

Diversity of Life

STARR AND TAGGART

BIOLOGY: THE UNITY AND DIVERSITY OF LIFE / EIGHTH EDITION



DIVERSITY OF LIFE

CECIE STARR / RALPH TAGGART

BIOLOGY
THE UNITY AND DIVERSITY OF LIFE
EIGHTH EDITION



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PREFACE

Not too long from now we will cross the threshold of a new millennium, a rite of passage that invites reflection on where biology has been and where it might be heading. About 500 years ago, during an age of global exploration, naturalists first started to systematically catalog and think about the staggering diversity of organisms all around the world. Less than 150 years ago, just before the start of a civil war that would shred the fabric of a new nation, the naturalist Charles Darwin shredded preconceived notions about life's diversity. It was only about 50 years ago that biologists caught their first glimpse of life's unity at the molecular level. Until that happened a biologist could still hope to be a generalist—someone who viewed life as Darwin did, without detailed knowledge of mechanisms that created it, that perpetuate it, that change it.

No more. Biology grew to encompass hundreds of specialized fields, each focused on one narrow aspect of life and yielding volumes of information about it. Twenty years ago I wondered whether introductory textbooks could possibly keep up with the rapid and divergent splintering of biological inquiry. James Bonner, a teacher and researcher at the California Institute of Technology, turned my thinking around on this. He foresaw that authors and instructors for introductory courses must become the new generalists, the ones who give each generation of students broad perspective on what we know about life and what we have yet to learn.

And we must do this, for the biological perspective remains one of the most powerful of education's gifts. With it, students who travel down specialized roads can sense intuitively that their research and its applications may have repercussions in unexpected places in the world of life. With that perspective, students in general might cut their own intellectual paths through social, medical, and environmental thickets. And they might come to understand the past and to predict possible futures for ourselves and all other organisms.

CONCERNING THE EIGHTH EDITION

Like earlier editions, this book starts with an overview of the basic concepts and scientific methods. Three units on the principles of biochemistry, inheritance, and evolution follow. The principles provide the conceptual background necessary for deeper probes into life's unity and diversity, starting with a richly illustrated evolutionary survey of each kingdom. Units on the comparative anatomy and physiology of plants, then animals, follow. The last unit focuses on the patterns and consequences of organisms interacting with one another and with their environment. Thus the organization parallels the levels of biological organization, from cells through the biosphere. We adhere to this traditional approach for good reason: it works.

As before, we identify and highlight the key concepts, current understandings, and research trends for the major fields of inquiry. Through examples of problem solving

and experiments, we give ample evidence of "how we know what we know" and thus demonstrate the power of critical thinking. We explain the structure and functioning of a broad sampling of organisms in enough detail so that students can develop a working vocabulary about life's parts and processes. We also updated the glossary.

CONCEPT SPREADS

In the first chapter, an overview of the levels of biological organization kicks off a story that continues through the rest of the book. Telling such a big, complex story might be daunting unless you remind yourself of the question "*How do you eat an elephant?*" and its answer, "*One bite at a time.*" We who have told the story again and again know how the parts fit together, but many students need help to keep the story line in focus within and between chapters. And they need to chew on concepts one at a time.

In every chapter we present each concept on its own table, so to speak. That is, we organize the descriptions, art, and supporting evidence for it on two facing pages, at most. Think of this as a concept spread, as in Figure A. Each starts with a numbered tab and ends with boldface statements to summarize the key points. Students can use these cues as reminders to digest one topic before starting on another. Well-crafted transitions between spreads help students focus on where topics fit in the larger story and gently discourage memorization for its own sake. The clear demarcation also gives instructors greater flexibility in assigning or skipping topics within a chapter.

By restricting the space available for each concept, we force ourselves to clear away the clutter of superfluous detail. Within each concept spread, we block out headings and subheadings to rank the importance of its various parts. Any good story has such a hierarchy of information, with background settings, major and minor characters, and high points and an ending where everything comes together. Without a hierarchy, a story has all the excitement, flow, and drama of an encyclopedia. Where details are useful as expansions of concepts, we integrate them into suitable illustrations to keep them from disrupting the text flow.

Not all students are biology majors, and many of them approach biology textbooks with apprehension. If the words don't engage them, they sometimes end up hating the book, and the subject. It comes down to line-by-line judgment calls. During twenty-two years of authorship, we developed a sense of when to leave core material alone and when to loosen it up to give students breathing room. Interrupting, say, an account of mitotic cell division with a distracting anecdote does no good. Plunking a humorous aside into a chapter that ties together the evolution of the Earth and life trivializes a magnificent story. Including an entertaining story is fine, provided that doing so reinforces a key concept. Thus, for example, we include the story of a misguided species introduction that resulted in wild European rabbits running amok through Australia.

BALANCING CONCEPTS WITH APPLICATIONS

Each chapter starts with a lively or sobering application that leads into an adjoining list of key concepts. The list is an advance organizer for the chapter as a whole. At strategic points, examples of applications parallel the core material—not so many as to be distracting, but enough to keep minds perking along with the conceptual development. Many brief applications are integrated in the text. Others are in *Focus* essays, which give more depth on medical, environmental, and social issues but do not interrupt the text flow.

FOUNDATIONS FOR CRITICAL THINKING

To help students develop a capacity for critical thinking, we walk them through experiments that yielded evidence in favor of or against hypotheses being discussed. The main index for the book will give you a sense of the number and types of experiments used (see the entry *Experiments*).

