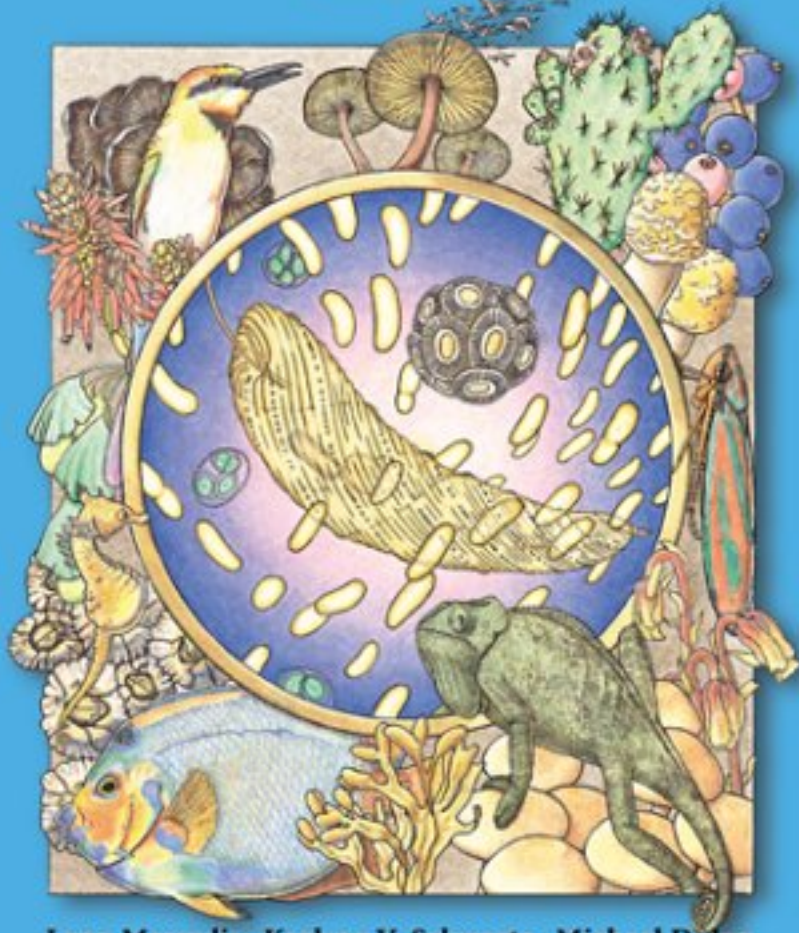


Diversity of Life

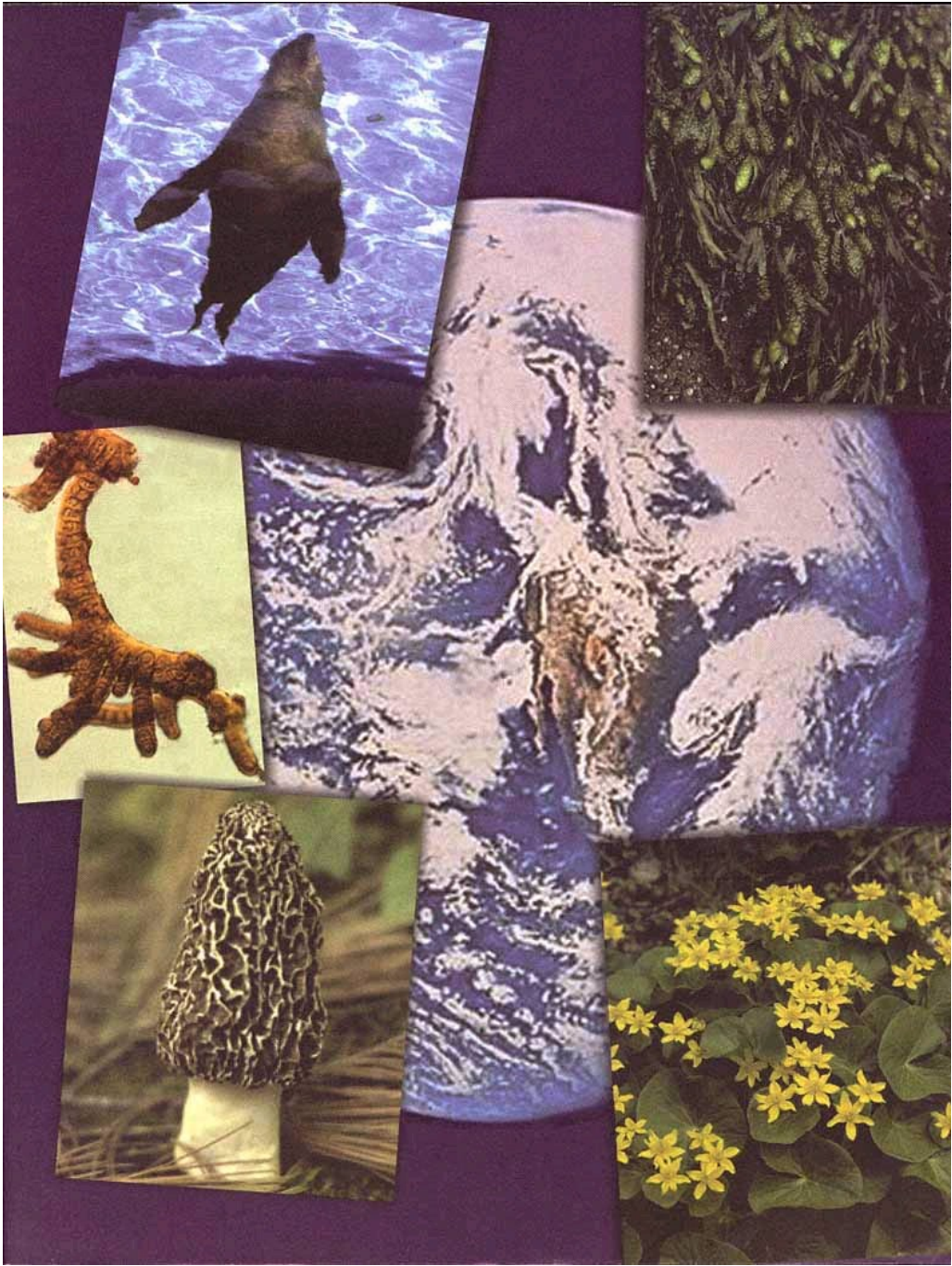
The Illustrated Guide to the Five Kingdoms

Second Edition



Lynn Margulis Karlene V. Schwartz Michael Dolan

Illustrated by Kathryn Delisle and Christie Lyons



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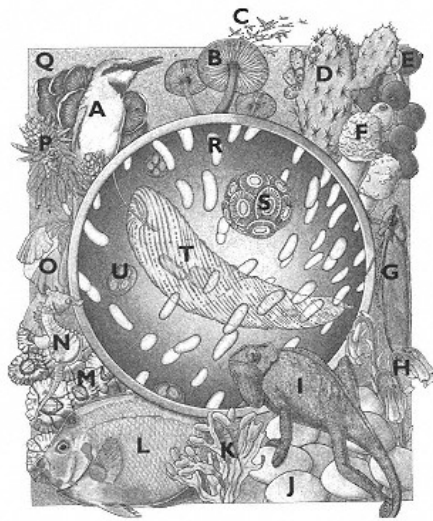
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Note to the Reader

As we burn rain forests for farm space, ranchland, and hardwood, as we drain ponds and level hills to accommodate housing projects and shopping malls, we encroach on the lives and living spaces of the other organisms with whom we share this planet. We are clearing out our planetmates faster than we are learning about them. The relentless increase of human beings at the cost of other organisms has inspired many eloquent scientists and concerned citizens to put the study of biodiversity—different kinds of life—high on the social agenda. This small guide outlines the basics of biodiversity. To introduce the reader to the diminishing life on Earth, we have selected at least one



- A—Rainbow bee-eater, *Merops ornatus*
 B—Velvet stem fungi, *Flammulina (Gollybia) velutipes*
 C—Lesser flamingos, *Phoeniconaias minor*
 D—Prickly-pear cactus, *Opuntia* sp.
 E—Viburnum shrub, *Viburnum nudum*
 F—basidiomycete fungus, *Amanita flavoconia*
 G—Leafhopper insect, *Graphocephala coccinea*
 H—Pinesap (Indian pipes), *Monotropa hypopitys*
 I—Ituri chameleon, *Chamaeleo ituriensis*
 J—Sulfur tuft mushrooms, *Naematoloma fasciculare*
 K—Rockweed, *Fucus vesiculosus*
 L—Atlantic queen angelfish, *Halacanthus ciliatus*
 M—Acorn barnacles, *Balanus balanoides*
 N—Sea horse, *Hippocampus* sp.
 O—Ginkgo, *Ginkgo biloba*
 P—Aloe, *Aloe* sp.
 Q—basidiomycete fungi, *Crepidotus variabilis*
 R—Proteobacteria, *Aeromonas hydrophila*
 S—coccolithophorid, *Emiliania huxleyi*
 T—euglenid, *Euglena spirogyra*
 U—cyanobacteria, *Gloeocapsa* sp.

Common name is followed by genus and species scientific names. "Sp." refers to the fact that the species in the genus is unknown.

Species List for Cover of Diversity of Life on Earth

member of each of the largest groupings, or phyla, of the five kingdoms and depicted it with the other members of its living community.

Designed for teachers and students, as well as the interested public, the book has a spiral binding that allows this book to lie flat for coloring or labeling. Because descriptions are subject to differing opinions and change as new information becomes available, no names or labels appear on the full-size illustrations. A smaller, labeled copy of each drawing accompanies the text that describes the organisms in their habitat. The genus (which comes first but is more like our family name) and species (second, but more like our personal name) of most organisms, as well as explanatory information, are provided. A complete list of species, genera, and phyla illustrated in this book appears in the Appendix, beginning on page 175. Members of some of the most abundant and familiar phyla (such as the molluscs, chordates, and angiosperms) are represented more than once.

Introduction

Biodiversity: All of Life

Although full of astounding beings, much of life on Earth remains a mystery. This guide introduces many unfamiliar organisms and describes many familiar ones. Through illustrations that show examples from each of the large groups, or phyla, the full range of living beings is discussed. This book is a primer in biodiversity.

Biodiversity (a short term for biological diversity) may be defined as the variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families, and even higher taxonomic groupings (Wilson, 1992). Biodiversity also encompasses ecosystems, that is, the community of organisms that inhabit a specific environment and the physical forces that impact those organisms. This book introduces the diversity of life in ecosystems around the world, illustrating the rich variety of bacteria, protocists, fungi, animals, and plants, and the five major kingdoms into which all organisms are classified.

Currently described in the literature of biology are approximately 1,450,000 species of terrestrial (land-dwelling) organisms, 318,000 species of aquatic (freshwater and oceanic) organisms, and 100,000 species of symbionts (organisms living on or in other live beings) (Reaka-Kudla et al., 1997). However these are believed to be only a small fraction of the extant species—those living on Earth today. Insects, animals with more than one million species, are the largest single group formally described by scientists; based on collections gathered in tropical rain forests the number of extant species of insects alone may top thirty to fifty million (Erwin, 1997). The marine equivalent of rain forests in terms of diversity of species are the coral reef communities. Probably millions more reef species are present than the 93,000 animals, algae, and other organisms described in reefs so far.

