in space (high levels of UV light, for example) may have contributed to the dominant synthesis of one chiral form over the other. It is plausible that organic molecules delivered to Earth on meteorites from space may have been the origin of homochirality.

Figure 1.8 Clay surfaces catalyze polymerization.

The charged, microscopic, layered structure of clay allows for the formation of relatively short polymers of proteins and nucleic acids.



1.2c Life Requires Polymers

Primordial Earth contained no atmospheric oxygen and, because of this, complex organic molecules could have existed for much longer than would be possible in today's oxidizing world. Oxygen (O_2) is a strong oxidizing molecule, which means it's very good at taking electrons away from other molecules, which fundamentally changes the molecule's structure and function. Even if they did accumulate on early Earth, molecules such as amino acids and nucleotides are **monomers**, which are simpler and easier to synthesize than the key chemical components of life, such as nucleic acids and proteins, which are polymers—macromolecules formed from the bonding together of individual monomers. Nucleic acids are polymers of nucleotide monomers, proteins are polymers of amino acid monomers, and polysaccharides (starch, cellulose) are polymers of simple sugars (e.g., glucose). Polymers are discussed further in *The Purple Pages*.

The synthesis of proteins and nucleic acids in a modern cell requires *enzymes* and results in macromolecules that consist of hundreds to many thousands of monomers linked together. So, how do you make the polymers that are required for life without sophisticated enzymes? A working hypothesis to address this question needs to be built from a perspective that the earliest forms of life must have been very basic, far simpler than a modern bacterium, for example. Scientists hypothesize that a polymer that consists of even 10 to 50 monomers may have been of sufficient length to impart a specific function (like a protein) or store sufficient information (like a nucleic acid) to make their formation advantageous to an organism. It is, however, doubtful that polymerization could have occurred in the aqueous environment of early Earth, as it would be very rare for monomers to interact precisely enough with one another to polymerize. It is more likely that solid surfaces, especially clays, could have provided the type of environment necessary for polymerization to occur (Figure 1.8). Clays consist of very thin layers of minerals separated by layers of water only a few nanometres thick. The layered structure of clay is also charged, allowing for molecular adhesion forces to bring monomers together in precise orientations that could more readily lead to polymer formation. Clays can also store the potential energy that may have been used for energy-requiring polymerization reactions. This *clay hypothesis* is supported by laboratory experiments that demonstrate that the formation of short nucleic acid chains and polypeptides can be synthesized on a clay surface.

Pause and Review

1. For understanding the origins of life, what was the significance of the Miller–Urey experiment?
2. What is the difference between a reducing atmosphere and an oxidizing atmosphere?

1.3 The First Life

In the previous section, we discussed how processes present on early Earth could have generated macromolecules crucial to the development of life. However, if we are to develop a comprehensive model for the origin of life, we need to explain the evolution of three key properties of a cell that go well beyond the synthesis of macromolecules. First, a mechanism to store information needed to evolve that could be replicated and passed on to progeny cells. Second, energy-transforming chemical reactions needed to be present that would enable primitive cells to capture energy from their surroundings and use it to do work (e.g., building macromolecules). Third, these processes would need to take place within defined compartments (e.g., cells) that are distinct and separate from the environment.

While simple chemical reactions important to life could have developed outside cells, even basic metabolic pathways would have had to be restricted to compartments where concentrations of molecules and conditions could be distinct from the external environment. While there remain a lot more questions than answers about how this all came about, what has been found is a habitat with a unique combination of characteristics that could have nurtured the earliest forms of life.

1.3a Alkaline Hydrothermal Vents May Have Been the Site of Earliest Life

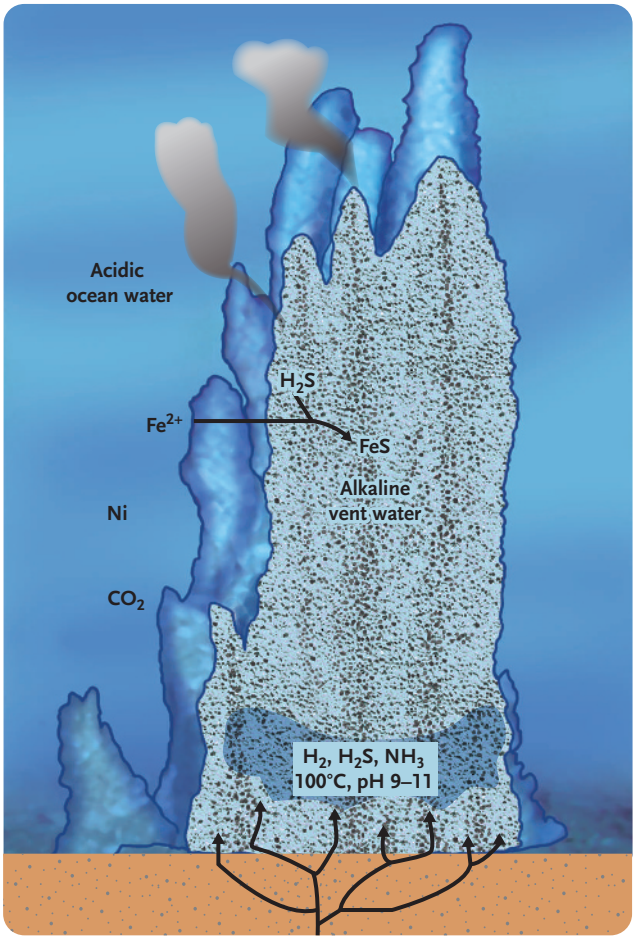
Over the past few decades, many scientists testing hypotheses related to the origin of life have come to agree that complex molecules necessary for life as well as life itself may have originated on the ocean floor at the sites of hydrothermal vents. These cracks in Earth's crust are found around the globe near sites of volcanic or tectonic activity. Most hydrothermal vents release superheated, nutrient-rich water at temperatures in excess of 300°C. Because of these high temperatures, hydrothermal vents have largely been dismissed as the likely sites where the first cells developed. However, more recently, researchers have discovered a different type of vent called an *alkaline hydrothermal vent*. Not only do these vents release water that is much cooler (100°C–150°C), the water is also strongly alkaline (pH 9–11) and rich in a range of molecules, including H_2, H_2S, and NH_3 (**Figure 1.9**). As we will see, these are all important characteristics conducive to the development of life.

One feature that makes alkaline vents a promising site for the development of life is that chemical reactions taking place where the vent water encounters ocean water causes calcium carbonate to precipitate out of the water forming chimneys that are honeycombed with microscopic pores that water moves through. These pores are only micrometres in diameter, which makes them comparable in size to a modern cell and provide a promising model for how the earliest cells could have evolved. One hypothesis suggests that the very first cells were not bound by lipid membranes like cells today but instead were surrounded by an inorganic casing composed of metal sulfides (NiS, FeS) that are readily found at the site of these vents. Laboratory experiments have shown that these metal sulfides produce bubbles when they precipitate that could have served as the first cell membranes. Such a primitive membrane would have allowed an important attribute of life to develop—compartmentalization. These early membranes would have trapped and concentrated organic molecules, allowing for more complex chemical reactions to take place.