We use certain chapter introductions as well as entire

chapters to show students some of the productive results of critical thinking. Among these are the introductions to the chapters on Mendelian genetics (11), DNA structure and function (14), speciation (19), immunology (40), and animal behavior (51).

Many *Focus on Science* essays provide more detailed, optional examples of how biologists apply critical thinking to problem solving. For example, one of these describes RFLP analysis (Section 16.3) and a few of its more jarring applications. Another essay (Section 21.4) helps convey to students that biology is not a closed book. Even when new research brings a sweeping story into sharp focus—in this case, the origin of the great prokaryotic and eukaryotic lineages—it also opens up new roads of inquiry.

This edition has *Critical Thinking* questions at the end of chapters. Katherine Denniston of Towson State University developed these thought-provoking questions. Chapters 11 and 12 also include a large selection of *Genetics Problems* that help students grasp the principles of inheritance.

To keep readers focused, we cover each concept on one or two facing pages, starting with a numbered tab . . .

5.1 MEMBRANE STRUCTURE AND FUNCTION

Earlier chapters provided you with a brief look at the structure of cell membranes and the general functions of their component parts. Here, we incorporate some of the background information in a more detailed picture.

The Lipid Bilayer of Cell Membranes

Fluid bathes the two surfaces of a cell membrane and is vital for its functioning. The membrane, too, has a fluid quality: it is not a solid, static wall between cytoplasmic and extracellular fluids. For instance, puncture a cell with a fine needle, and its cytoplasm will not ooze out. The membrane will flow over the puncture site and seal it!

How does a fluid membrane remain distinct from its fluid surroundings? To arrive at the answer, start by reviewing what we have already learned about its most abundant components, the phospholipids. Recall that a **phospholipid** has a phosphate-containing head and two fatty acid tails attached to a glycerol backbone (Figure 5.2a). The head is hydrophilic; it easily dissolves in water. Its tails are hydrophobic; water repels them. Immerse a number of phospholipid molecules in water, and they will interact with water molecules and with one another until they spontaneously cluster in a sheet or film at the water's surface. Their jostling may even force them to become organized in two layers, with all fatty acid tails sandwiched between all hydrophilic heads. This **lipid bilayer** arrangement, remember, is the structural basis of cell membranes (Section 4.1 and Figure 5.2c).

The organization of each lipid bilayer minimizes the total number of hydrophobic

groups exposed to water, so the fatty acid tails do not have to spend a lot of energy fighting water molecules, so to speak. A "punctured" membrane exhibits sealing behavior precisely because a puncture is energetically unfavorable. It leaves far too many hydrophobic groups exposed to the surrounding fluid.

Ordinarily, few cells get jabbed by fine needles. But the self-sealing behavior of membrane phospholipids is good for more than damage control. Among other things, it functions in vesicle formation. For example, as vesicles bud away from ER or Golgi membranes, phospholipids interact hydrophobically with cytoplasmic water. They get pushed together, and the rupture seals. You will read more about vesicle formation later in the chapter.

Fluid Mosaic Model of Membrane Structure

Figure 5.3 shows a bit of membrane that corresponds to the **fluid mosaic model**. By this model, cell membranes are a mixed composition—a "mosaic"—of phospholipids, glycolipids, sterols, and proteins. The phospholipid heads as well as the length and saturation of the tails are not all the same. (Recall that unsaturated fatty acids have one or more double bonds in their backbone and fully saturated ones have none.) The glycolipids are structurally similar to phospholipids, but their head incorporates one or more sugar monomers. In animal cell membranes, cholesterol is the most abundant sterol (Figure 5.2b). Phytosterols are their equivalent in plant cell membranes.

Also by this model, the membrane is "fluid" owing to the motions and interactions of its component parts.

Figure 5.2

(a) Structural formula of phosphatidylcholine, a phospholipid that is one of the most common components of the membranes of animal cells. Orange indicates its hydrophilic head; yellow indicates its hydrophobic tails.
(b) Structural formula of cholesterol, the major sterol in animal tissues.
(c) Diagram showing how lipids that are placed in liquid water may spontaneously organize themselves into a bilayer structure.

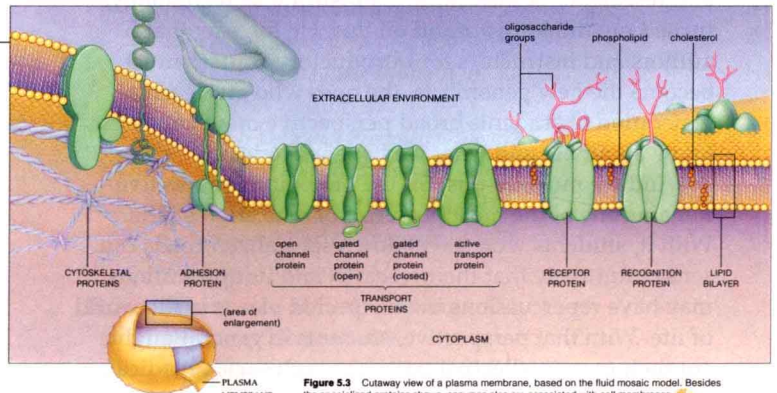
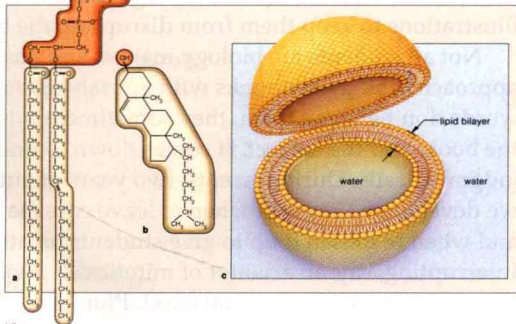


Figure 5.3 Cutaway view of a plasma membrane, based on the fluid mosaic model. Besides the specialized proteins shown, enzymes also are associated with cell membranes.