Unlike other books on biodiversity, this work places each organism in its habitat, that is, its natural environmental context. From photosynthetic bacteria to amebas and slime molds, from horsetails to tube worms and velvet worms, each being is depicted in its own surroundings, which includes other members of its community. Ecological, taxonomic, and structural information are presented together in the context of natural history.

For all of the richness in diversity of plants and animals, the microscopic organisms—the microbial world of fungi, protocists, and bacteria—provide a vast contrast, another level of diversity. Microbes are diverse not only because of their dense populations and specialized metabolisms, but also because so many microbes have evolved specific symbiotic associations with large beings. Just as Charles Darwin could identify dozens of plant species from seeds in a ball of mud on a bird's wing, microbiologists can detect dense concentrations of microbes from small samples. From a 0.1 milliliter particle suspension derived from 1.0 gram of tropical leaf litter, 145 fungal species were reported (Rossman, 1997). Some 69,000 species of fungi are described in scientific journals, but a total of 1.5 million fungal species are estimated by extrapolation: so many fungi form specific symbioses with plants, insects, and other organisms (Hawksworth, 1991). Similarly, at least ten percent of insects harbor specific bacterial symbionts that have co-evolved with the animals (Amann et al., 1995). All scientists agree that the diversity in prokaryotes (bacteria) is extensive and poorly known. Half of the major taxa of bacteria have few or no representatives in laboratory culture with which they can be compared. Probably ninety-nine percent of bacteria cannot be cultivated by routine techniques (Pace, 1997).

We tend to take nonhuman life for granted, even though many little-known species are essential to human survival. Our food, shelter, and pharmaceuticals come from other living beings. Coal and petroleum products, including gasoline, plastics, and motor oil, all come from traces of bygone life that were left on Earth's surface when great algal crusts or giant forests died and were buried before they decayed. Thirty to fifty million, perhaps even one hundred, species of organisms in total are estimated to be living today; more than 99.9 percent of all species that have ever lived are now extinct. Present-day insects are astonishingly diverse—more than 751,000 species abound. As many as 250,000 species of protocists are estimated to exist. As for bacteria, the biological literature lists some 10,000 types. Because genes are exchanged between different groups of bacteria, the species concept does not apply to these organisms as it might to plants and animals, so we simply refer to bacterial types.

Some half million species of plants have been described (Margulis and Schwartz, 1998). Because new species are found each year, probably another half million plant species await discovery. The extent of biodiversity attributed to plants moves continually upward, with discovery of previously undescribed tropical forest species. Forces that generate plant diversity include hybridization and polyploidy, which is occurrence of more than two sets of chromosomes in an individual plant; a polyploid plant is genetically distinct from its parent. Polyploid plants amount to more than fifty percent of the total species of plants (Raven et al., 1999). Plant diversity is maintained by genetic isolation and by geographic isolation—individuals are barred from breeding by genes or by geographic features such as a river. Reduction of genetic isolation, reduction of geographic isolation, and habitat destruction reduce plant diversity. Striking examples of habitat destruction are observed in coral reefs and in tropical rain forests. About forty-five percent of the original rain forest has been destroyed and more than 100,000 square kilometers are cut and burned each year; that one percent (100,000 km²) of the total remaining tropical forest is more than the area of Maryland, Vermont, and New Hampshire combined. The first International Plant Survey announced in 1998 that one

in eight of the world's 270,000 plant species are globally threatened with extinction by pollution, habitat destruction, and logging.

Similar human-made and natural forces shape animal species diversity, just as they generate plant diversity. Animal biodiversity is generated and maintained by direct and indirect effects among predators, prey, and their food plants; by genetic isolation; by geographic isolation; and by habitat destruction and fragmentation. What is the extent of biodiversity in the animal kingdom? A total of 1,032,000 animal species have been formally described, compared to an estimated thirty to one hundred million total living species. Of the 1,032,000 animal species, approximately nine-tenths are animals that lack backbones. The remaining tenth are vertebrates—animals that have backbones, such as aardvarks and zebras. More than 25 percent of the mammals and more than 10 percent of the birds are globally threatened with extinction. Extinguished biological diversity is genetic variability forever lost. Numbers of species are declining in most of planet Earth's natural communities at rates unprecedented since the Mesozoic era.

Life in all of its variety is dynamic, shaped by human-made and natural forces that are complex but are not unknowable. Forces that generate and maintain biodiversity are not always obvious to us. What we do know is that biodiversity is critical to sustain life. Biologists are beginning to comprehend the science of biodiversity and to design strategies to protect biodiversity, to maintain Earth's life support, the organisms that share Earth with us.

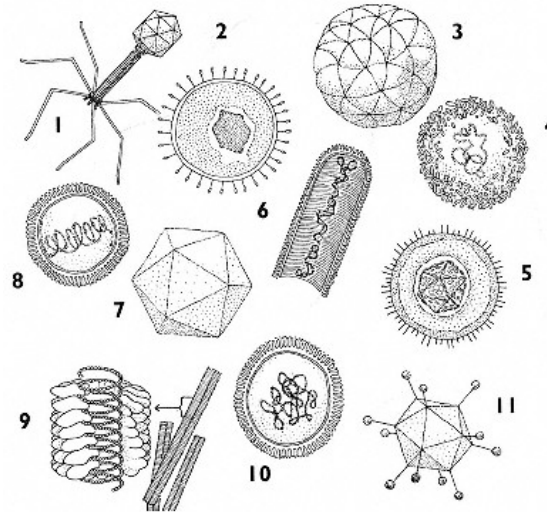


Figure 1

Viruses are particles of DNA or RNA enclosed in a protein coat. Because they are not made of cells, viruses are not considered to be living organisms. Although they reproduce, they can do so only by entering a cell and using its living machinery to replicate themselves. Outside of the cell a virus cannot reproduce, feed, or grow. The viruses pictured here are (1) bacteriophage, (2) human immunodeficiency virus (HIV), (3) polio virus, (4) pox virus, (5) herpes virus, (6) rhabdovirus, (7) picorna virus, (8) orthomyxovirus, (9) tobacco mosaic virus (TMV), in cross section (left) and whole (right), (10) paramyxovirus, and (11) adenotype 2 virus. *Kathryn Delisle*

Viruses

All organisms of the five kingdoms are composed of either prokaryotic (nonnucleated) cells (i.e., bacteria) or eukaryotic (nucleated) cells (i.e., protocists, fungi, animals, and plants). The cell, the smallest living form of life, maintains and reproduces itself if environmental conditions permit. The chemistry of self-maintenance is called metabolism. Viruses, much smaller and much less complex than cells, are not self-maintaining or autopoietic as are cells. Some viruses are depicted in Figure 1. Viruses cannot metabolize, even when fed, watered, and supplied with chemical or light energy. Viruses can replicate inside cells but cannot reproduce on their own. Because they are not cellular

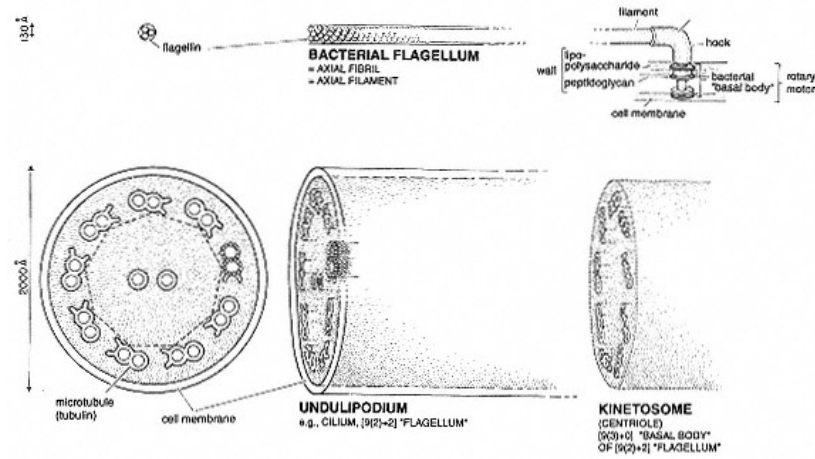


Figure 2

Although both move the cell through its environment, prokaryotic (bacterial) flagella (top) and eukaryotic undulipodia (bottom) differ fundamentally in structure. *Laszlo Meszoly*

entities, viruses do not belong to any of the five kingdoms of organisms. Alternatively, viruses may be thought of as inanimate parts of the cells that they infect and hence can be classified with these cells.

Cells and Movement: Flagella and Undulipodia

The parts of living cells move. Whether the cell is prokaryotic or eukaryotic, its components bounce around by random jiggling called Brownian motion. In addition, some bacterial cells glide slowly (by an unknown mechanism) if in contact with a surface, whereas others swim using their rotary motor flagella (Figure 2).

Bacterial cells lack active intracellular movement, whereas in all nucleated cells, directed internal cell motion occurs, including that of mitosis. Most bacterial cells divide directly by a process called binary fission. Although eukaryotic cells also divide in two, their genetic organization (DNA on chromosomes within a nucleus) requires that cells divide by mitosis. In many organisms, during mitotic cell divisions, at the ends (poles) of the cells are two or four dotlike bodies called centrioles. Magnified, these bodies show a characteristic array of microtubules: nine triplet microtubules in a cylindrical pattern (Figure 2). The centriole structure of nine groups of three microtubules each and no central microtubules is called the $[9(3)+0]$ array. Eukaryotic cells swim using wavy structures called cilia or other kinds of undulipodia. These organelles—whether oviduct cilia, sperm tails, or amebomastigote undulipodia—show the same pattern in cross section under an electron microscope. The kinetosome that lies under the undulipodium is identical to the centriole, but the shaft, with its nine groups of two

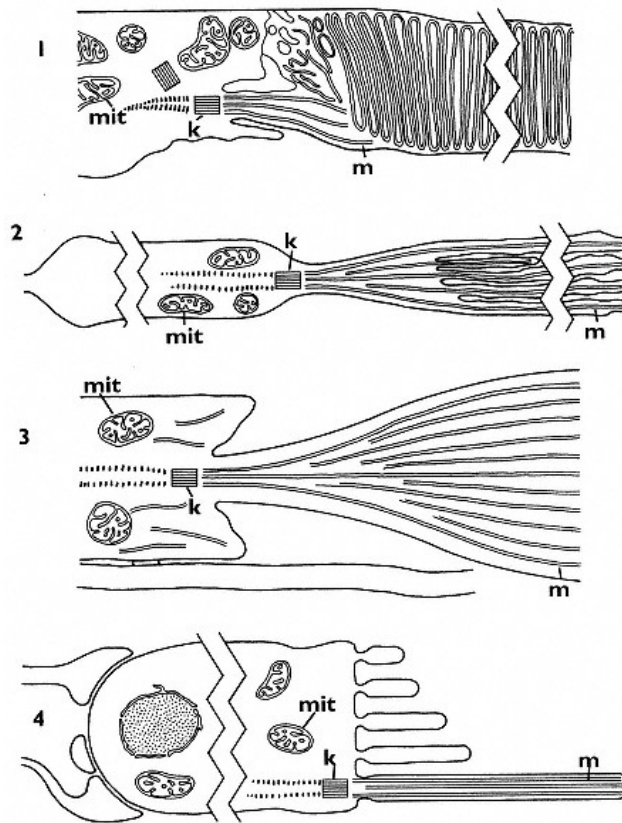


Figure 3

Four general types of animal sensory cells based on cilia (a type of undulipodium). All contain modified undulipodia with microtubules. (1) Rod cell of the eye (vision). (2) Olfactory cell (smell). (3) Mechanoreceptor cell (touch). (4) Inner-ear cell (hearing). **k** = kinetosome; **m** = microtubule; **mit** = mitochondrion; zig-zags represent omissions in long structures.