At some point the inorganic nature of the first membrane would have been replaced by one dominated by lipid molecules

Figure 1.9 Alkaline hydrothermal vent

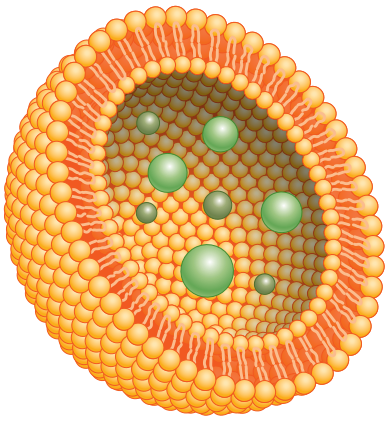
When water is released from a vent in the ocean floor and encounters ocean water, calcium carbonate precipitates out of the water, forming chimneys. The vent water is alkaline and carries hydrogen, hydrogen sulfide, and ammonia to the surface. The surrounding ocean water is cool and contains CO_2 and a wide range of trace metals. Reactions among these various molecules could have produced the first cell membranes and contributed to the development of the first metabolic reactions.



produced by biosynthetic reactions within the cell. The earliest lipid membranes could have been similar to a liposome, which is a lipid vesicle in which the lipid molecules form a bilayer very similar to a cell membrane (Figure 1.10). Given a mixture of lipid molecules, liposomes can form spontaneously (i.e., without the need for energy) and would be selectively permeable—allowing only some molecules to move in and out. As well, liposomes have been shown to swell and contract depending on the osmotic conditions of their environment. The development of lipid membranes would have been critical to the earliest cells gaining the ability to live independently and away from the vent structure.

Figure 1.10 Liposome

(a) An artist's rendition of a liposome, which is composed of a lipid bilayer. Liposomes can assemble spontaneously under simulated primordial conditions. **(b)** Electron micrograph image of a preparation of liposomes.



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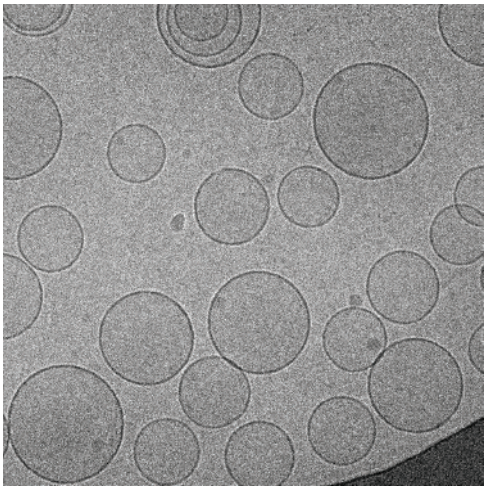


b.

Science History Images / Alamy Stock Photo

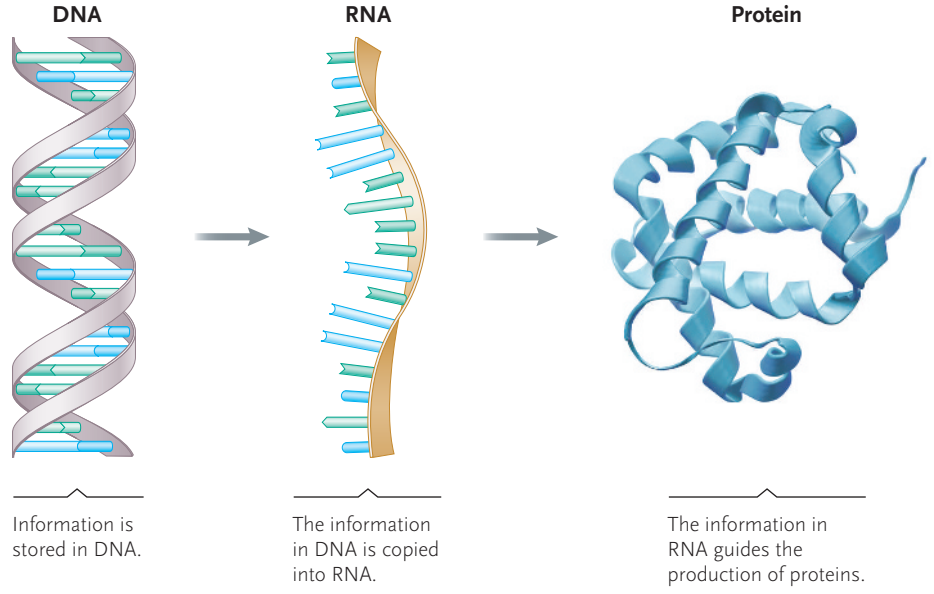
1.3b RNA Can Carry Information and Catalyze Reactions

As we will discuss starting in Chapter 11, DNA is the molecule that provides every cell with the instructions necessary to function. A specific sequence of nucleotides of DNA, called a *gene*, is copied into a unique molecule of RNA. Some of these RNA molecules in turn provide information for the synthesis of particular proteins. Even the simplest bacterium today contains thousands of genes, RNA molecules, and proteins. The flow of information from DNA to RNA to protein is common to all forms of life and is referred to as the *central dogma* (Figure 1.11). But there is an inherent paradox with this system. Each step of the information flow requires the involvement of enzymes that catalyze the transcription of DNA into RNA, and the translation of the RNA into protein. But enzymes are proteins.

So how did such a system evolve when the final products, proteins, are required to catalyze each step (e.g., transcription, translation) of the process? A breakthrough came in the early 1980s when Thomas Cech and Sidney Altman, working independently, discovered a group of RNA molecules that could themselves act as catalysts. This group of RNA catalysts, called **ribozymes**, are found in all

Figure 1.11 The central dogma

Information in DNA is used to synthesize proteins through an RNA intermediate. How did such a system evolve when the products, proteins, are required in modern-day cells to catalyze each step?

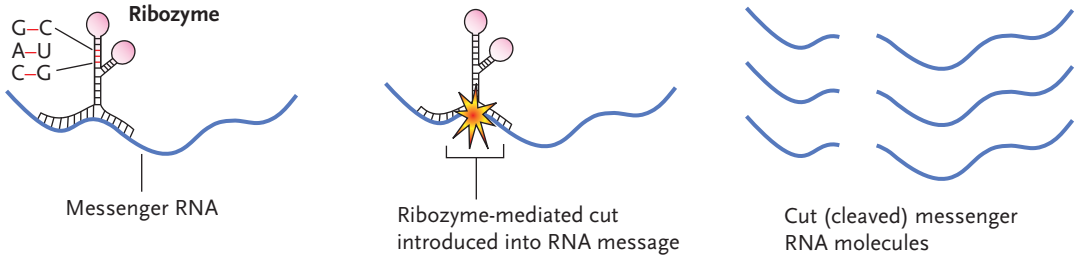


forms of life. They are not as common as enzymes, but they carry out critical reactions related to the control of gene expression and protein synthesis.

The precise catalytic properties of a ribozyme are determined by its shape, which is based on the hydrogen bonding between specific nucleotides of the RNA molecule. This is referred to as complementary base pairing: the nucleotide adenine (A) can only bind to uracil (U), while guanine (G) only binds to cytosine (C) (see **Figure 1.12**). The link between nucleotide sequence, shape, and thus function is analogous to an enzyme. The specific reaction catalyzed by an enzyme is dependent on its precise three-dimensional shape, which is dictated by its unique amino acid sequence. All ribozymes recognize their target by specific base pairing between the ribozyme nucleotide sequence and the nucleotide sequence of the target molecule (Figure 1.12). Within cells today, ribozymes serve a diversity of functions; some are responsible processing newly formed RNA molecules into their final form while others are, for example, major components of the ribosome and play a key role in protein synthesis.

Figure 1.12 **Ribozyme-mediated RNA cleavage**

At left, a ribozyme acquires a unique three-dimensional structure by complementary base pairing with itself. It binds to a specific sequence on a target RNA molecule also through complementary base pairing. Within a modern-day cell, such reactions help control gene expression by altering the abundance of functional messenger RNA (mRNA) molecules.