The hydrophobic interactions that give rise to most of a membrane's structure are weaker than covalent bonds. This means most phospholipids and some proteins are free to drift sideways. Also, the phospholipids can spin about their long axis and flex their tails, which keeps neighboring molecules from packing together in a solid layer. Short or kinked (unsaturated) fatty acid tails also contribute to membrane fluidity.

The fluid mosaic model is a good starting point for exploring cell membranes. But bear in mind, membranes differ in the details of their molecular composition and arrangements, and they are not even the same on both surfaces of their bilayer. For example, oligosaccharides and other carbohydrates are covalently bonded to protein and lipid components of a plasma membrane, but only on its outward-facing surface (Figure 5.3). Moreover, they differ in number and kind from one species to the next, even among the different cells of the same individual.

Overview of Membrane Proteins

The proteins embedded in a lipid bilayer or attached to one of its surfaces carry out most membrane functions. Many are enzyme components of metabolic machinery. Others are **transport proteins** that allow water-soluble substances to move through their interior, which spans the bilayer. They bind molecules or ions on one side of the membrane, then release them on the other side.

The **receptor proteins** bind extracellular substances, such as hormones, that trigger changes in cell activities.

For example, certain enzymes that crank up machinery for cell growth and division become switched on when somatotropin, a hormone, binds with receptors for it. Different cells have different combinations of receptors.

Diverse **recognition proteins** at the cell surface are like molecular fingerprints; their oligosaccharide chains identify a cell as being of a specific type. For example, "self" proteins pepper the plasma membrane of your cells. Certain white blood cells chemically recognize the proteins and leave your own cells alone, but they attack invading bacterial cells having "nonself" proteins at their surface. Finally, **adhesion proteins** of multicelled organisms help cells of the same type locate and stick to one another and stay positioned in the proper tissues. They are glycoproteins with oligosaccharides attached. After tissues form, the sites of adhesion may become a type of cell junction, as described earlier in Section 4.10.

A cell membrane has two layers composed mainly of lipids, phospholipids especially. This lipid bilayer is the structural foundation for the membrane and also serves as a barrier to water-soluble substances.

Hydrophilic heads of the phospholipids are dissolved in fluids that bathe the two outer surfaces of the bilayer. Their hydrophobic tails are sandwiched between the heads.

Proteins associated with the bilayer carry out most membrane functions. Many are enzymes, transporters of substances across the bilayer, or receptors for extracellular substances. Other types function in cell-to-cell recognition or adhesion.

FIGURE A A concept spread from this edition.

. . . and ending with one or more summary statements.

VISUAL OVERVIEWS OF MAJOR CONCEPTS

While writing the text, we simultaneously develop the illustrations as inseparable parts of the same story. This integrative approach appeals to students who are visual learners. When they can first work their way through a visual overview of some process, then reading through the corresponding text becomes less intimidating. Over the years, students have repeatedly thanked us for our hundreds of overview illustrations, which contain step-by-step, written descriptions of biological parts and processes. We break down the information into a series of illustrated steps that are more inviting than a complex, "wordless" diagram. Figure B is a sample. Notice how simple descriptions, integrated with the art, take students through the stages by which mRNA transcripts become translated into polypeptide chains, one step at a time.

Similarly, we continue to create visual overviews for anatomical drawings. The illustrations integrate structure and function. Students need not jump back and forth from the text, to tables, to illustrations, and back again in order to comprehend how an organ system is put together and what its parts do. Even individual descriptions of parts are hierarchically arranged to reflect the structural and functional organization of that system.

COLOR CODING

In line illustrations, we consistently use the same colors for the same types of molecules and cell structures. Visual consistency makes it easier for students to track complex parts and processes. Figure C is the color coding chart.

ZOOM SEQUENCES

Many illustrations in the book progress from macroscopic to microscopic views of the same subject. Figure 7.2 is an example; this zoom sequence shows where the reactions of photosynthesis proceed, starting with a plant growing by a roadside. As another example, Figures 38.19 and 38.20 move down through levels of skeletal muscle contraction, starting with a muscle in the human arm.

ICONS

Within the text, small diagrams next to an illustration help relate the topic to the big picture. For instance, in Figure A, a simple representation of a cell subtly reminds students of the location of the plasma membrane relative to the cytoplasm. Other icons serve as reminders of the location of reactions and processes in cells and how they

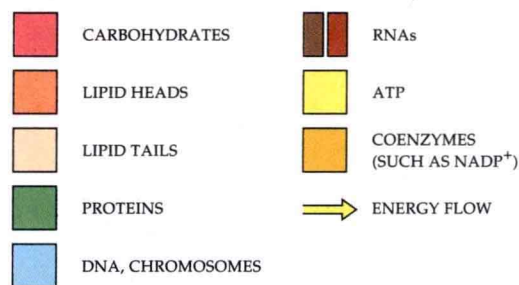


FIGURE C Color coding chart for the diagrams of biological molecules and cell structures.

Step-by-step art with simple descriptions helps students visualize a process before reading text about it.