Kathryn Delisle

fused microtubules each, surrounding two separate central microtubules, differs slightly (Figure 2).

Undulipodial shafts have $[9(2)+2]$ cross sections made of longitudinally aligned microtubules. Evolution has modified undulipodia into a fantastic variety of functional structures, including the sensory hairs of lobster antennules and the cilia on the gills of marine animals (Figure 3). The term used to describe mitotic centrioles and cilia basal bodies is centriole-kinetosome. Centriole-kinetosomes, undulipodia,

mitosis, and [9(2)+2] arrays are entirely absent in prokaryotes—that is, they do not occur in members of the Kingdom Bacteria. Although microtubules and mitosis are present in fungi, centriole-kinetosomes and undulipodia are always absent.

Because of the confusion surrounding the names of these structures, we define them as follows:

Flagella (Greek: "whip"), **s. flagellum**. Solid bacterial organelles of motility composed of flagellin, intrinsically nonmotile. Rotary locomotion is generated at the points of insertion of organelle into the cell. Flagella are extracellular in that they always extend externally beyond the plasma membrane of the prokaryotic cell. Diameter: fifteen to thirty nanometers. Includes the axial filaments or axial fibrils of spirochetes. In these latter microbes the flagella are situated in the periplasm, the space between the outer and the inner (plasma) lipoprotein membranes of the Gram-negative cell wall.

Undulipodia (from Latin: *undula*, "a little wave," and Greek: *podos*, "foot": "little waving feet"), **s. undulipodium**. Cilia and [9(2)+2] flagella: Long slender tubulin-containing intracellular organelles of motility of eukaryotes, intrinsically motile throughout their length, capable of movement when severed from the cell. Diameter: 0.25 micrometers (250 nanometers). The axoneme is the [9(2)+2] shaft of the undulipodium; that is, it is the undulipodium lacking its surrounding membrane.

Many biologists retain "flagellum" and "basal body" for the ninefold symmetrical microtubular motility organelles of eukaryotes. We suspect that they are reluctant to change because they do not generally confront bacteriologists. In the past the term flagellum has referred to the undulipodium/cilium found in animals, plant sperm, and many protocists, as well as to the rotating bacterial organelle. This ambiguous use of the term has led to confusion, which we here avoid by using two different terms.

Modes of Nutrition: Autotrophy and Heterotrophy

The existence of photosynthetic animals such as *Convoluta roscoffensis* and heterotrophic plants such as Indian pipes (*Monotropa*) makes clear that nutritional mode alone cannot be used to define kingdoms or phyla. Indeed, bacteria (monerans) display a remarkable diversity of nutritional modes (Table 1). With the exceptions of photoheterotrophy and chemotrophy, every nutritional mode is represented among the protocists.

Photoheterotrophs use organic compounds as food sources while simultaneously employing visible light to generate ATP directly, whereas chemoautotrophs can exclusively use carbon dioxide and other inorganic compounds as sources of carbon and energy. In strict chemoautotrophy (e.g., methanogenesis, methylotrophy, ammonia oxidation, sulfide oxidation, and the like), neither the source of carbon nor the source of energy is from carbon-hydrogen (organic) compounds. These two metabolic modes—photoheterotrophy and chemoautotrophy—are found only in bacteria. Thus, although protocists display a greater range of nutritional types than do plants, fungi, or animals,

TABLE 1*Modes of Nutrition*

Organisms have evolved various ways of obtaining energy and carbon—the two requirements for growth and reproduction.

MODE/EXAMPLE	ENERGY SOURCE	CARBON SOURCE
Autotrophy Plants, algae, and cyanobacteria	Light	Atmospheric CO ₂
Sulfide-, methane-, and ammonia-oxidizing bacteria	Inorganic compounds (H ₂ S, CH ₄ , and NH ₃)	Atmospheric CO ₂
Heterotrophy Fungi, protists (ciliates, mastigotes, slime nets, etc.) and animals (molluscs, hydras, fish)	Organic compounds (containing C, H, N, O)	Organic compounds (containing C, H, N, O)

protocists are far more limited in energy- and nutrient-gathering capability than are bacteria. Bacteria are by far the most nutritionally diverse organisms; photosynthesis and motile heterotrophy (a typical animal trait) first evolved in bacteria.

All five kingdoms include organisms that exhibit biomineralization—the production of minerals by live cells and the incorporation of those minerals into their bodies or protective coverings (Table 2).

Populations, Communities, and Ecosystems

Populations of organisms are the members of the same species found in the same place at the same time, such as a herd of bison on the plains or all the daisies in a meadow. Communities of organisms are composed of the populations of organisms of different species in a common environment at the same time. The habitat scenes of this book illustrate communities simplified in terms of number of species represented. Communities form ecosystems—major interacting systems that involve both living organisms and their physical environment. Ecosystems may alternatively be defined as the smallest volumes in nature that entirely cycle elements crucial for life, such as the ocean, cloud forest, jungle, or desert. Carbon (C) in carbon dioxide (CO₂) is fixed into organic compounds such as sugars; these are transformed into metabolic intermediate compounds until carbon dioxide is again produced. Nitrogen (N), as in N₂, is converted to amino acids and proteins. The elements C and N cycle faster inside an ecosystem than between ecosystems. Each organism lives in an ecosystem with its producers, consumers, and decomposers.

Together, all live organisms on the face of the Earth, from the bottom of the abyss to the air at the top of the atmosphere, make up the biota—all living matter on Earth at a given time. Paleontology is the study of the past biota, the 99.9 percent of all species that ever lived on Earth and are now extinct. The biota and all of its natural habitats together are called the biosphere.

The biosphere thus is the sum total of all of Earth's ecosystems. When all of Earth's ecosystems taken together interact as a very active planetwide system of life, certain

TABLE 2

Biomining: Biologically Controlled Mineral Precipitation by Cells

Each of the five kingdoms contains organisms that can mobilize minerals and incorporate them into their bodies and support structures. A few examples are given here (see Lowenstam and Wiener, 1989, in Resources, page 217). (The aid of John Stolz and Heinz Lowenstam in developing this table is gratefully acknowledged.)

MINERAL	BACTERIA	PROTOCTISTA	FUNGI	ANIMALIA	PLANTAE
Calcium					
Calcium carbonate (CaCO_3 : aragonite, calcite, vaterite)	Extracellular precipitate Sheath precipitates	Ameba tests Foraminiferan tests	Extracellular precipitates	Corals Mollusc shells Echinoderm skeletons Calcareous sponges Some kidney stones	Precipitates
Calcium phosphate (CaPO_4)			Extracellular precipitates	Brachiopod "lamp shells" Vertebrate teeth and bones Some kidney stones	
Calcium oxalate (CaC_2O_4)				Most kidney stones	<i>Dieffenbachia</i>
Silicon					
Silicon dioxide (SiO_2)	Precipitates	Diatom tests Radiolarian tests Silicomastigote scales		Glass-sponge spicules	Grass phytoliths
Iron					
Magnetite (Fe_3O_4)	Magnetosomes			Arthropods Molluscs Vertebrates	
Greigite (Fe_3S_4)	Magnetosomes				
Siderite (FeCO_3)					
Vivianite ($\text{Fe}_3[\text{PO}_4]_2 \cdot 8\text{H}_2\text{O}$)	Extracellular precipitates				
Goethite ($\text{FeO} \cdot \text{OH}$)			Extracellular precipitates	Chitons	
Lepidocrocite ($\text{FeO} \cdot \text{OH}$)			Extracellular precipitates	Chitons	
Ferrihydrite ($5\text{Fe}_2\text{O}_3 \cdot 9\text{H}_2\text{O}$)				Molluscs	Angiosperms
Manganese					
Manganese dioxide (MnO_2)		Intracellular or extracellular precipitates around spores			
Barium					
Barium sulfate (BaSO_4)		Algal-plastid gravity sensors Xenophyophore skeletons		Sense organs: statoliths (otoliths)	
Strontium					
Strontium sulfate (SrSO_4)		Acantharian tests		Mollusc shells	

physiological properties emerge. The geophysiology chiefly derives from the profound influence of the biota on environmental conditions: the surrounding temperature, acidity (pH), and moisture content. We hypothesize that the biota, the sum of life on Earth, helps to control the partial pressures and oxidation states of the atmospheric gases and (through regulation of greenhouse gases and ozone) the air and water temperature. By producing ammonia as waste, the biota lowers acidity. Organism growth and behavior may even help control ocean salinity. The tendency of the biota to modulate conditions in its immediate environment has been called Gaia. More specifically, Gaia is the largest composite ecosystem of all, the sum of the smaller ecosystems on Earth, composed of all the life forms with their interactions tending to modulate their immediate environments. This book introduces the components of Gaia (all of our planetmates) about most of which we tend to be completely unaware.

The five-kingdom groupings here reflect as much as possible the reorganization of the biological sciences: molecular biological detail, ultrastructural and genetic analysis, and paleobiology. The unambiguous classification of the diversity of life requires recognition of the key importance of microorganisms, especially the poorly known protocists, in the evolution and present-day distribution of life on Earth.

Biomes and Planet Earth

Biomes are huge, contiguous territories that are geographically identifiable—the world ocean, the northern tundra, or the equatorial tropical rain forests. Biomes are composed of ecosystems; for example, coastal zones, open ocean, and abyssal plains are all part of the ocean biome. The sum of all biomes is the biosphere, which is the twenty-kilometer-deep, hollow sphere of water, air, and land at Earth's surface in which life resides.

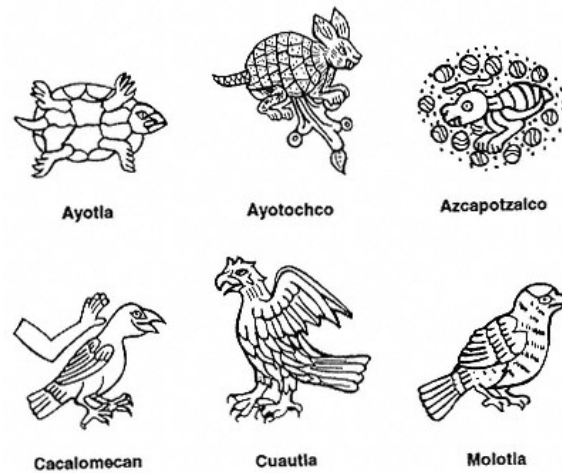


Figure 4
Ancient Mexicans named all the organisms around them and specified their usefulness. The knowledge in the Nahuatl language was recorded in the sixteenth century by Fray Bernardino de Sahagún in the *Florentine Codex*: "... 2nd chapter, which telleth of all the different kinds of birds ... 4th paragraph, which telleth of all the birds of prey. ... The eagle is fearless, a brave one. ... It can face the sun. ... It is brave, daring, a screamer, a wing-beater. ... It constantly grooms itself." From R. L. Castro and F. Garrido. 1984. *Escribir con Imágenes: Antiguos Nombres Mexicanos para Iluminar. Ediciones del Ermitaño, Tlacopec, Mexico.*

Systematics: Classification and Naming of Organisms

Every society has a classification system that often is based on the organism's direct relationship to people (Figure 4). Our modern system of classifying organisms began with the Swedish scientist Carl von Linné (1707–1778), known by the Latin version of his name, Carolus Linnaeus. Linnaeus revolutionized the naming and identification of organisms by giving each type two names, a generic name and a specific name. Binomial ("two-name") nomenclature is the proper term for Linnaeus's system, which is still in use today. Every known organism is identified by its two-part technical name, always written in italics and usually derived from Latin or Greek. The first part of the name refers to the larger group (genus) to which an organism belongs. The two words together refer to its species. The genus is often abbreviated as in *E. coli*.