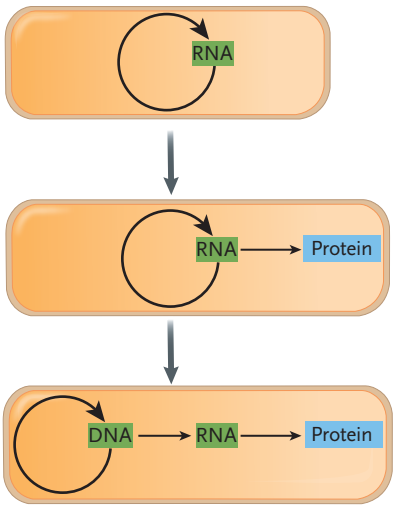
The discovery of ribozymes revolutionized our thinking about the origin of life. Instead of the contemporary system that requires all three molecules—DNA, RNA, and protein—early life may have existed in an "RNA world." RNA could have served both as a carrier of information, by virtue of its nucleotide sequence, and as a structural/catalytic molecule due to its ability to fold on itself and form unique three-dimensional shapes. Before the discovery of ribozymes, enzymes were the only known biological catalysts. For their remarkable discovery of RNA catalysts, Sidney Altman and Thomas Cech shared the Nobel Prize in Chemistry in 1989.

1.3c RNA Is Replaced by DNA for Information Storage and Proteins for Catalysis

If life developed in an environment where RNA served as both an information carrier and a catalyst, why is it that all modern organisms use DNA to store genetic information, and why do proteins (e.g., enzymes) catalyze the vast majority of biological reactions? The simple answer is that they do the respective jobs of information storage (DNA) and catalysis (protein) far better than RNA does by itself. The evolution of these other molecules would give organisms a distinct advantage over others that relied solely on RNA.

A possible scenario for the development of today's system of information transfer is shown in **Figure 1.13**. The first cells may have contained only RNA, which could make copies of itself (*self-replicating*) and could catalyze a small number of reactions critical for survival. It is hypothesized that a small population of RNA molecules then evolved that could catalyze the formation of very short proteins before the development of ribosomes. In modern cells, the ribosome is the site of protein synthesis: it binds mRNA molecules and uses the information in the nucleotide sequence to generate a protein built from a

Figure 1.13 **Possible scenario for the evolution of the flow of information from DNA to RNA to protein**



pool of amino acids. It is interesting to note that the catalytic component of the ribosome that joins individual amino acids together is itself an RNA molecule. So, in fact, the ribosome is a type of ribozyme.

Cells that evolved the ability to use the information present in RNA to direct the synthesis of even small proteins would be at a tremendous advantage because proteins are far more versatile than RNA molecules for three reasons. First, the catalytic power of most enzymes is much greater than that of a ribozyme. A typical enzyme can catalyze the same reaction using a pool of substrate molecules many thousands of times a second. By comparison, the rate of catalysis of most ribozymes is one-tenth to one-hundredth that of an enzyme. Second, the cell can make a far greater diversity of proteins. Twenty different kinds of amino acids, in different arrangements, can be incorporated into a protein, whereas an RNA molecule is composed of different combinations of only four nucleotides. Third, amino acids can interact chemically with each other in more complex and varied bonding arrangements not possible between nucleotides. For these reasons, proteins are the dominant structural and functional molecule of a modern cell.

Continuing with the possible scenario shown in Figure 1.13, the evolution of DNA would have followed that of proteins. Compared with RNA, molecules of DNA are more structurally complex. Not only is DNA double stranded, but it also contains the sugar deoxyribose, which is more difficult to synthesize than the ribose found in molecules of RNA. A possible sequence begins with DNA nucleotides being produced by random removal of an oxygen atom from the ribose subunits of RNA nucleotides. At some point, the DNA nucleotides paired with the RNA informational molecules and were assembled into complementary copies of the RNA sequences. Some modern-day viruses carry out this RNA-to-DNA reaction using enzyme reverse transcriptase (see Chapter 25). Once the DNA copies were made, selection may have favoured DNA as it is a much better way to store information than RNA for two reasons: First, each strand of DNA is chemically more stable and thus less likely to degrade than a strand of RNA. This is because the oxygen in ribose is reactive, while having deoxyribose, which lacks that oxygen atom, makes DNA less likely to undergo chemical changes. Second, DNA is double stranded. So, in the case of a random introduction of the wrong base in one strand during DNA replication, the information contained on the complementary strand can be used to correctly repair the damaged strand. It's like having two copies of the same book in the library.

The remarkable stability of DNA is illustrated by the fact that intact DNA can be successfully extracted from tissues that are many thousands of years old. The well-known novel and movie *Jurassic Park* are based on this demonstrated ability. By comparison, RNA needs to be isolated quickly from cells and stored at very low temperatures to prevent its degradation.

1.3d Evolution of Metabolism

To think about how life started, it's helpful to consider the fundamentals of metabolism that we find in organisms today. The foundation of the biosphere includes microbes and plants that use photosynthesis to take electrons from water molecules and use them to reduce CO_2 into organic compounds, such as glucose:

$$6H_2O + 6CO_2 \xrightarrow{\text{energy}} C_6H_{12}O_6 + 6O_2$$

The importance of synthesizing organic molecules like glucose is twofold: First, using a range of biochemical pathways, cells can convert glucose into other organic molecules such as fatty acids, nucleic acids, and amino acids. Second, because they are reduced (the molecules have gained electrons), organic molecules can be used as a source of energy. For example, cellular respiration is the process that oxidizes glucose to generate adenosine triphosphate (ATP), the main molecule in cells where energy is stored.

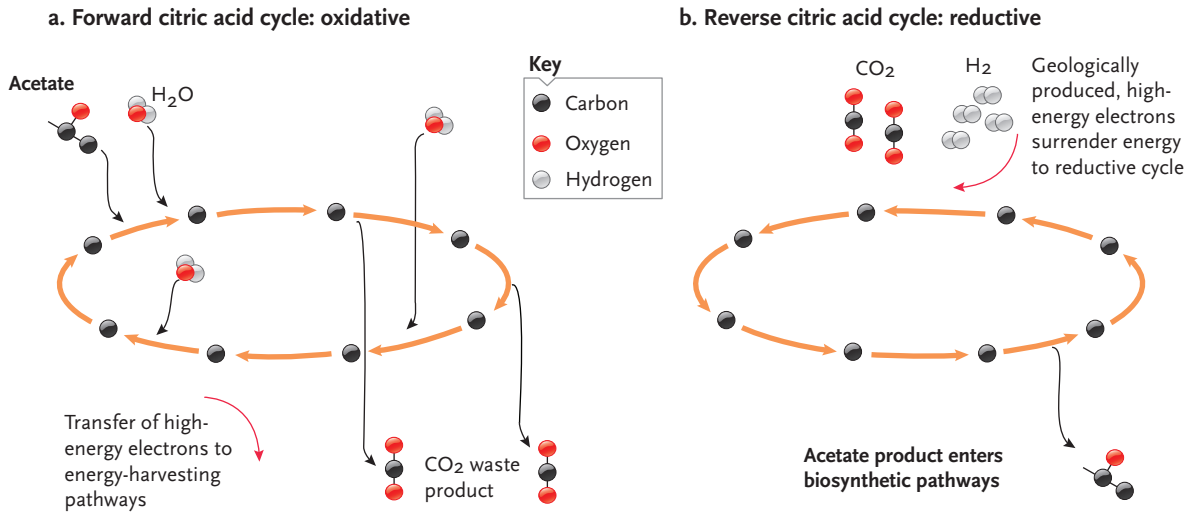
The chemical reaction shown above doesn't just occur by itself; to split molecules of water and extract the electrons takes a lot of energy and that energy typically comes from sunlight. In fact, photosynthesis is a very sophisticated process and because of that, it probably was not the first process that evolved to reduce CO_2 to energy-rich carbon molecules. There is a much simpler set of reactions that can do this is related to that the *citric acid cycle* (or Krebs cycle). In the *citric acid cycle* of cellular respiration, organic molecules (e.g., acetyl-CoA) are oxidized, releasing electrons, CO_2, and water. The electrons released are in turn used further along in the respiratory pathway to provide energy to generate ATP. You will learn all about this in more detail in Chapter 5.