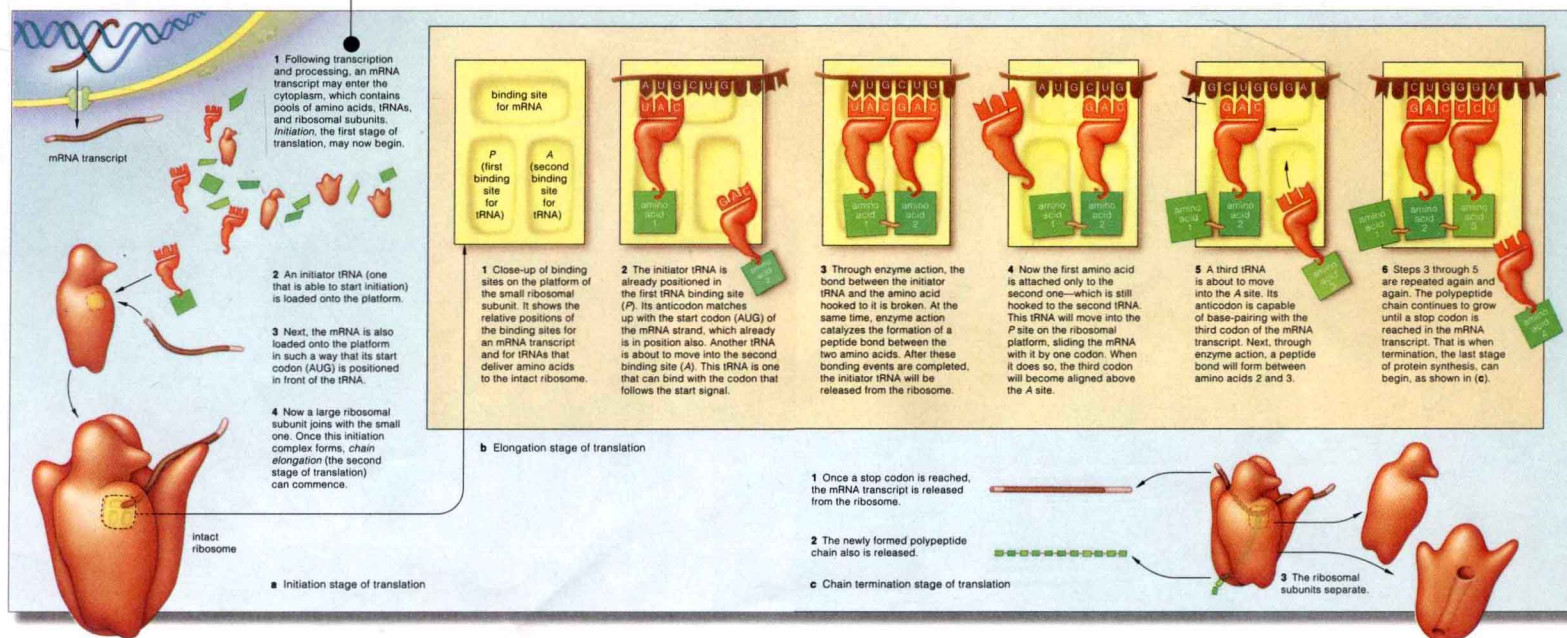


FIGURE B A visual overview from this edition.

interrelate to one another. Still others remind students of the evolutionary relationships among groups of organisms, as in Chapter 26.

New to this edition are icons that invite students to use multimedia. One icon directs them to art in the CD-ROM enclosed with each student copy, another to supplemental material on the Web, and a third to InfoTrac:

CD-ROM
ICON:



WEB
ICON:



INFOTRAC
ICON:



END-OF-CHAPTER STUDY AIDS

The end-of-chapter study aids are designed to reinforce the key concepts. Each chapter ends with a summary in list form, review questions, a self-quiz, critical thinking questions, selected key terms, and a list of readings. Italicized page numbers tie the review questions and key terms to relevant text pages.

END-OF-BOOK STUDY AIDS

At the book's end, the detailed classification scheme in Appendix I is helpful for reference purposes. Appendix II includes metric-English conversion charts. Appendix III has answers to the self-quizzes at the end of each chapter.

A Glossary includes boldfaced terms from the text, with pronunciation guides and word origins to make the formidable words less so. The Appendixes as well as the Glossary are printed on paper that is tinted different colors to preclude frustrating searches for where one ends and the next begins. The Index is detailed enough to help readers find doors to the text more quickly.

CONTENT REVISIONS

Instructors who use *Biology: The Unity and Diversity of Life* may wish to evaluate this overview of key modifications. Overall, conceptual development is more integrated. The writing is still crisp but not too brief, because some topics can confuse students when presented in insufficient detail. New research called for some adjustments in the overall framework. For example, we subscribe to the six-kingdom classification scheme, which now has exceptional support from comparative biochemical studies. Even the end-of-chapter Critical Thinking questions incorporate current material.

UNIT IV. EVOLUTION AND DIVERSITY Chapter 21 has a tree of life adapted to the six-kingdom scheme. Ediacaran and Cambrian forms are defined, and gymnosperm dominance is more clearly correlated with the Mesozoic. The global broiling theory is correlated with the K-T asteroid impact. Besides being a conceptual and chronological framework for the diversity chapters, this survey chapter may help students sense their place in nature. The greatly revised diversity chapters have crisp evolutionary story lines, a more balanced text-to-art ratio, and riveting applications (see Section 22.9 on infectious diseases). Chapter 23 states how opinions differ on which organisms are protists. In keeping with current consensus, we treat chytrids, water molds, and algae in that chapter. We have a new red algal life cycle. Chapter 24 includes a better treatment of lichens. Chapter 25 includes more on the Carboniferous and new spreads on existing seed-bearing plants. In the Chapter 26 introduction, I shamelessly segue from my grandchild to the early invertebrates. The chapter has new sections on animal origins, molluscan evolution, and adaptations of arthropods. Chapter 27 is reorganized for clarity, as in the sections on vertebrate evolutionary trends, reptiles, and mammals. Chapter 28 integrates new fossil evidence.