The genus to which most soup beans belong is *Phaseolus*, although the larger faba beans belong to the genus *Vicia*. Chimpanzees and gorillas belong to the genera *Pan* and *Gorilla*, respectively. Chimps, gorillas, and humans all belong to the mammalian order Primates. *Homo sapiens* refers to human beings; *Homo* is the genus name, and *Homo sapiens* our species name (in Latin *Homo* means "human," and *sapiens* means "wise"). Species are grouped into genera, genera into families, families into orders, orders into classes, and classes into phyla. Each phylum can be assigned to one of the five kingdoms.

Dogs, for example, are canids; they belong to Kingdom Animalia, phylum Chordata, class Mammalia, order Carnivora, and family Canidae. Their genus is *Canis*. *Canis familiaris*, *Canis lupus*, and *Canis latrans* are the scientific names of the domesticated dog, the wolf, and the coyote, respectively. No matter from what country naturalists or scientists come, they use the genus and species names. An important benefit of taxonomy is its universal scientific terminology. Even scientists who write with Japanese or Russian letters use the Latin alphabet for these scientific names. If the technical genus and species name is always the same worldwide, everyone knows without a doubt which organism is meant, even if it has a different common name in each language. Lightning bugs and fireflies are flying insects that glow in the dark. Are lightning bugs and fireflies the same? To be certain, one needs to use the scientific name.

The inadequacy of the Aristotelean two-kingdom system (e.g., plants and animals) has been known since the nineteenth century, when the German scientist Ernst Haeckel (1834–1919) created three kingdoms: Protista, Plantae, and Animalia. All modern scientists agree that bacteria, fungi, and other microscopic organisms do not fit into a two-kingdom scheme, although the details of the overall taxonomy of life are still being worked on today. Our summary, of course subject to revision, is in the Appendix, which begins on page 175.

Five Kinds of Life

Bacteria are strange. Electron microscopy has shown that not only are bacteria very different from plants, animals, and fungi, but bacteria are also very different from each other and from the microscopic prototists (the protists). All scientists put bacteria in their own kingdom: Bacteria, or Procaryotae, or Monera. Unlike all other organisms on

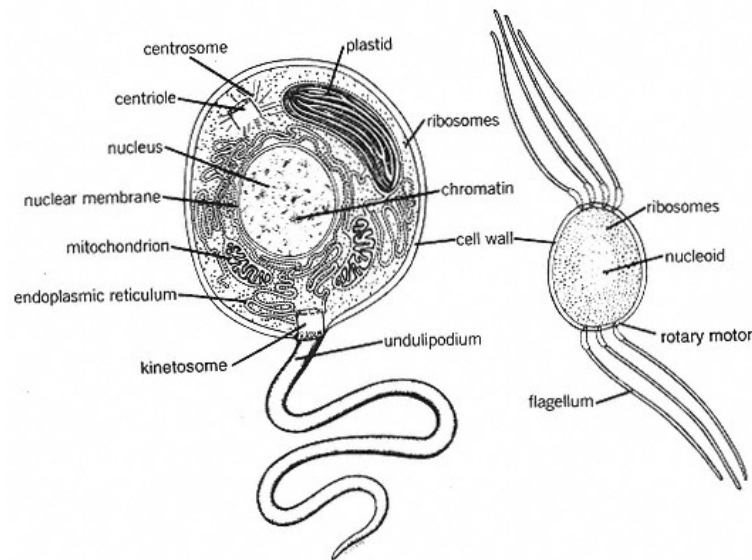


Figure 5

The bacterial cell (right) is nonnucleated, or prokaryotic. Its DNA is dispersed throughout the cell, and it has a flagellum for locomotion. By contrast, the eukaryotic cell (left) has a nucleus, which contains its DNA in the form of chromosomes. Its organelle of locomotion is the undulipodium. The details of the rotary motor flagellum and the far larger whiplike undulipodium are shown in Figure 2 (page 4). *Christie Lyons*

Earth, bacteria lack nuclei in their cells (Figure 5). Also unlike the other kingdoms of organisms on the planet, all bacteria can, in principle, trade genes with each other. Still, even until the 1960s most biologists grouped bacteria together with all the other nonanimals; because bacteria were alive but were not animals, it was logical to call them plants. Haeckel's recognition of microbes as an altogether different kind of life is now catching on.

The first adoption of Haeckel's ideas in the United States came in 1956 when biologist H. P. Copeland (1902–1968) separated Haeckel's one kingdom Protista into two. Copeland wrote a book presenting a four-kingdom classification of organisms—which nearly no one read at the time. Copeland placed bacteria into one kingdom and prototists (which included the fungi) into another kingdom of microscopic beings. Copeland and other biologists realized that all organisms are made of cells that either have nuclei (eukaryotes) or do not have nuclei (prokaryotes). Improved microscopes made it easier to determine the presence or absence of nuclei. Because all plant, animal, and fungal cells have nuclei, these diverse groups of organisms are really much more closely related to one another than to bacteria.

By 1959 Cornell University Professor R. H. Whittaker (1924–1980) had thoroughly read Copeland's little book on the "classification of the lower organisms." Whittaker proposed a five-kingdom system that divided life forms into the groups that we present here. Through his study of pine forests in New Jersey and deserts in the southwestern

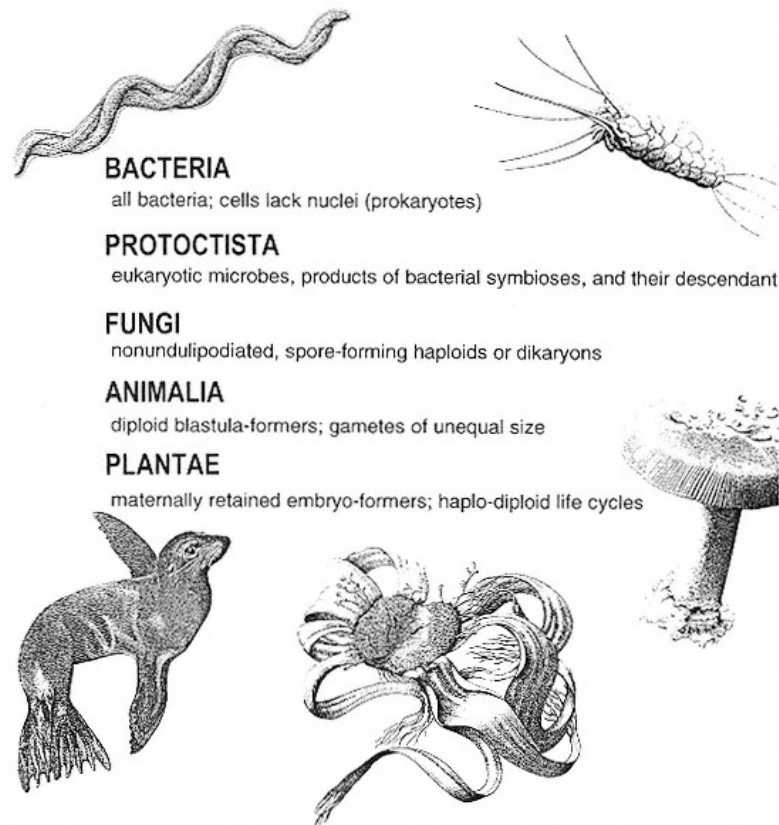


Figure 6

Five kinds of life. Clockwise from top left: *Cristispira* (spirochete), *Mallomonas* (golden-yellow alga), *Cantharellus cibarius* (chanterelle), *Welwitschia mirabilis* (gnetophyte), *Zalophus* (California sea lion). Protists are the smallest prototists from which all the other prototists, as well as fungi, animals, and plants, evolved.
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United States, Whittaker found bacteria and fungi to be so unlike plants that he could no longer call them plants. He therefore erected new kingdoms for bacteria and fungi. Yet his system is still limited to an accessibly small number of kingdoms.

This book is based on Whittaker's five kingdoms: (1) Monera, (2) Protocista, (3) Fungi, (4) Animalia, and (5) Plantae. These correspond to (1) bacteria; (2) algae, ciliates, and approximately forty other groups of microbes and related larger organisms that are not members of the plants, animals, or fungi; (3) molds, yeasts, and mushrooms; (4) animals; and (5) plants (bryophytes and tracheophytes). These are the five major kinds of life on Earth (Figure 6).

The only slight change we have made is to follow Copeland rather than Whittaker in recognizing the great protocist kingdom. We recognize the limitation of multicellularity evolved from unicellularity on many different occasions, and so place all protists with their multicellular descendants into inclusive groups. We recognize Copeland's revival of Hogg's Kingdom Protocista, which makes sense now that these organisms are better studied. This change allows us to include larger nonanimal, nonfungal, and nonplant organisms with their smaller relatives. We reunite the smaller members of the kingdom, the protists (single cells with nuclei), with their larger immediate descendants by calling them all protocists, including the many-celled organisms with nuclei that do not conform to the descriptions of plants, animals, or fungi.

Multicellular animals used to be called metazoans, whereas "unicellular animals" were called protozoans. In the five-kingdom system, however, there is no such thing as a one-celled animal. In the five-kingdom system all animals develop from a mother's egg that has been fertilized by a swimming, smaller cell (called a sperm) from the father. The fertile egg develops into a blastula, which is a small, hollow ball of cells that usually goes on to develop a gastrula, an embryo with the beginnings of a digestive system that generally goes on to form tissues. Thus, all animals are multicellular.

Geological Time Scale

All organisms have bacterial ancestors. Prokaryotes first appeared in the fossil record approximately 3,500 million years ago. From some protocists, the first new organisms to form from these prokaryotes, emerged members of the other eukaryotic kingdoms: Animalia and Fungi from unknown heterotrophs, and Plantae from green algae (Figure 7). These three kingdoms, which in general appear later in the geological record than protocists do, are defined in this book, and the dates of their earliest fossils are illustrated (Figure 8).