What is really interesting about the citric acid cycle is that, in addition to working in an "oxidative mode" like it does in cellular respiration, in some bacteria it can actually run in reverse, in a "reductive mode" (**Figure 1.14**). It can take in energy in the form of high energy electrons from hydrogen gas (H_2) for example, and use those electrons to reduce CO_2 into organic molecules, including the important metabolic intermediates pyruvate and acetate. So, in the oxidative mode, the input is reduced organic molecules and the output is chemical energy and CO_2; in the reductive mode, the input is chemical energy and CO_2, and the output is more reduced organic molecules.

By running the citric acid cycle in reverse you end up doing what the far more sophisticated process of photosynthesis achieves: converting CO_2 into organic molecules. A key difference is H_2 gas is much easier to extract electrons from (to oxidize) than the H_2O used photosynthesis. The advantage photosynthesis would eventually have is that H_2O is so much more abundant on Earth than H_2 gas. But at particular sites, such as alkaline vents, H_2 gas is released in high amounts and therefore represented a

Figure 1.14 Forward and reverse citric acid cycle

(a) The reactions and molecules of the citric acid cycle are found in all modern organisms. (**b**) In some microbes, the cycle runs in reverse. Instead of oxidizing a fuel molecule (e.g., acetate) and releasing CO_2 as waste, the reverse cycle incorporates CO_2 in organic molecules by using geologically produced molecules such as H_2, which represent a rich source of usable electrons. The reverse citric acid cycle may have been the mechanism that early organisms used to generate complex molecules.



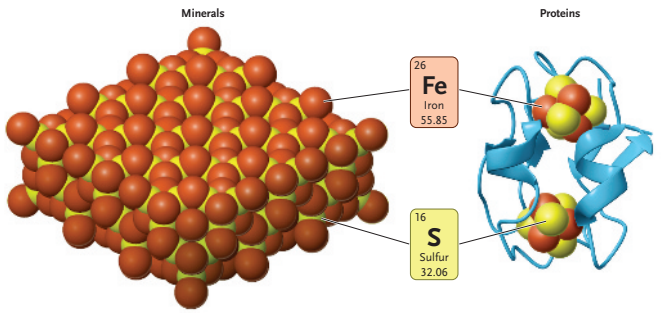
readily available source of energy that the earliest forms of life could rely on to generate complex organic molecules—the sugars, amino acids, nucleotides, and fatty acids that are the building blocks of cells.

Like all metabolic pathways, the reverse citric acid cycle found in bacteria today requires enzymes to catalyze the conversion of one intermediate of the cycle into the next. Could the pathway have operated in very primitive cells in the absence of enzymes? Laboratory experiments have shown that the rate of these chemical reactions can be sped up without enzymes by the presence of certain metal–mineral complexes. One particular complex that could have served as a catalyst before enzymes developed is iron–sulfur (Fe–S) clusters. These could have been easily formed from a reaction between hydrogen sulfide (H_2S) and iron (Fe), which are dissolved in the alkaline vent water (look back at Figure 1.9). What is really exciting about this hypothesis is Fe–S clusters are essential to life today. They are key cofactors in what are referred to as *FeS proteins* (**Figure 1.15**), which play critical roles in enzyme catalysis, as well as in electron transfer, as components of both photosynthetic and respiratory electron transport chains.

In addition to iron, many other metals (zinc, copper, nickel, molybdenum, etc.) are required in trace amounts for the function of many proteins, and thus are essential for life. The reliance of all organisms on these metals may reflect how modern biochemistry is linked to the geochemistry of the hydrothermal vents where life may have started.

Figure 1.15 Greigite, an iron–sulfur (Fe–S)-containing mineral (left), is structurally very similar to the iron–sulfur (Fe–S) cofactors found in some present-day enzymes (right).

The FeS mineral cluster itself may have played a key role in early catalysis prior to the development of proteins and then, in turn, the evolution of enzymes.



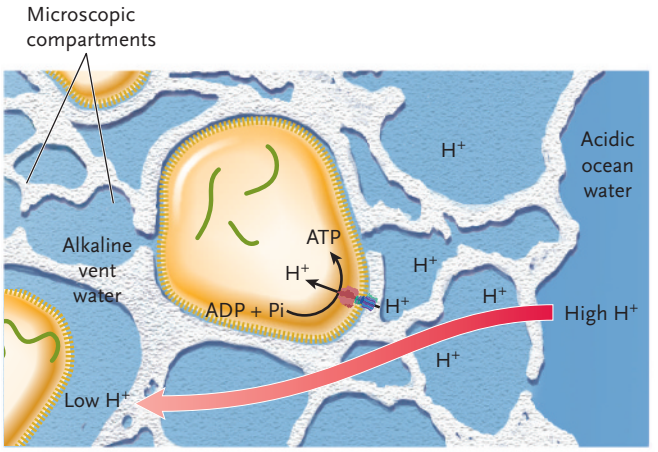
In almost all forms of life today a central mechanism to transform energy is *chemiosmosis*: using a difference in proton (H^+) concentration across a membrane to do work. As we will discuss in Chapter 5, membranes are impermeable to protons, so having more protons on one side than the other produces an

electrochemical gradient that can be harnessed to do energy-requiring processes, including generating ATP from adenosine diphosphate (ADP) and phosphate (PO_4^{3-}, abbreviated Pi). In organisms today, cells need to expend energy to pump protons across a membrane to generate proton gradients, but if the earliest cells evolved in the environment of alkaline hydrothermal vents, the gradient would come for free as it's being generated by geological processes. Recall that the water coming out of these vents has a low concentration of protons (the water is alkaline), whereas the surrounding ocean water has a proton concentration that is estimated to be about 1000-fold greater (**Figure 1.16**).

Today, the chemiosmotic synthesis of ATP from ADP and Pi is a reaction that is catalyzed by a membrane-localized enzyme complex, ATP synthase. Being a key component of both photosynthesis and cellular respiration, ATP synthase is found across all domains of life, which suggests that it evolved very early in the development of life. It's hard to explain how such an elaborate enzyme complex could have evolved so early but it is worth reminding ourselves that even the earliest forms of life must have been quite sophisticated. The ribosome, which is the organelle responsible for protein synthesis, is another key feature of all cells that is very complex. The evolution of these two key cellular machines must have relied on two key features: easy access to a supply of usable energy and an environment where molecules could have been synthesized in a confined space. The alkaline vent system of 4 billion years ago may very well have supplied both of those features.

Figure 1.16 **An example of an early cell within the microscopic pores of the vent system**

They could have harnessed the geochemically produced proton gradient to generate ATP through development of ATP synthase-like complex.



Pause and Review

1. What are the characteristics of an alkaline hydrothermal vent?
2. Explain the difference between the forward citric acid cycle and the reverse citric acid cycle.
3. RNA may have been the first information-carrying molecule, but it was replaced by DNA. Why?
4. How was the proton gradient within the earliest cells produced?

1.4 The Tree of Life

As we saw in the previous section, the alkaline hydrothermal vent system is a very promising geological feature where early life may have developed. Along with looking at the physical features present on Earth, insights into early life can come from studying the huge diversity of life that we find on Earth today and developing hypotheses around how different organisms may be related. To trace the evolutionary history of organisms, what is referred to as *phylogeny,* researchers build branching diagrams called *trees* that show the relationship among different groups of species. We will discuss evolutionary histories more in Chapter 19.

Considering that life has existed for about 4 billion years and species change over time, building a reasonably accurate evolutionary tree that includes all major groups of organisms, a so-called tree of life, seems like a daunting task. And it shouldn't surprise you that, as the research tools and techniques used to assess relatedness among organisms have improved, so has the accuracy of the evolutionary trees that are built as a result of that research. We will see in this section that through the use of modern molecular techniques we are able to infer a great deal about what our most ancient ancestors might have been like.