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EVOLUTION AND DIVERSITY **IV**



In The Beginning . . .

Some clear evening, watch the moon as it rises from the horizon and think of the 380,000 kilometers between it and you. *Five billion trillion times* the distance between the moon and you are galaxies—systems of stars—at the boundary of the known universe. Wavelengths traveling through space move faster than anything else—millions of meters per second. Yet the long wavelengths that originated from faraway galaxies many billions of years ago are only now reaching the Earth.

By every known measure, all the near and distant galaxies suspended in the vast space of the universe are moving away from one another, which means that the universe is expanding. And the prevailing view of how the colossal expansion came about accounts for every bit of matter in the universe, in every living thing.

Think about how you rewind a videotape on a VCR, then imagine “rewinding” the universe. As you do this, the galaxies start moving back together. After 12 to 15

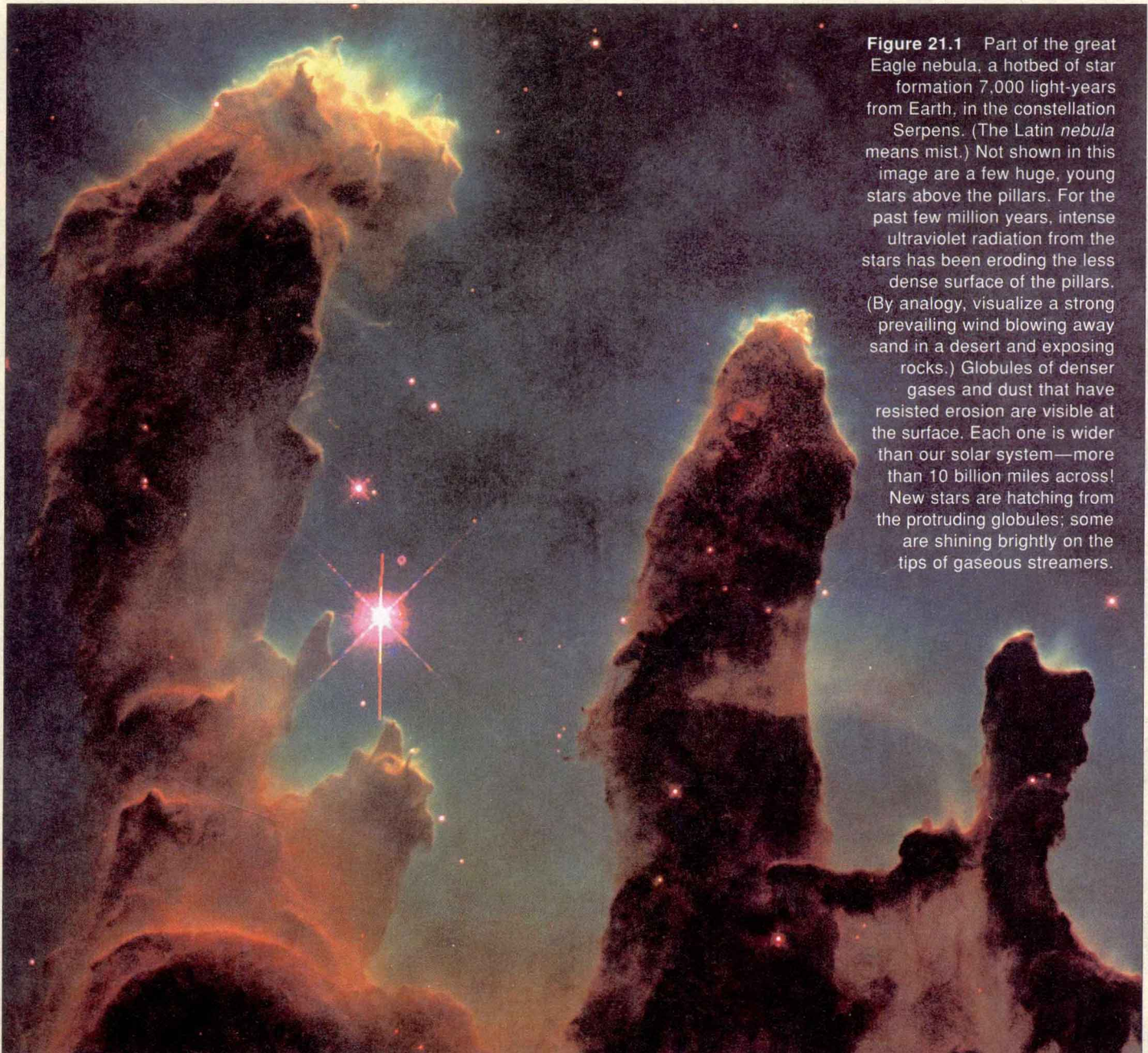


Figure 21.1 Part of the great Eagle nebula, a hotbed of star formation 7,000 light-years from Earth, in the constellation Serpens. (The Latin *nebula* means mist.) Not shown in this image are a few huge, young stars above the pillars. For the past few million years, intense ultraviolet radiation from the stars has been eroding the less dense surface of the pillars. (By analogy, visualize a strong prevailing wind blowing away sand in a desert and exposing rocks.) Globules of denser gases and dust that have resisted erosion are visible at the surface. Each one is wider than our solar system—more than 10 billion miles across! New stars are hatching from the protruding globules; some are shining brightly on the tips of gaseous streamers.

billion years of rewinding, all galaxies, all matter, and all of space are compressed into a hot, dense volume about the size of the sun. You have arrived at time zero.