Animals (diploid organisms developing from blastula embryos) from the Ediacaran biota (see Figure 12, p. 50) are found in the fossil record of more than 500 million years ago. Fungi (haploid and dikaryotic organisms developing from desiccation-tolerant spores and lacking undulipodia at all stages in their life cycles) appear, primarily in association with plant roots, in the late Silurian or lower Devonian, some 450 million years ago. Plants (organisms that develop from embryos that are not blastulas and that are surrounded by maternal tissue, and in which the haploid alternates with the diploid generation) also appeared in the lower Paleozoic era. Fossils interpreted to be robust walled cysts of protocists are recorded in the fossil record more than a billion years

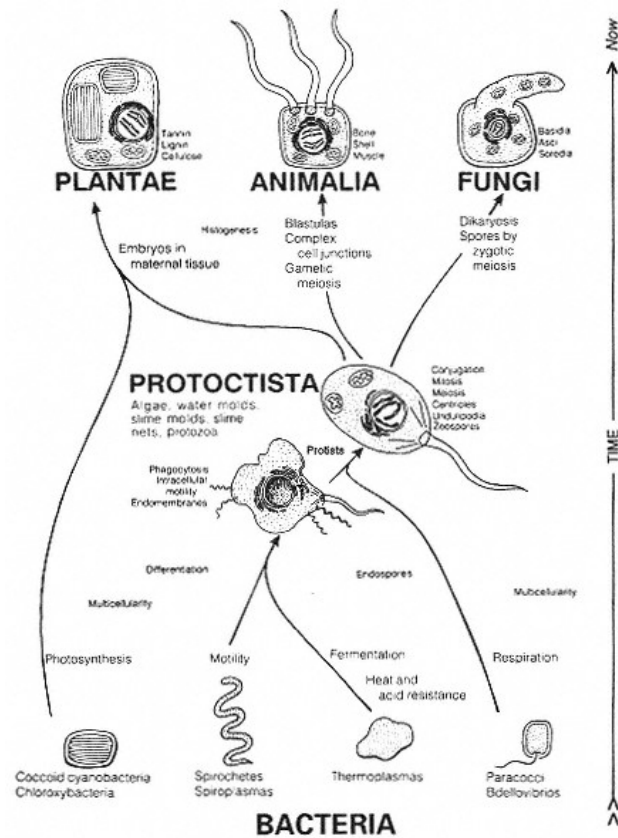


Figure 7

This phylogeny, or family tree, of life on Earth indicates the ancient bacterial (prokaryotic) lineages, as well as lineages of those of their eukaryotic descendants that evolved by fusion of lineages (i.e., by symbiogenesis to form protists). The protist cells are ancestral to all other prototists, as well as to the plants, animals, and fungi. This diagram thus depicts what is referred to as the serial endosymbiosis theory (SET) of evolution. The joining of arrows indicates the origin of cells by symbiogenesis. *Laszlo Meszoly*

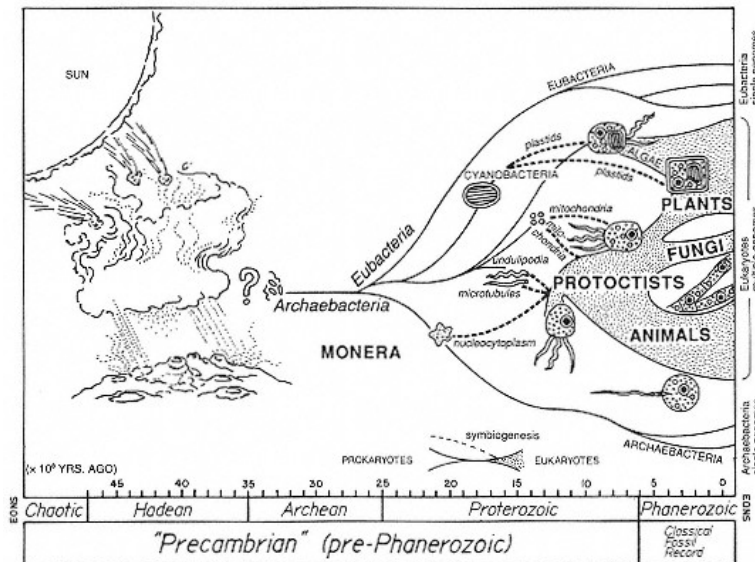


Figure 8

In this geological time scale phylogeny, the evolution of life, is plotted along the geological time scale at the bottom. Eukaryotic kingdoms, those that evolved by symbiogenesis, are shaded. The symbiotic origins of eukaryotic organelles from bacteria are indicated by dashed lines.

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ago. *Grypania*, a coiled tube fossil visible to the unaided eye, may be a two-billion-year old photosynthetic protocist.

Size

As a group, members of the microbial kingdoms (bacteria, protocists, and fungi) range enormously in size. From the smallest coccoids, which measure 0.09 micrometer in diameter, to the giant kelps, these organisms extend in size over eight orders of magnitude. Botanists and marine biologists do not like to call the gigantic members of the kingdom protists, a term that connotes the very small. In the history of biology the term protist once included the prokaryotes. In this work the term protist is informal, referring to members of Kingdom Protocista that require the use of a microscope to be visualized.

Associations

All organisms depend on others to provide their food, remove their waste, and produce their breathable gas. No species can survive in the absence of others, although the details vary from organism to organism. Some plants require certain insect or mammalian species for pollination, but the contact between the sexual parts of the plant and the pollinating bee or bat, for example, may be brief. Some protocists (e.g., myxosporans and apicomplexans) derive all of their nutrition from members of

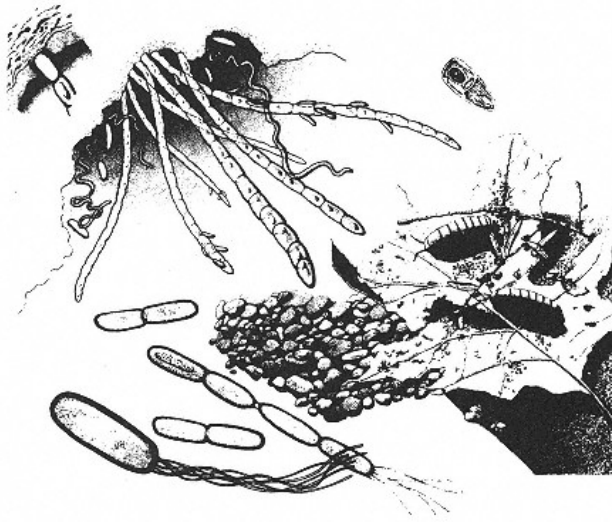


Figure 9

Intestines of animals often harbor spore-forming bacteria. *Arthromitus* sp. (Endospora) attach to the hindgut wall of the termite *Pterotermes occidentis* (upper left). A related *Arthromitus* sp., whose spores are shown in soil particles, was isolated from the guts of sowbugs, *Porcellio scaber* (lower right). Christie Lyons

different kingdoms and phyla; they are symbiotrophs. Organisms that kill or seriously threaten fellow organisms in their living community are called necrotrophs.

Symbionts are organisms of different species living in long-term association. The nature of symbiotic relationships changes from casual to permanent, from temporary to obligate, depending on many factors—of which environmental conditions and evolutionary history may be the most important. Symbiogenesis is the origin of new form and function that emerges from long-term symbiosis (e.g., the appearance of the rumen in the ancestors of cattle or of the trophosome in pogonophoran worms).

Spores

Production of spores is a common means of propagation and dispersal by microorganisms (bacteria, protocists, and fungi) and plants. Spores are small packages containing the organism's genome and are resistant to heat and desiccation. Animals' digestive tracts are fertile habitats for spore-forming microbes (Figure 9). The microbes' life histories often consist of inert stages as spores in soil or water, with growth and reproductive stages confined to the gut. Spores of fungi (Figure 13) and plants (Figure 15) are described in Chapters 3 and 5.

Chapter 1— Bacteria

The kingdom Bacteria comprises all the bacteria—the subvisible prokaryotic, or nonnucleated, organisms. Most are simple unicellular organisms, such as the proteobacteria. The most complex bacteria undergo developmental changes in form: Unicellular bacteria may come together in packets of millions and metamorphose into stalked structures that release resistant sporelike microcysts (e.g., Myxobacteria, see page 36). Some grow long, even, branched filaments; others form fat, sessile bodies that bud off

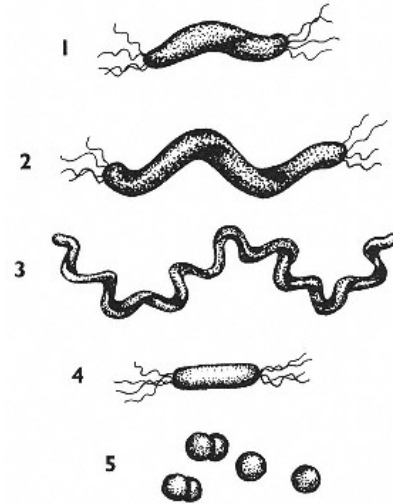


Figure 10
Bacterial shapes. (1) *Vibrio*, curved. (2)
Spirillum, helical, external flagella. (3)
Spirochete, helical, internal flagella. (4)
Bacillus, rod-shaped. (5) Cocci, spherical. *J.*
Steven Alexander

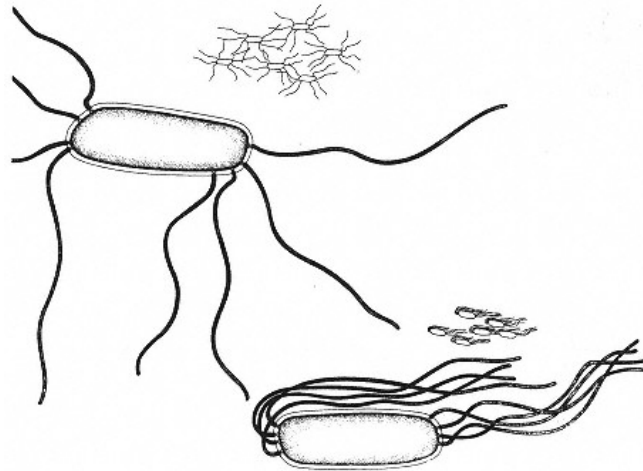


Figure 11
 Bacterial flagella exhibit two basic types of movement: They twiddle (top left), in which the flagella move in an uncoordinated way and the bacterium remains stationary, and they run (lower right), in which the flagella move in a coordinated and synchronized way, propelling the cell in a certain direction (here to the left).
 Christie Lyons

swimming, flagellated, single-celled offspring (Figure 10). The distinctive type of movement displayed by flagellated bacteria is shown in Figure 11.

Noted for their complex chemistry, bacteria effect many chemical transformations. Metabolically, bacteria are far more diverse than all the eukaryotes (protocists, fungi, animals, and plants) taken together. Some monerans—such as the methanogenic, halophilic, and thermoacidophilic bacteria—are genetically distinct enough to be considered a subkingdom: Archaea. This distinction is based mainly on comparing the sequence of nucleotides in ribosomal RNA (rRNA). This universally distributed molecule is believed to have mutated relatively slowly through 3.6 billion years of evolutionary time; thus, its nucleotide sequence—based on comparison of bacterial rRNA to that of plants, animals, protocists, and fungi—is relatively unchanged. By comparing the RNA sequences of different groups of organisms, we can estimate how closely related they are.

Although the nomenclature of bacteria is in dispute, more than 10,000 "species," including the cyanobacteria, have been named and described in the bacteriological literature. Many more are still unidentified; most bacteriologists agree that the majority of bacteria have not been grown and studied. Very few descriptions of bacteria in their natural communities are available.

Concerned with organisms important to medicine and agriculture, bacteriologists rely mainly on a practical manual, *Bergey's Manual of Systematic Bacteriology*. They do not conform their nomenclatural and taxonomic practices to those of other biologists.

Thus, some of the groupings in this text are simplified from those found in the standard reference works (see Resources, page 217) so that the taxonomic level of phylum is conceptually comparable throughout the five kingdoms. We recognize eighteen prokaryotic phyla—fewer than those of the animals or protoctists but more than those of the plants or fungi. These phyla group the bacteria by easily distinguishable, ecologically important characteristics, both morphological and metabolic. Where molecular evolutionary information is available, we keep genetically related groups together. Unlike change through time in other organisms, in bacteria evolutionary change seems to be reversible. In eukaryotes the appearance of new species seems to be an irreversible process. Bacteria, which transfer their genes back and forth to other bacteria throughout the biosphere, group themselves into communities or guilds that form a global network, as Sonea and Panisset (1983) describe.