1.4a Earth Is 4.6 Billion Years Old

Let's go back to the very start. Earth was formed about 4.6 billion years ago, at the same time as the rest of the planets in the solar system. The age of our planet has been arrived at using the technique of *radiometric dating*, which looks at specific isotopic ratios in rocks and knowledge of their rate of decay (see *The Purple Pages* for more detail on isotopes). The decay of uranium to lead in particular has been used to age Earth. To give us some sense of just how long 4.6 billion years is, as well as the relative timing of some

major events in the history of life on Earth, **Figure 1.17** condenses the entire history of Earth into a unit of time that we are more familiar with: 1 year. With 4.6 billion years condensed into a single year, each day represents an interval of 12.6 million years!

Using our condensed version of the history of Earth, we set the date of the formation of Earth as January 1 at 12:00 a.m. As previously discussed, scientists estimate that life evolved approximately 4 billion years ago. This translates to mid-March in our one-year calendar. The first clear fossil evidence of prokaryotic cells, cells that without a nucleus and other membrane-bound organelles, occurs in late March, or about 3.5 billion years ago. Fossil evidence of eukaryotes—organisms containing cells with nuclei and other membrane-bound organelles—has been dated to about 2 billion years ago, which is not until early July using our 1-year analogy. Perhaps surprisingly, animals do not make an appearance until mid-October (about 525 million years ago) and land plants until the following month (about 450 million years ago). The extinction of dinosaurs, which was completed by about 65 million years ago, does not occur until late December. What about humans? We may think humans, *Homo sapiens,* have been around a long time but, relative to other forms of life, the roughly 300 000 years that modern humans have existed is a very short period of time—a blip on our time scale. Using our one year analogy, modern humans have existed only since December 31; more precisely, since December 31 at 11:43 p.m.!

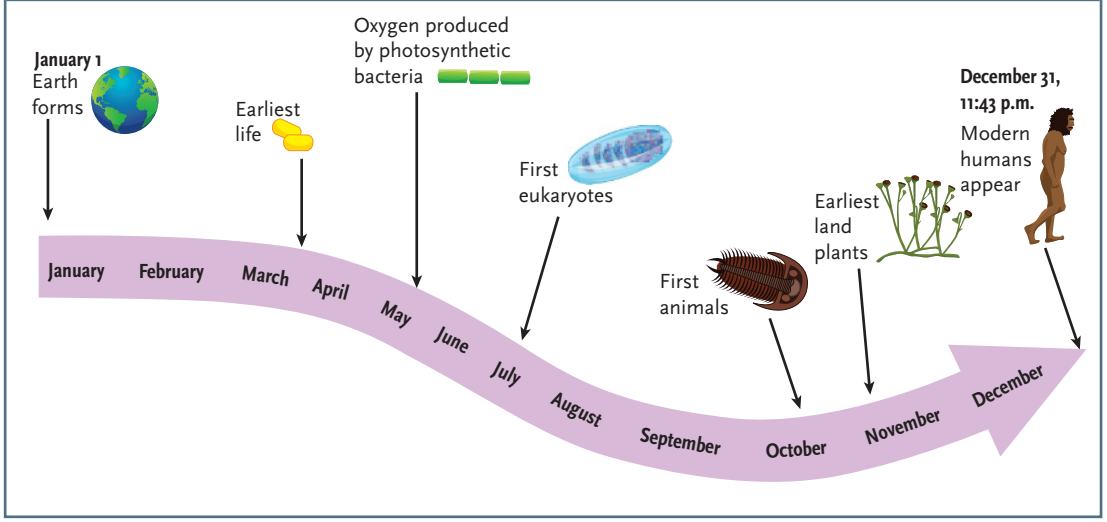
1.4b Analyses of Gene Sequences Have Revealed the Branching Pattern of the Entire Tree of Life

When it comes to looking at the relationships among the major groups of organisms, the way we understood things about 50 years ago made everything seem so simple. All life could be divided into two clear camps: eukaryotes and prokaryotes. The eukaryotes were the organisms that we were most familiar with—the animals, plants, and fungi—each defined their own kingdom but were united into a single larger group by having cells that contained membrane-bound organelles, most importantly, the nucleus. Fifty years ago, *prokaryotes* meant only one thing—bacteria. Single-celled, structurally and metabolically simple, bacteria were largely hidden from our everyday world because they were microscopic. But everything changed when researchers started to apply the tools and techniques of molecular biology to the study of evolutionary relationships (phylogenetics) among groups of organisms.

For centuries, biologists had built phylogenetic trees based on how organisms looked: organisms that have similar structures and features (what we call *morphology*) were grouped more closely together than organisms that looked less similar. But, two organisms that look similar may in fact not share a similar evolutionary history. By the 1970s, researchers realized that a more objective and powerful approach to building trees was to use differences in DNA sequence—the order of the four nucleotides that make up DNA: adenine (A), guanine (G), cytosine (C), and thymine (T). Let's look at this a little closer. During the process of speciation (discussed in Chapter 18), two distinct populations of one species, for example, become more and more isolated from each other and accordingly their DNA sequences would become less similar. As they continue to diverge over time, these two populations would eventually become separate species. If organisms representing two different species don't have a lot of differences in their DNA then you can reasonably conclude that the two species likely diverged quite recently. If there are a lot of differences, they are likely to be more distantly related.

If you want to use differences in DNA to build a tree of life, the first question you need to consider is: *What is the DNA sequence that I want to compare?* You could determine the sequence of the entire genomes of organisms representing the different species you want to include in your tree, but even today that can get expensive, and looking for similarities and differences between the millions or billions of bases that make up whole genomes can take a long time. Instead, scientists have focused on looking at differences in the sequence of just one gene. But which one should they pick? There are two major criteria you need to consider: First, the specific gene you choose

Figure 1.17 The history of life on Earth condensed into one year



needs to be present in all organisms. It would make little sense to use a gene required for eye development, for example, to build a tree of life since 99.99% of species on Earth don't have eyes. Second, the gene has to be relatively long (at least a thousand bases would be good). The longer the DNA sequence, the more information it contains to make comparisons among species. For example, having a gene made up of only six nucleotides (say, GAGCCT) isn't very useful because many unrelated species would have that sequence simply by chance.

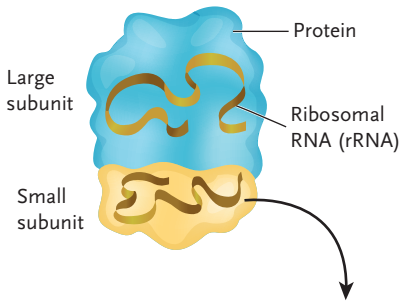
One of the first researchers to use a DNA sequence to build phylogenetic trees was Carl Woese, a microbiologist at the University of Illinois. He focused his attention on a cell component that is common to all life: the ribosome - the organelle at the centre of protein synthesis that uses the information in mRNA molecules to synthesize its corresponding protein. The structure of a ribosome is built by a combination of protein and a specific kind of RNA called *ribosomal RNA* (rRNA), and these components are remarkably similar across all organisms (**Figure 1.18**). Woese settled on the gene that codes for the rRNA molecule that makes up the small subunit of the ribosome. The DNA sequence for this gene is about 1500 nucleotides in length, so it provides lots of information with which to compare species and build the tree. A small portion of this sequence is seen in Figure 1.18.

In 1990, Woese and his colleagues published the first tree of life based on rRNA sequence data. It surprised many in the scientific community because, instead of showing 5 or 7 or maybe 10 distinct kingdoms of life, it clearly showed that all life could actually be grouped into 3 "superkingdoms" called **domains**: Bacteria, Archaea, and Eukarya (**Figure 1.19a**). The most surprising finding of what has become known as the *three-domain tree of life* is that it showed not one but two major groups of organisms that have prokaryotic cell structure: the Bacteria and Archaea. The Bacteria include many well-known microbes, including *Escherichia coli* (*E. coli*), and the domain Archaea includes microorganisms that are far less common and are often found in harsh environments, such as hot springs and salt marshes. The domain Eukarya includes the familiar animals, plants, and fungi and protists. We will discuss the major distinguishing features of the Bacteria, Archaea, and Eukarya in the next chapter, as we delve more deeply into cell structure and function.