That incredibly hot, dense state lasted only for an instant. What happened next is known as the **big bang**, a stupendous, nearly instantaneous distribution of all matter and energy everywhere, through all of the known universe. About a minute later, temperatures dropped to a billion degrees. Fusion reactions produced most of the light elements, including helium, which are still the most abundant elements throughout the universe. Radio telescopes have detected relics of the big bang in the form of cooled and diluted background radiation, left over from the beginning of time.

Over the next billion years, stars started forming as gaseous material contracted in response to the force of gravity. When stars became massive enough, nuclear reactions were ignited in their central region, and they gave off tremendous light and heat. As massive stars continued to contract, many became dense enough to promote the formation of heavier elements.

All stars have a life history, from birth to an often spectacularly explosive death. In what might be called the original stardust memories, the heavier elements released during the explosions became swept up during the gravitational contraction of new stars, and they became raw materials for the formation of even heavier elements. Even as you are reading this page, the Hubble space telescope is providing astounding glimpses of star-forming activity, as in the dust clouds of Orion, Serpens, and other constellations (Figure 21.1).

Now imagine a time long ago, when explosions of dying stars ripped through our galaxy and left behind a dense cloud of dust and gas that extended trillions of kilometers in space. As the cloud cooled, countless bits of matter gravitated toward one another. By 4.6 billion years ago, the cloud had flattened out into a slowly rotating disk. At the dense, hot center of that disk, the shining star of our solar system—the sun—was born.

The remainder of this chapter is a sweeping slice through time, one that cuts back to the formation of the Earth and the chemical origins of life. It is the starting point for the next four chapters, which will take us along lines of descent that led to the present range of species diversity. The story is not complete. Even so, all the available evidence, from many avenues of research, points to a principle that can help us organize separate bits of information about the past: *Life is a magnificent continuation of the physical and chemical evolution of the universe, of galaxies and stars, and of the planet Earth.*

KEY CONCEPTS

1. A great body of evidence suggests that life originated more than 3.8 billion years ago. Its origin and subsequent evolution have been linked to the physical and chemical evolution of the universe, the stars, and the planet Earth.
2. All of the inorganic and organic compounds necessary for self-replication, membrane assembly, and metabolism—that is, for the structure and functioning of living cells—could have formed spontaneously under conditions that existed on the early Earth.
3. The history of life, from its chemical beginnings to the present, spans five intervals of geologic time. It extends through two great eons—the Archean and the Proterozoic—and the Paleozoic, Mesozoic, and Cenozoic eras.
4. Not long after life originated, divergences led to two great prokaryotic lineages, called the archaeobacteria and eubacteria. Shortly afterward, the ancestors of eukaryotes diverged from the archaeobacterial lineage.
5. Archaeobacteria and eubacteria dominated the Archean and Proterozoic eons. Eukaryotic cells originated late in the Proterozoic era and became spectacularly diverse. A theory of endosymbiosis helps explain the profusion of specialized organelles that arose in eukaryotic cells.
6. All six kingdoms of organisms are characterized by the persistences, extinctions, and radiations of many different lineages over time.
7. Throughout the history of life, asteroid impacts, drifting and colliding continents, and other environmental insults have had profound impact on the direction of evolution.

Origin of the Earth

Cloudlike regions of the universe, as shown in Figure 21.1, are mostly hydrogen gas. These clouds also contain water, iron, silicates, hydrogen cyanide, ammonia, methane, formaldehyde, and some other simple organic and inorganic substances. The contracting cloud from which our solar system evolved probably was similar in composition. Between 4.6 and 4.5 billion years ago, the periphery of the cloud cooled. Mineral grains and ice orbiting the sun started to clump together as a result of electrostatic attraction and the pull of gravity (Figure 21.2). In time, larger, faster clumps started colliding and shattering. Some became more massive by sweeping up asteroids, meteorites, and the other rocky remnants of collisions, and gradually they evolved into planets.



Figure 21.2 Representation of the cloud of dust, gases, and clumps of rock and ice around the early sun.

As the Earth was forming, much of its inner rocky material melted. Asteroid impacts as well as its own internal compression and radioactive decay of minerals could have generated the heat necessary to do this. As the rocks melted, nickel, iron, and other heavy materials moved to the Earth's interior; lighter ones floated to the surface. This process produced a crust, mantle, and core. The **crust** is an outer region of basalt, granite, and other low-density rocks. It envelops the intermediate-density rocks of the **mantle**, which wraps around a core of very high-density, partially molten nickel and iron.