Pasture

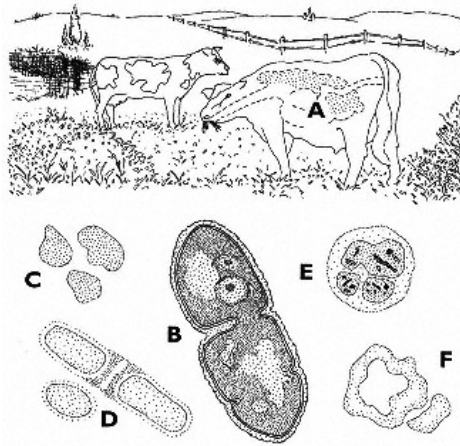
Phylum: Euryarchaeota-Methanogens

To date, two great groups, or phyla, of subkingdom Archaea have been recognized: (1) Euryarchaeota, comprising methanogenic bacteria, which produce methane gas and live in the absence of oxygen, and salt-loving halophils, which do not produce methane; and (2) Crenarchaeota, hot sulfur/acid-tolerant bacteria. Some scientists believe that archaea are the oldest form of life on Earth, which is why they were given a name that means "ancient ones." The methanogens shown here got their name because they produce methane, the same gas that we pipe into our stoves for fuel.

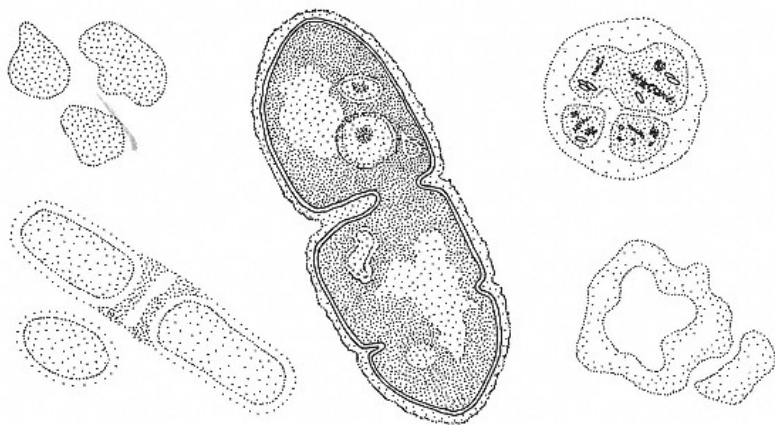
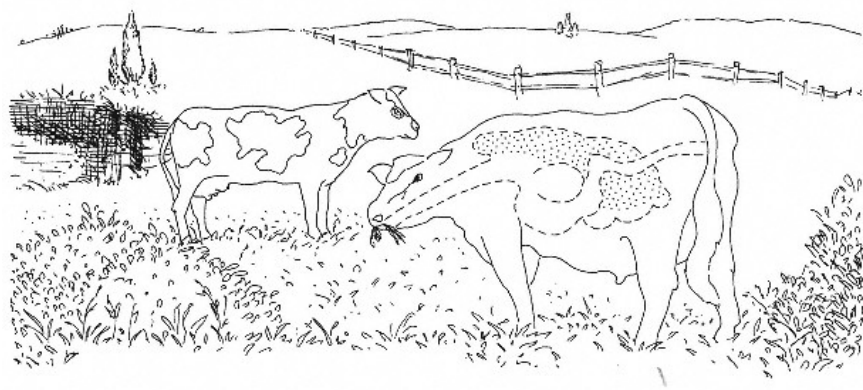
Because they are poisoned by oxygen, methanogens are restricted to anoxic environments: sewage, marine, and freshwater sediments, and the intestinal tracts of some animals, such as the rumen of the four-chambered stomach of cattle (*Bos taurus*, **A**). (The shaded area indicates where bacteria that can break down cellulose live.) Because they can act on only a limited number of substrates, methanogens depend on other bacterial fermenters to convert a wide range of organic compounds into the hydrogen and carbon dioxide gases they need to produce methane. Of the 400×10^{12} to 600×10^{12} grams of methane released into the air each year, an estimated 74 percent comes directly from methanogens.

Many different methanogens reside as symbiotic bacteria that have become organelles in ciliates (see page 94). Such methanogenic ciliates live in anoxic sea water, mud, lake sediment, or sewage water. Each cell of *Plagiopyla frontata* and *Cyclidium porcatum*, for example, contains hundreds of methanogenic bacteria.

The methanogens comprise nineteen genera; fifty species have been named. Pictured here are *Methanobacterium ruminantium* (**B**, in cross section, dividing), *Methanogenium marirgen* (**C**), *Methanobacterium* (**D**), *Methanosarcina* (**E**), and *Methanogenium cariaci* (**F**).



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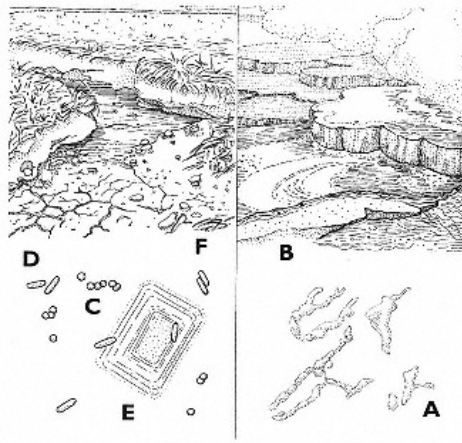
Mud Flats and Hot Springs

Phylum: Euryarchaeota—Halophils

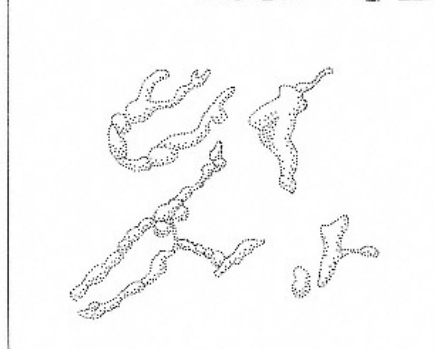
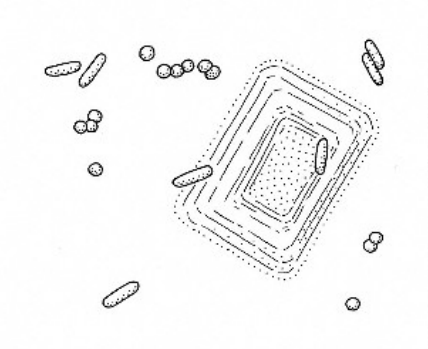
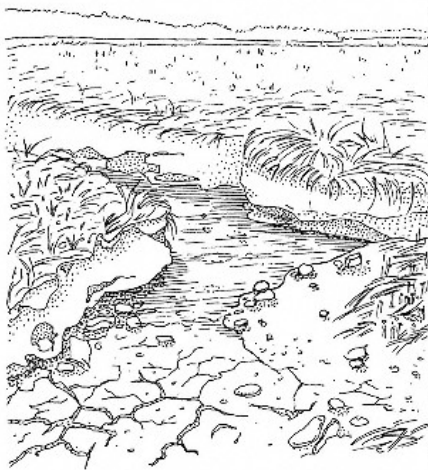
Halophils are incapable of methane production and require salt to live. Halophilic bacteria, such as the spherical *Halococcus sp.* (C) and the rod-shaped *Halobacterium sp.* (D), both much smaller than the salt crystals that surround them (E), live on mud flats in salt marshes (F). The cell membranes of halophils are strong: special components, such as derivatives of glycerol diether, allow them to withstand high salt concentrations. When exposed to low salt concentrations, however—even the fresh water of rain—many cells of halophils burst open. Because, like carrots, halophils make pigments called carotenoids that color their cells bright pink or orange, at high population densities halophils can be spotted from airplanes and orbiting satellites as pink scum on salt flats.

Phylum Crenarchaeota—Thermoacidophilic Bacteria

Thermoacidophilic bacteria, for example, *Thermoplasma acidophilum* (A), which lives in habitats such as this hot spring in a geyser pool at Yellowstone National Park (B), grow vigorously at 60°C and at pH values from 1 to 2 (the pH of concentrated sulfuric acid). At room temperature they freeze and die immediately. Although *Thermoplasma* is a bacterium (and all bacteria are prokaryotes), its DNA, like that of eukaryotes, has a protein coat that probably protects its genes from the hot acid.



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Barnyard

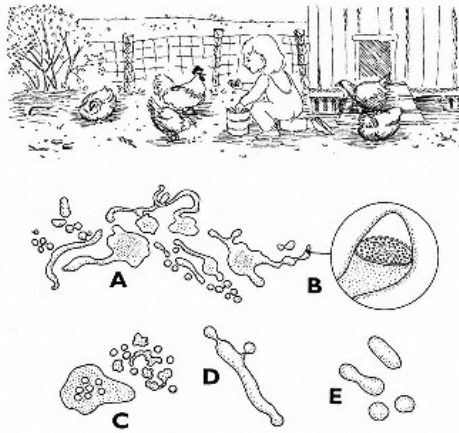
Phylum: *Aphragmabacteria*

Because of their chemical constituents, aphragmabacteria are classified as eubacteria rather than as archaea. Most bacteria—in fact all except those already depicted: the methanogens (see page 20), the halophils, and the thermoacidophiles (see page 22)—are eubacteria. Because they lack cell walls, however, aphragmabacteria differ from all other eubacteria.

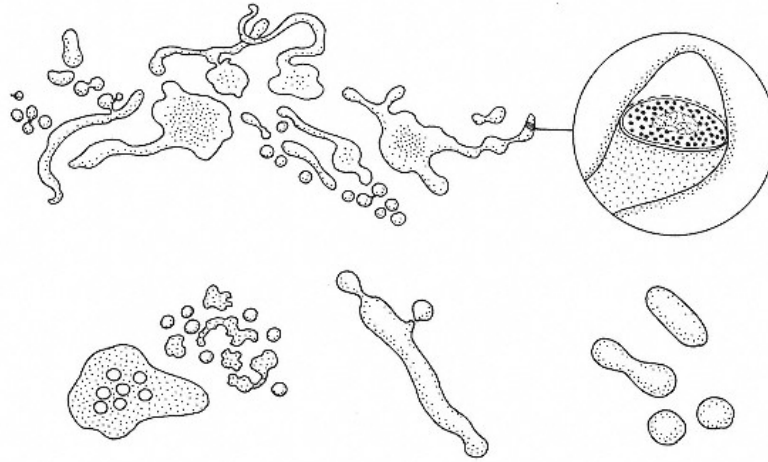
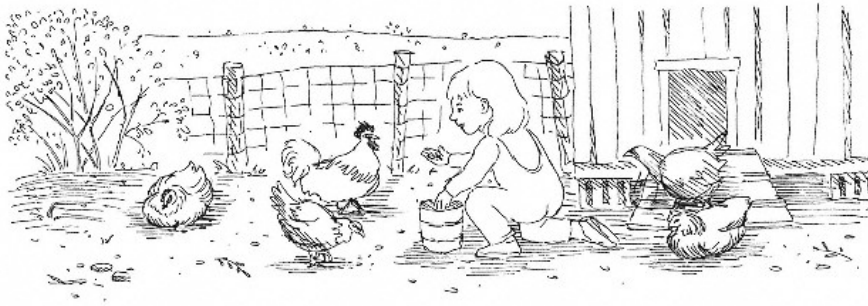
Like all other living beings, aphragmabacteria have flexible membranes made up of fat and protein structures, but they lack rigid walls outside of those membranes. They are therefore resistant to penicillin and other antibiotics that inhibit cell wall formation. When aphragmabacteria grow, their cells usually pile up on each other to form colonies of cells that look like fried eggs (**A**). Members of one group of aphragmabacteria, the mycoplasmas, have unusually high concentrations of cholesterol in their lipid membranes, suggesting a long association between these bacteria and animal tissue rich in lipids. A cross section of a cell from the genus *Mycoplasma* (**B**) reveals its nucleoid, ribosomes, cell membrane, and fuzz on its surface.