Before moving on, it's worth mentioning the scientific impact of the three-domain tree of life. First, it illustrated the power of using molecular data to produce evolutionary trees; data that unlike morphology, could be more accurately interpreted. Second, the use of molecular data such as gene sequences allowed for the classification of microbes that are difficult to describe in other ways. Not only because they are microscopic but also because some are very difficult to grow and study in

Figure 1.18 The ribosome is made of two subunits, each composed of protein and ribosomal RNA (rRNA).

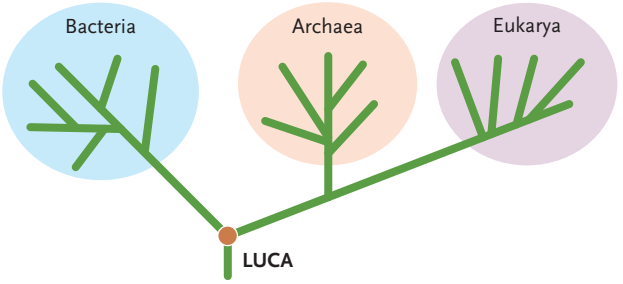
The sequence of the rRNA gene of the small subunit is widely used to infer evolutionary relationships among species. In the example shown here of a small portion of the sequence, Species 3 has more differences (shown in red) than Species 1 or 2. Based on these data, we can conclude that Species 3 is more distantly related to Species 1 than Species 2.



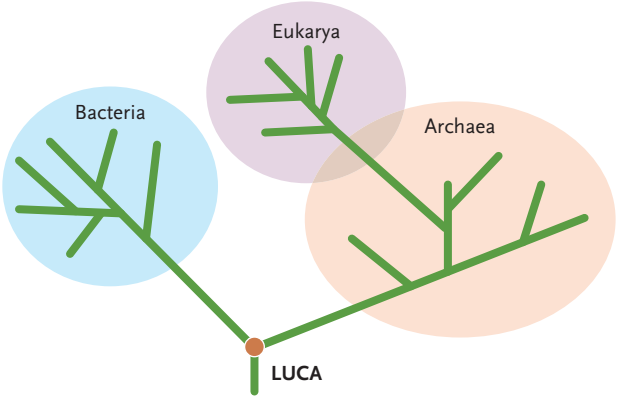
Species 1 ... ATCCGCTAGGCTGACGGCTTAGCCCATATCGAC...
Species 2 ... ATCCGGTAGGCTGACGGCTTTGCCCATATCGAC...
Species 3 ... ATCCGCTACGCAGATGGCTTAGCCGATAACGAC...

Figure 1.19 Trees of life with domains

(a) Three-domain tree of life. rRNA sequence comparisons suggest that Bacteria, Archaea, and Eukarya are three domains of living organisms, and that Eukarya are more closely related to Archaea than to Bacteria. **(b) Two-domain tree of life**. The discovery of the Asgard group of archaeans that have key eukaryotic traits suggests that eukaryotes evolved from within the Archaea. LUCA stands for Last Universal Common Ancestor and is discussed in the text.



a. Three-domain tree



b. Two-domain tree

the laboratory. Third, and perhaps most surprisingly, it showed that archaeans are more closely related to eukaryotes than they are to bacteria. Before the use of molecular tools, few scientists expected that to be the case.

Since it was first published, the three-domain tree of life has been well supported by additional gene sequencing projects, as well as detailed analyses showing how distinct the cell structure and physiology of archaeans are compared to bacteria. But microbiologists had long suspected that the bacteria and archaea that had been studied so far represented only a tiny fraction of the total microbial diversity on Earth. Microbes are microscopic, many live in extreme habitats, and many are difficult to culture in a laboratory, making them particularly difficult to study.

Sediment cores taken in 2010 near a hydrothermal vent in the Arctic Ocean contained previously uncharacterized specimens of archaeans that have since been assigned to a subgroup called Asgard. DNA sequencing of these samples showed something shocking: while the data clearly confirmed they were archaeans, the data also showed that these organisms forming the Asgard subgroup contained genes that were previously thought to be present only in eukaryotes. These so-called "eukaryotic signature proteins" included genes involved in building the cytoskeleton, the process of phagocytosis, and various aspects of transcription and translation that were previously thought to be unique to eukaryotes.

The analysis of the Asgard genes suggest that archaeans and eukaryotes are in fact much more closely related than previously thought. The data have led to an updated version of the tree of life, which consists of only two primary domains: Bacteria and Archaea. Eukaryotes are now considered to be a subgroup evolving from within the Archaea (**Figure 1.19b**). The establishment of the two-domain tree of life will be scrutinized as sequence data from a wider range of organisms become available.

1.4c All Present-Day Organisms Are Descended from a Common Ancestor, LUCA

There are clear differences in the structure and function between bacteria, archaeans, and eukaryotes that we will discuss in detail in Unit 5. But underlying these differences, all organisms across the tree of life share some fundamental characteristics. These similarities include (1) cells defined by a membrane composed of a bilayer of lipid molecules; (2) a genetic system based on DNA; (3) a system of information transfer: DNA to RNA to protein; (4) ribosomes as the central feature of a protein assembly machinery that uses the information in messenger RNA (mRNA) and transfer RNA (tRNA) to produce peptide chains from a pool of amino acids; (5) reliance on proteins as the major structural and catalytic molecule; (6) use of ATP as the currency of chemical energy; and (7) common pathways of energy transformation (e.g., glycolysis, substrate-level phosphorylation, chemiosmosis).

Given that all organisms on Earth share these seven characteristics, what is the likelihood that these traits developed independently during the evolution of each of the three major groups of life? For example, each group developed by themselves exactly the same biochemical pathway to breakdown glucose (e.g., glycolysis). The likelihood of this is essentially 0. Instead, it is an almost certainty that all life today is descended from a single ancestral organism that had already developed these seven traits. This one organism is referred to as the Last Universal Common Ancestor, or LUCA, and is estimated to have lived between 3.5 and 3.8 billion years ago. Looking back at Figure 1.19, you will see that LUCA is consistent with both the three-domain tree of life and the two-domain tree of life.

! Concept Fix: You may think that LUCA was the first form of life to exist on Earth, but that is not the case. Calling something the *last* common ancestor is like saying the *last* team to win the Stanley Cup; what we mean is the *most recent*. LUCA is the most recent ancestor that gave rise to all the organisms we see on Earth today. Given that LUCA was quite complex in both structure and function, it was likely to have been preceded by other, simpler forms of life (**Figure 1.20**). Also, as shown in Figure 1.20, it is likely that life arose more than once on the early Earth; each form perhaps having only some of the seven attributes we see in all forms of life today. For example, perhaps a form of life arose that did not use ATP as a common source of chemical energy, or perhaps never developed DNA as the repository of genetic information. The similarities across all domains of life present today indicate, however, that only one of these primitive life forms has descendants that survive today.

Figure 1.20 Life before LUCA

It is likely that there were many independent origins of life and many forms of life that predated LUCA. As indicated by the light green part of the figure, all of these are now extinct, as well as others that have become extinct more recently.