Four billion years ago, the Earth was a thin-crusted inferno (Figure 21.3a). In less than 200 million years, life had originated on its surface! We have no record of the event. As far as we know, movements in the mantle and crust, volcanic activity, and erosion obliterated all traces of it. Still, we can put together a plausible explanation of how life originated by considering three questions:

First, *when life originated, what physical and chemical conditions prevailed on Earth?*

Second, *based on physical, chemical, and evolutionary principles, could large organic molecules have spontaneously formed and then evolved into molecular systems displaying the fundamental properties of life?*

Third, *can we devise experiments to test whether living systems could have emerged by chemical evolution?*

The First Atmosphere

When the first patches of crust were forming, hot gases blanketed the Earth. This first atmosphere probably was a mix of gaseous hydrogen (H_2), nitrogen (N_2), and carbon monoxide (CO), as well as carbon dioxide (CO_2). Was gaseous oxygen (O_2) also present? Probably not. Rocks release oxygen when they are subjected to the intense heat of volcanic eruptions, but not much. Besides, free oxygen would have reacted at once with other elements. At first, water at the Earth's molten surface must have evaporated into the atmosphere. After the crust cooled and solidified, rains from the clouds blanketing the Earth drenched the parched rocks. For millions of years the runoff eroded mineral salts and other compounds from the rocks. And salt-laden waters gradually collected in depressions in the crust and formed the early seas.

If the early atmosphere and seas had not been free of oxygen, then the organic compounds that became organized into the first cells might not have formed on their own. Oxygen would have attacked them, in the manner described in the introduction to Chapter 6. If liquid water had not accumulated, then cell membranes could not have formed. Cells are the basic units of life. *Each has a capacity to survive and reproduce on its own.*

Synthesis of Organic Compounds

Reduce a cell to its lowest common denominator and all that remains are proteins, complex carbohydrates and lipids, and nucleic acids. Existing cells assemble these molecules from smaller organic compounds: the simple sugars, fatty acids, amino acids, and nucleotides. Energy from the environment drives the synthesis reactions. Were small organic compounds also present on the early Earth? Were there sources of energy that spontaneously drove their assembly into the large molecules of life?

Mars, meteorites, the Earth's moon, and the Earth all formed at the same time, from the same cosmic cloud. Rocks collected from Mars, meteorites, and the moon contain precursors of biological molecules, so the same precursors must have been present on the Earth. If this were indeed the case, *then energy from sunlight, lightning, or even heat escaping from the crust could have been enough to drive their combination into organic molecules.*

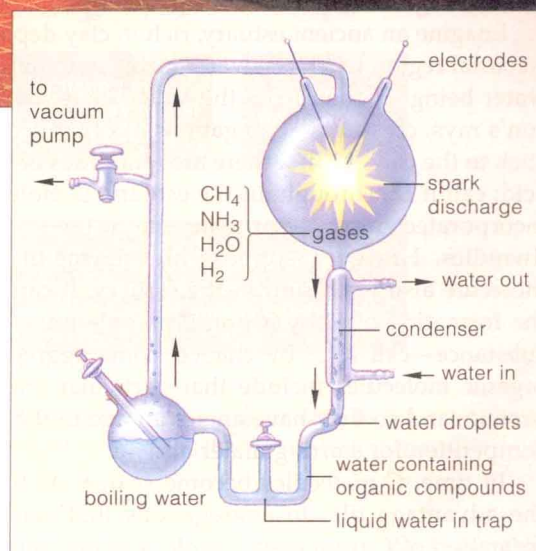
Stanley Miller conducted the first experimental test of that prediction. First he mixed methane, hydrogen,



a

Figure 21.3 (a) Representation of the Earth during its formation, when the moon's orbit was much closer than it is today. If the Earth had condensed into a planet of smaller diameter, its gravitational mass would not have been great enough to hold onto an atmosphere. If it had settled into an orbit closer to the sun, water would have evaporated from its hot surface. If the Earth's orbit had been more distant from the sun, its surface would have been far colder, and water would have been locked up as ice. Without liquid water, life as we know it never would have originated on Earth.

(b) Stanley Miller's experimental apparatus, used to study the synthesis of organic compounds under conditions that presumably existed on the early Earth. The condenser cools circulating steam so that water droplets form.



b

ammonia, and water inside a reaction chamber of the sort depicted in Figure 21.3b. Then he kept the mixture circulating and bombarded it with a spark discharge to simulate lightning. In less than a week, amino acids and other small organic compounds had formed.

In other experiments that simulated conditions on the early Earth, glucose, ribose, deoxyribose, and other sugars formed spontaneously from formaldehyde, and adenine from hydrogen cyanide. Ribose and adenine are found in ATP, NAD, and other nucleotides vital to cells.

However, if *complex* organic compounds had formed directly in the seas, they would not have lasted long. The spontaneous direction of the necessary reactions would have been toward hydrolysis, not condensation, in water. How did more lasting bonds form?

By one hypothesis, clay in the rhythmically drained muck of tidal flats and estuaries served as templates (structural patterns) for the spontaneous assembly of proteins and other complex organic compounds. Clay consists of thin, stacked layers of aluminosilicates with metal ions at their surfaces, which attract amino acids. Expose amino acids to some clay, warm the clay with rays from the sun, then alternately moisten and dry it. Condensation reactions will proceed at its surfaces and yield proteins and other complex organic compounds.

By another hypothesis, complex organic compounds formed spontaneously near hydrothermal vents on the seafloor, where species of archaeobacteria are thriving

today. As experimental tests by Sidney Fox and others show, when amino acids are placed in water and then heated, they spontaneously order themselves into small protein-like molecules, which Fox calls "protenoids."

However the first proteins formed, their molecular structure dictated how they would interact with other compounds. Suppose some proteins had the structure to function as weak enzymes. That is, they were able to hasten bond formation between amino acids. Enzyme-directed synthesis would have a selective advantage. In the chemical competition for available amino acids, the protein configurations that promoted reactions would win. Also, proteins have the capacity to bind metal ions and other carbon-based compounds. As you will see next, such chemical modification was the foundation for the evolution of metabolism. For now, simply reflect on the possibility that selection was at work before the origin of living cells, favoring the chemical evolution of enzymes and other complex organic compounds.