Some aphragmabacteria can cause pneumonia in humans and birds and may even cause diseases in plants. *Spiroplasma*, another mycoplasma, can be isolated from diseased citrus tree leaves and grown alone in culture tubes in the laboratory, but whether it actually causes the disease is unknown.

Aphragmabacteria reproduce in several ways: They form small coccoids inside parent cells (**C**), they bud (**D**), or they divide into two equal-size offspring by binary fission (**E**). Some aphragmabacteria have very little total DNA, about ten times less than other bacteria. These organisms—the tiniest, wall-less creatures—which lack any fixed shape, are the most minimal kind of life on Earth.



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Clam Camp

Phylum: Spirochaetae

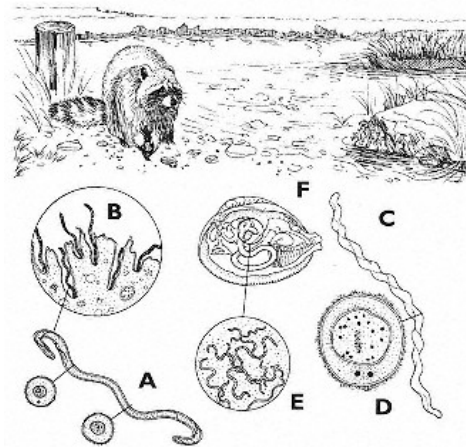
Spirochetes are bacteria that swim very rapidly, but unlike spirilla and other fast-moving bacteria, spirochetes have their flagella inside the outer membrane of their cell walls. Sometimes this design is referred to as the "snake-in-a-bag" arrangement. Some spirochetes are found in marine or freshwater environments; many are symbionts of animals. One type, *Treponema pallidum*, is found in great numbers in the genital sores of people who have symptoms of the venereal disease syphilis.

The three major groups of spirochetes—leptospire, spirochaetales, and pillotinas—are pictured here. The leptospire (A, *Leptonema* or *Leptospira*) are one of the few types of spirochete that require gaseous oxygen. Certain leptospire are found in the kidney tubules (B) of mammals, such as raccoons (*Procyon*) and rats, which may have a disease called leptospirosis.

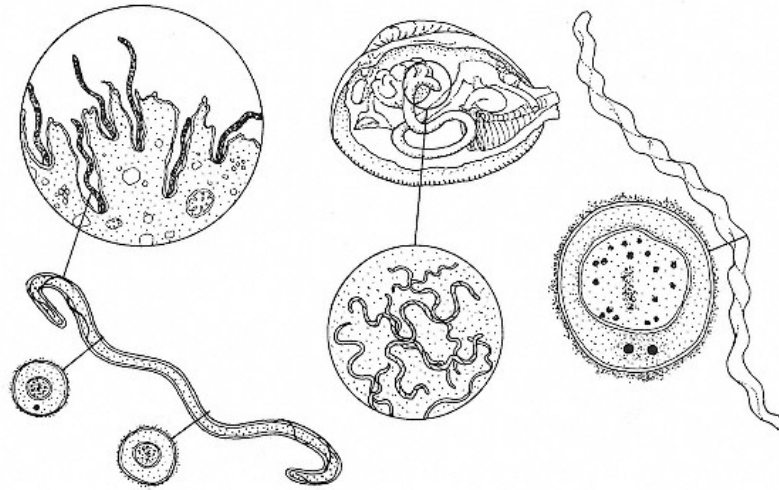
Twelve different spirochaetales genera have been described, including the smallest, most familiar types such as *Spirochaeta* (C). *Spirochaeta* is free-living and very similar in structure to the symbiotic *Treponema*. *Serpulina* is a similar spirochete that lives in the digestive system of pigs. The cross section of *Spirochaeta* (D) shows the flagella between the inner and outer cell wall membranes of these typical Gram-negative bacteria.

The pillotinas (E) are much larger than the leptospire or the spirochaetales some are symbiotic with marine molluscs (see page 148), such as oysters and clams. Pillotinas include cristispires, which inhabit a large gelatinous translucent structure called the crystalline style at the front of the stomach of the mollusc (F). The style, which helps molluscs grind algae for food, provides food and a haven for large numbers of the huge spirochete *Cristispira*, as well as for two smaller types of bacteria (a mycoplasma and a spirillum). *Cristispira* has as many as 300 flagella.

Other spirochete genera include *Borrelia* (in ticks and mammals, some associated with Lyme disease); the large spirochetes that live in the intestines of termites: *Clevelandina*, *Diplocalyx*, *Hollandina*, and *Pillotina*; the small *Mobilifilum*, with ten flagella; and the huge *Spirosymplokos*, with a unique composite structure.



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Rocky Brook

Phylum: *Proteobacteria*—*Thiopneutes*

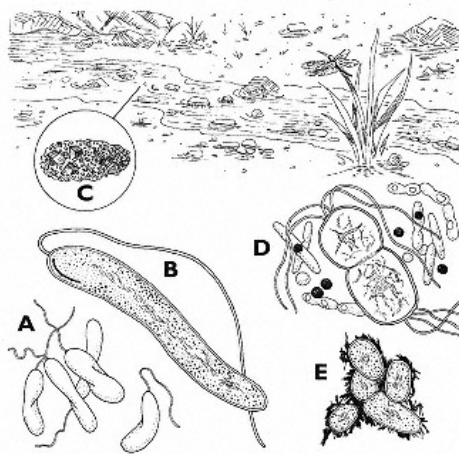
Thiopneutes feed on organic matter, but instead of breathing oxygen and producing water as humans do, they take in elemental sulfur or sulfate and produce hydrogen sulfide. Just as with inhaling oxygen, however, taking in sulfate involves the disposal of waste hydrogen atoms. Thus, members of this phylum, such as *Desulfovibrio* (A), are important in the worldwide movement of the sulfur compounds that are necessary for their own proteins and those of all other organisms.

Shaped like commas, these Gram-negative bacteria invariably are found in the muds of sulfur-rich environments. The longitudinal section of *Desulfovibrio* (B) shows its flagella, ribosomes, cell wall, and nucleoid, as well as a comma-shaped structure associated with flagellar motility called the polar membrane. Many thiopneutes release pungent gases such as hydrogen sulfide (H_2S), which smells like rotten eggs, making it easy to detect their presence indirectly. In iron-rich water, the hydrogen sulfide formed by these bacteria reacts with the iron, leading to the deposition of pyrite (iron sulfide, also known as fool's gold, C).

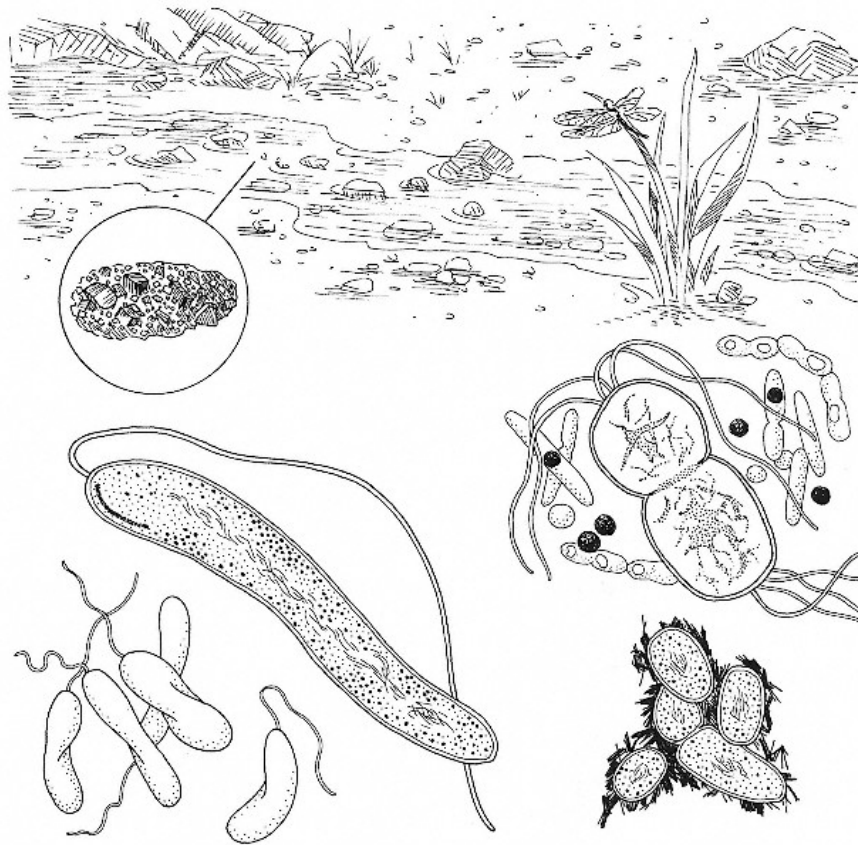
Phylum: *Endospora*

To belong to the phylum Endospora, a bacterium must be at least a part-time aerobe, and it must produce endospores, which are resistant propagules that permit the distribution of these bacteria to all sorts of dry, barren places that the more sensitive growing cells cannot survive. The most notable genus of aerobic, endospore-forming bacteria is *Bacillus* (D), to which at least forty distinguishable kinds of rod-shaped bacteria have been assigned, making the bacillus group more diverse than some entire animal phyla.

A *Bacillus* parent cell produces only one airborne spore, which may land anywhere; in this dormant stage, bacilli can survive for years without water and nutrients. The *Bacillus* cells shown (E) are depositing manganese. One *Bacillus* species, *B. anthracis*, is associated with symptoms of a serious human lung disease called anthrax. This airborne disease caused about 60,000 deaths per year during the Middle Ages, especially among people who worked with domesticated animals. (A certain life stage of *B. anthracis* may grow in the intestines of sheep and goats, just as its relative, the fermenting bacterium *Arthromitus*, grows attached to the intestinal wall of wood-eating termites.) Today anthrax still affects 20,000 to 100,000 people a year, most of whom work with farm animals.



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Pond Scum

Phylum: Proteobacteria—Anaerobic Phototrophic Bacteria

The bacteria in this phylum are phototrophs, primary producers in the world ecosystem. They derive their energy directly from sunlight and their carbon from carbon dioxide in air. Most require no organic compounds for food. There are three main groups of anaerobic photosynthesizers: green sulfur bacteria, purple sulfur bacteria, and purple nonsulfur bacteria.

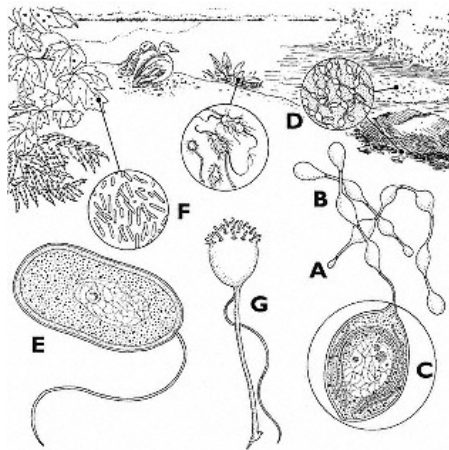
Both green and purple sulfur bacteria (generally found living above the green sulfur bacteria in layers of mud) require sulfur, usually in the form of hydrogen sulfide (H_2S), as a source of hydrogen atoms so that they can reduce carbon dioxide into foodstuff carbon. The purple nonsulfur bacteria, on the other hand, use small organic molecules such as pyruvate or lactate as hydrogen donors.