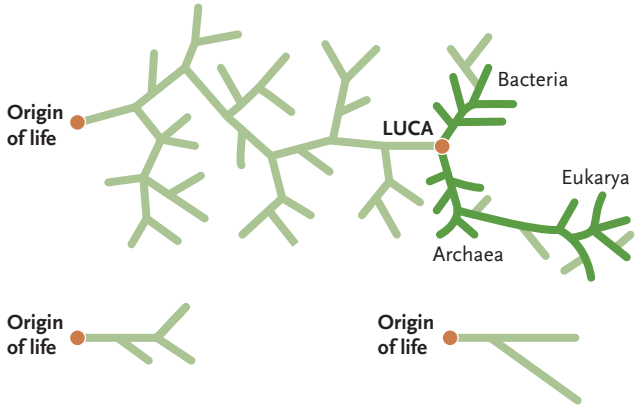
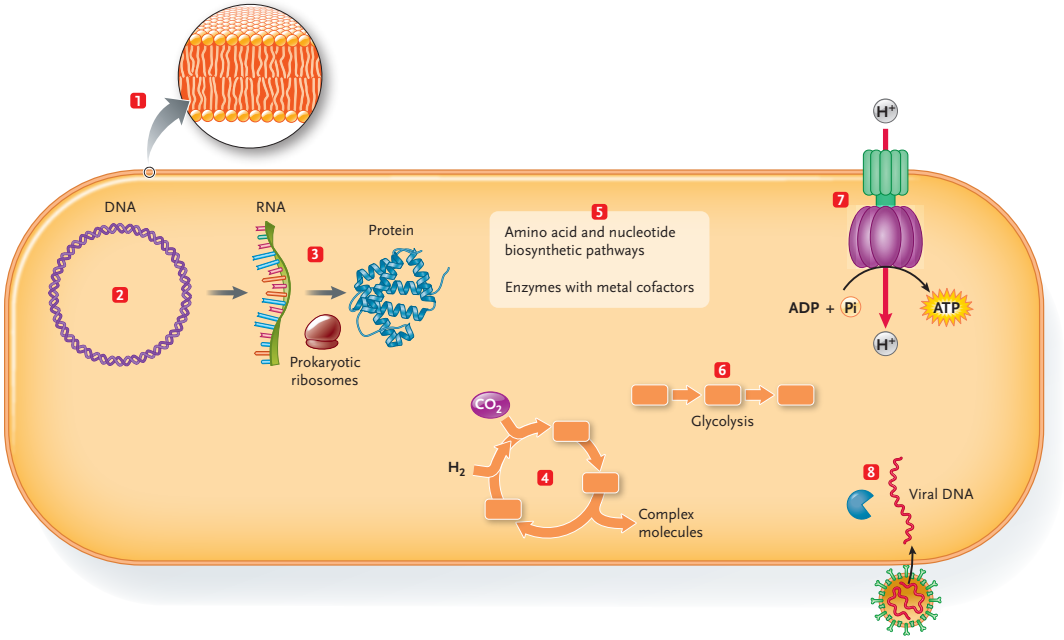


Figure 1.21 **A model of LUCA based on reconstruction of its genome based on analysis of data from a range of modern-day bacteria and archaeans**

Based on this analysis, LUCA had the following characteristics: **(1)** A simple phospholipid cell membrane; **(2)** A DNA genome encoding approximately 2600 proteins, making it similar in size to a bacterial genome; **(3)** Molecular machinery, including prokaryotic-like ribosomes for building proteins; **(4)** Reverse citric acid cycle, allowing it to use CO_2 and H_2 in the environment to synthesize complex organic molecules; **(5)** A range of biosynthetic pathways related to amino-acid and nucleotide biosynthesis employing enzymes, some of which had metal (e.g., Fe, Ni) cofactors; **(6)** Glycolysis, enabling it to extract energy from molecules such as glucose; **(7)** ATP synthase complex, allowing it to utilize an environmentally produced proton gradient to generate ATP from ADP and Pi; **(8)** A basic immune system to fight viral infection.



Based on the similarity that exists among all living organisms, we are certain that LUCA existed. And yet, unlike dinosaurs, for example, we have no actual physical evidence of LUCA to work with. Instead, researchers have used the tools of molecular biology to piece together a view of what LUCA was actually like. To reconstruct the structure, biochemistry, and ecology of LUCA, researchers compared the sequenced genomes of hundreds of modern bacteria and archaeans. The researchers found that there was a core group of proteins that were present in all the species they studied. That these proteins were widely distributed across all bacterial and archaeal species suggests that these are ancient and likely evolved from related proteins present in LUCA. This and other genomic analyses have allowed researchers to develop this picture of what LUCA was like (**Figure 1.21**). LUCA was anaerobic—relying on mechanisms of metabolism that did not need O_2. It had a DNA genome similar to a modern-day bacterium coding for as many as 2600 proteins. This enabled the synthesis of a range of structures and processes that are the foundation of many of the attributes we see in modern-day cells (Figure 1.21). This molecular research also suggests that LUCA thrived in a hot environment, which supports the hypothesis that LUCA developed in a vent-like setting and took advantage of the abundance of molecules produced by a range of geochemical processes.

Pause and Review

1. What is the advantage of using DNA sequence over morphology as the data used to build an evolutionary tree?
2. We have moved recently from a three-domain tree of life to a two-domain tree of life. What caused the shift in thinking?
3. LUCA wasn't the first form of life to develop, so why is it so important to our understanding of the evolution of life?

1.5 The Fossil Record

We need to remind ourselves that, so far in this chapter, everything we have discussed about the origins of life and LUCA is based on inference—researchers do not have actual physical evidence of the early life forms that inhabited Earth. What we know about LUCA has been discovered through inference and chemical detective work rather than by studying the organismal remains. This section provides an overview of what we actually do know about the history of life on Earth as reflected by the remains of organisms that have been preserved in the fossil record.

1.5a The Fossil Record Is Invaluable but Incomplete

The fossil record provides the only direct evidence about what life was like millions of years ago. Fossilized skeletons, shells, stems, leaves, and flowers tell us about the size and appearance of ancient animals and plants. The fossil record has also allowed scientists to see how species have changed over time as it chronicles the proliferation and extinction of evolutionary lineages, and it provides data on the geographical distribution of extinct species. As discussed in Chapter 16, Darwin's ability to compare fossil specimens with living relatives was very influential in his development of the notion of evolution through natural selection.

Obviously, the fossil record is an invaluable resource to understand the past, but it is important to note that it represents only a small fraction of the organisms that once lived on Earth, and thus it vastly underrepresents the diversity of life. The fossil record only really represents a record of a subset of organisms; those that were very abundant, had wide distributions, and possessed hard parts that could be fossilized. Soft-bodied organisms with small geographic distributions or that lived in environments where erosion was a dominant process are underrepresented in the fossil record—if they are in it at all.

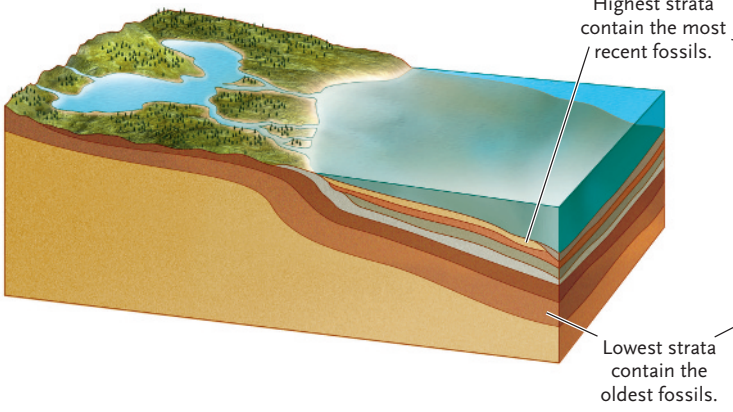
1.5b Fossils Form When Organisms Are Buried by Sediments or Preserved in Oxygen-Poor Environments

Most fossils are found in sedimentary rocks. Rain and runoff constantly erode the land, carrying fine particles of rock and soil downhill and downstream to a swamp, a lake, or the sea. Particles settle to the bottom of waterbodies and low-lying areas as sediments, forming successive layers, called *strata*, over millions of years (**Figure 1.22**). The weight of newer sediments compresses the older layers beneath them into a solid matrix: sand into sandstone, or mud into shale. Fossils form within the layers when the remains of organisms are buried in the accumulating sediments. Because sedimentation superimposes new layers over old ones, the lowest strata in a sedimentary rock formation are usually the oldest, and the highest layers are the newest.