Many diverse experiments yield indirect evidence that the complex organic molecules characteristic of life could have formed under conditions that existed on the early Earth.



Origin of Agents of Metabolism

A defining characteristic of life is metabolism. The word refers to all the reactions by which cells harness energy and use it to drive their activities, such as biosynthesis. During the first 600 million years or so of Earth history, enzymes, ATP, and other organic compounds may have assembled spontaneously, and they may have done so in the same physical locations. If so, their close association would have naturally promoted chemical interactions and the beginning of metabolic pathways.

Imagine an ancient estuary, rich in clay deposits. It is a coastal region where seawater mixes with mineral-rich water being drained from the land. There, beneath the sun's rays, countless aggregations of organic molecules stick to the clay. At first there are quantities of an amino acid; call it *D*. Throughout the estuary, *D* molecules get incorporated into new proteins—until the supply of *D* dwindles. However, suppose an enzyme-like protein molecule also is present in the estuary. It can promote the formation of *D* by acting on an abundant, simpler substance—call it *C*. By chance, some aggregations of organic molecules include that particular enzyme-like protein, and so they have an advantage in the chemical competition for starting materials.

In time, *C* molecules become scarce. At that point, the advantage tilts to aggregations that can promote formation of *C* from even simpler organic substances *B* and *A*—say, from carbon dioxide and water. As you know, carbon dioxide and water occur in essentially unlimited amounts in the atmosphere and in the seas. Chemical selection has favored a synthetic pathway:



Finally, suppose some aggregations are better than others at absorbing and using energy. Which molecules could bestow such an advantage? Think of the energy-trapping pathway that now dominates the world of life: photosynthesis. It starts at pigments called chlorophylls. The light-absorbing and electron-donating portion of a chlorophyll molecule is called a porphyrin ring structure. Porphyrins are also present in cytochromes, which are part of electron transport systems in all photosynthetic and aerobically respiring cells. Porphyrin molecules can spontaneously assemble from formaldehyde—one of the molecular legacies of cosmic clouds (Figure 21.4). Was porphyrin an electron transporter of some of the early metabolic pathways? Perhaps.

Origin of Self-Replicating Systems

Another defining characteristic of life is a capacity for reproduction, which now starts with protein-building instructions in DNA. The DNA molecule is fairly stable,

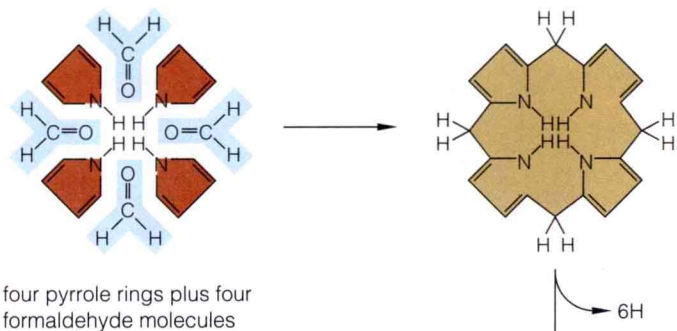
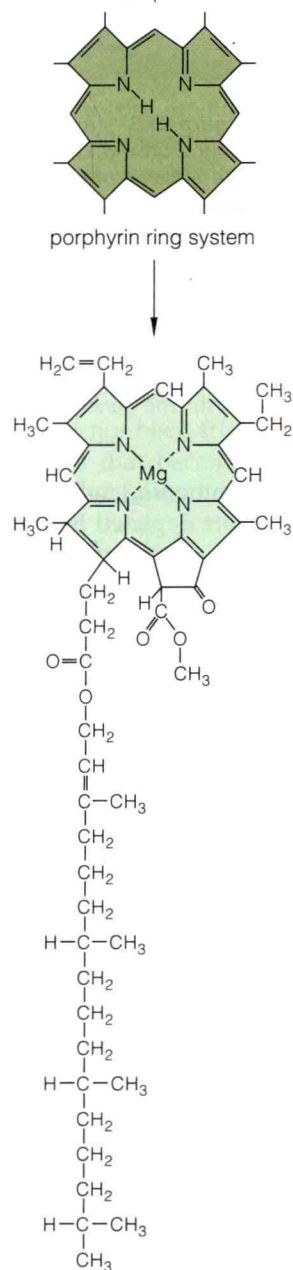


Figure 21.4 One hypothetical sequence by which formaldehyde, an organic compound, underwent chemical evolution into porphyrin. Formaldehyde was present when the Earth formed. Porphyrin is the light-trapping and electron-donating component of all existing chlorophyll molecules. It also is a component of cytochrome, which is a protein component of electron transport systems that are part of many metabolic pathways.

and it is easily replicated before each cell division. As you know from earlier chapters, arrays of enzymes and RNA molecules operate together to carry out DNA's encoded instructions.

Most existing enzymes are assisted by the small organic molecules or metal ions that are called coenzymes. Intriguingly, some types of coenzymes have a structure that is identical to that of the RNA nucleotides. Another clue: Heat nucleotide precursors and short chains of phosphate group together, and they will self-assemble into strands of RNA. On the early Earth, energy from the sun or from geothermal events would have been sufficient to drive the spontaneous formation of RNA molecules.

Very simple self-replicating systems of RNA, enzymes, and coenzymes have been created in some laboratories. Did RNA later become the information-storing templates for protein



chlorophyll a, one of the light-trapping pigments of photosynthetic plant cells