Figure 1.22 Sedimentation and geological strata

(a) Sedimentation deposits successive layers at the bottom of a lake or sea. **(b)** Over millions of years, the upper layers compress those below them into rock. When the rocks are later exposed by uplifting or erosion, the different layers are evident as geological strata.

a. Sedimentation



b. Geological strata in the Painted Desert, Arizona

HABesen/Getty Images

The process of fossilization is a race against time because the soft remains of organisms are quickly consumed by scavengers or decomposed by microorganisms. Thus, fossils usually preserve the details of hard structures, such as the bones, teeth, and shells of animals and the wood, some leaves, and pollen of plants. During fossilization, dissolved minerals replace some parts molecule by molecule, leaving a fossil made of stone (**Figure 1.23a**); other fossils form as moulds, casts, or impressions in material that is later transformed into solid rock (**Figure 1.23b**).

In some environments, the near absence of oxygen prevents decomposition, and even soft-bodied organisms are preserved. Some plants, insects, and tiny lizards and frogs are embedded in *amber*, the fossilized resin of coniferous trees (**Figure 1.23c**). Other organisms are preserved in glacial ice, deeply frozen soil, coal, tar pits, or the highly acidic water of peat bogs (**Figure 1.23d**). Sometimes organisms are so well preserved that researchers can examine their internal anatomy, cell structure, food in their digestive tracts, and even their DNA sequences.

1.5c The Earliest Fossils

The earliest indirect evidence of life, which predates any actual fossil evidence, comes from research looking at the carbon composition of ancient rocks. Early photosynthetic organisms would have had the ability to take CO_2 from the atmosphere and use it to synthesize various organic molecules (see Chapter 6 for details). During photosynthesis, organisms preferentially incorporate the carbon-12 isotope (^{12}C) over other, heavier isotopes of carbon such as carbon-13 (^{13}C). (See *The Purple Pages* for a discussion of isotopes.) Researchers have discovered sedimentary rocks originating from the ocean floor that contain deposits that have lower levels of the ^{13}C isotope than expected. The most likely explanation is that the deposits are actually the remains of organic carbon molecules from ancient microbes. These sediments have been dated to approximately 3.9 billion years ago. If correct, this would push the origins of life to perhaps as early as 4 billion years ago, approximately 600 million years after Earth was formed.

The earliest conclusive evidence of life is found in the fossilized remains of structures called *stromatolites*, the oldest being formed about 3.5 billion years ago. A **stromatolite** is a type of layered rock formed when microorganisms bind particles of sediment together, forming thin sheets (**Figure 1.24**). Modern stromatolites are found in habitats characterized by warm shallow water and are most common in Australia. Modern-day stromatolites are formed by the action of a specific group of photosynthetic bacteria called *cyanobacteria*. We will see in Chapter 2 that cyanobacteria were the ancestors of the modern-day chloroplast found in all plants and algae. Unlike their photosynthetic predecessors, cyanobacteria could utilize water as an electron donor for photosynthesis, which results in the release of O_2 into the atmosphere.

Figure 1.23 Fossils

(a) Petrified wood in Arizona formed when minerals replaced the wood of dead trees, molecule by molecule. These forests lived during the late Triassic period, about 225 million years ago. **(b)** The remains of a fern (Sphenopteris) from the Carboniferous period, 300 million years ago, were preserved in coal. **(c)** These 10-million-year-old mosquitoes were trapped in the oozing resin of a coniferous tree and are now encased in amber. **(d)** A frozen baby mammoth that lived about 40 000 years ago was discovered embedded in Siberian permafrost in 1977.

a. Petrified wood (Araucariaceae)

Prisma by Dukas Presseagentur GmbH / Alamy Stock Photo

b. *Sphenopteris*

David Lyons / Alamy Stock Photo

c. Flying insects in amber

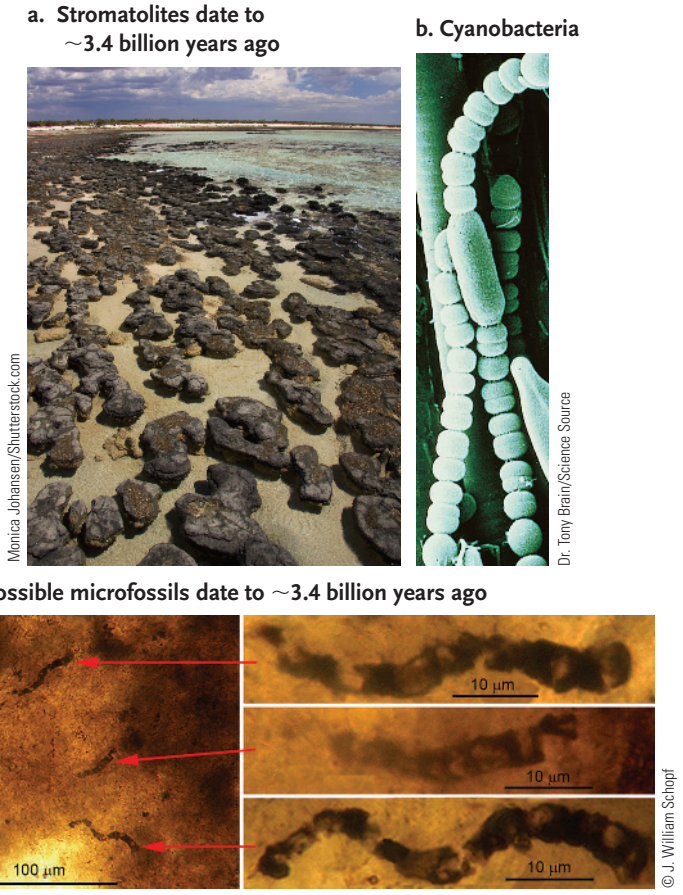
Tobkatrina/Shutterstock.com

d. Mammoth (*Mammuthus*)

South China Morning Post/Getty Images

Figure 1.24 **Early fossil evidence of life**

(a) Stromatolites exposed at low tide in Western Australia's Shark Bay. These mounds, which consist of mineral deposits made by cyanobacteria, are about 2000 years old; they are highly similar in structure to fossil stromatolites that formed more than 3 billion years ago. **(b)** Modern cyanobacteria filaments. These photosynthetic bacteria use water as an electron donor for photosynthesis and, as a by-product, release oxygen. **(c)** Microfossils. The left panel shows a cross-section through rock from Western Australia that has been dated to 3.4 billion years ago. On the right are further magnifications of three microfossils that have been interpreted as filamentous, possibly cyanobacteria.



1.5d Scientists Assign Relative and Absolute Dates to Geological Strata and the Fossils They Contain

The sediments found in any one place form recognizable *strata* (layers) that differ in colour, mineral composition, particle size, and thickness. If they have not been disturbed, the strata are arranged in the order in which they formed, with the youngest layers on top.

Geologists of the early 19th century deduced that the fossils discovered in a particular sedimentary stratum, no matter where on Earth it is found, represent organisms that lived and died at roughly the same time in the past. Because each stratum formed at a specific time, the sequence of fossils in the lowest (oldest) to the highest (newest) strata reveals their relative ages. Geologists originally used the sequence of strata and their distinctive fossil assemblages to establish the geological time scale (Table 1.1).

Although the geological time scale provides a relative dating system for sedimentary strata, it does not tell us how old the rocks and fossils actually are. But many rocks contain unstable radioisotopes, which, from the moment they