The phototrophic bacteria are morphologically diverse. Some are single cells that swim; others are immotile. Some group together in packets, and others, such as the purple sulfur bacterium *Rhodospirillum rubrum* (A), named after the great Dutch-American microbiologist Cornelis van Niel (1897–1985), form stalked budding structures. The septa that divide individual cells (B) are shown here. The cross section of *R. rubrum* (C) shows what it looks like under an electron microscope. Its cell wall, cell membrane, nucleoid with DNA fibrils, ribosomes, and thylakoid membranes are visible.

Some phototrophic bacteria form extensive sheets of cells in which the spaces between cells are filled with coverings, or sheaths, made of a gelatinous mucous material. The pond scum shown here (D) is a sign that prodigious numbers of phototrophic bacteria are present.

Phylum: Proteobacteria—Pseudomonads

The pseudomonads are a group of ubiquitous Gram-negative, flagellated, rod-shaped bacteria that have an astounding ability to break down organic compounds of all kinds, including organic ring compounds such as those in petroleum. The cross section of one species, *Pseudomonas multivorans* (E), shows its cell wall, cell membrane, nucleoid, DNA fibrils, ribosomes, and flagellum.



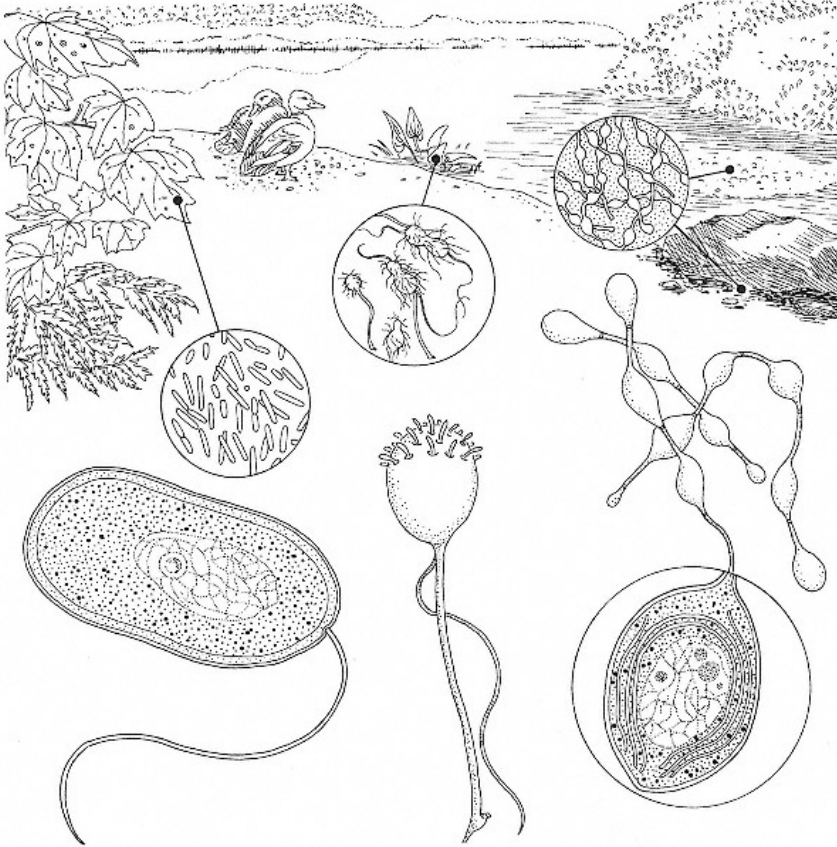
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Members of the genus *Xanthomonas* (F) are serious plant pathogens, causing the rapid wilting and death of many food plants under conditions optimal for the bacterium. Other genera of the phylum include *Zoogloea* and *Bdellovibrio*. *Bdellovibrio* is a small, predatory bacterium that penetrates and enters the periplasm of many other Gram-negative bacteria. An aerobe, it reproduces in the periplasm of its victim by using the victim's cell material to make more of itself. After the victim's resources are exhausted, many new, healthy bdellovibrios burst out of its diminished remains and swim away to find new victims.

Phylum: *Pirellulae*

Newly discovered bacteria belonging to the group (phylum) *Pirellulae* have proteinaceous walls distinct from the typical peptidylglycan-muramic acid walls of most bacteria. First recognized to be distinct on the basis of their 16S-rRNA gene sequences, the three best known genera among these new freshwater heterotrophs are *Planctomyces* (misnamed because it is not at all a "myces," which means "fungus"), *Pirellula* (**G**) shown here with its holdfast, which allows it to hang onto rocks and water plants) and *Gemmata*. *Gemmata* is unique in that, like eukaryotes, it has a membrane that surrounds all of its DNA. However, this is a nucleoid, not a nucleus, because all other features of the *Gemmata obscuriglobus* cells are bacterial in nature.

Isosphaera, with equal sizes of spherical cells, was thought at first to be a member of the cyanobacteria because it resembles them morphologically. It is now known to be a member of the *Pirellulae* group, which lives in the ocean.



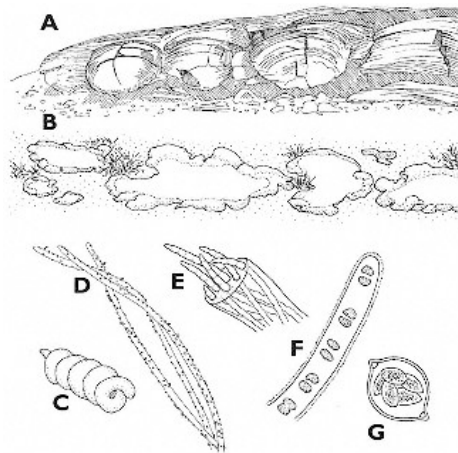
Salt Marsh

Phylum: Cyanobacteria

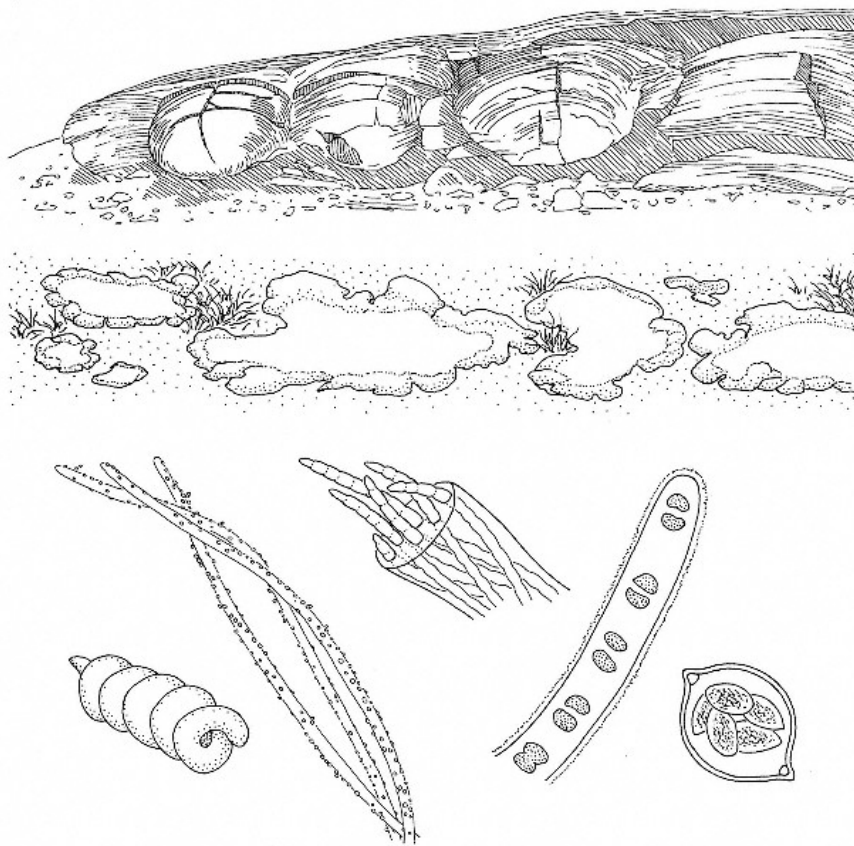
Together with the anaerobic phototrophic bacteria (see page 30), the prototistan photosynthesizers (algae), and the photosynthesizers that bear embryos (plants), cyanobacteria sustain all life on Earth by converting solar energy and carbon dioxide into food. Unlike the bacteria that produce sulfur and sulfate as waste products of photosynthesis, however, cyanobacteria release the gas oxygen (O_2) into the air (just as plants and algae do). Cyanobacteria are one of several bacterial groups that can fix atmospheric nitrogen into organic matter.

During the Proterozoic eon (2,500 million to 590 million years ago) a diversity of bacteria, the most productive of which were the phototrophs, produced layered sediments. These muddy and sandy banded sediments, preserved as layered rocks that are interpreted to be fossils produced by the metabolic activity of microorganisms, are called stromatolites (**A**). Live cyanobacterial communities that grow in layered sedimentary structures such as these are called microbial mats (**B**). Today microbial mats are found in the Persian Gulf, the Bahamas, Western Australia, northeastern Spain (Catalonia), the west coast of Mexico, and other seaside areas in semitropical and tropical regions.

Some of the most important cyanobacteria that make up these communities are *Spirulina* (**C**), *Oscillatoria limnetica* (**D**, with sulfur globules on its surface), and *Microcoleus* (**E**), in which many filaments (called trichomes) are inside a common covering (called a sheath). The large-filament *Johannesbaptista* (**F**) has coin-shaped cells, and the cells of the coccoid *Gloeotheca* (**G**) are inside a spherical sheath. In many of these productive microbes the sheath acts like a pair of sunglasses, protecting the cells from fierce sunlight, yet letting enough light in so that photosynthesis can go on.



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South Pacific Coral Reef

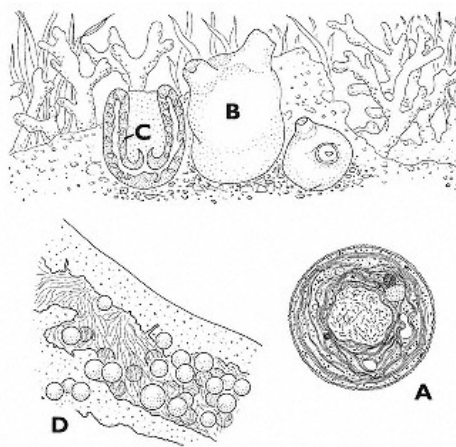
Phylum: Cyanobacteria—Chloroxybacteria

Although once thought to comprise a phylum of their own, the chloroxybacteria have been shown to belong to a subphylum of the cyanobacteria (see page 32), which they resemble in every way except in their pigments. Very few genera of the chloroxybacteria (also called Prochlorophyta) are known because these bacteria were discovered only in the 1960s. The three genera that have been described are *Prochlorococcus*, *Prochloron*, and *Prochlorothrix*.

Unlike other bacteria but just like plants these organisms have bright green chlorophyll: chlorophyll *a* and chlorophyll *b*. They lack both the blue-green pigments and the phycobiliproteins that make up the structures called phycobilisomes, which are found in all other cyanobacteria. Although the details of their photosynthetic apparatus are very similar to those of the chloroplasts of green algae and plants, the rest of their features—in particular the presence of a bacterium-style cell wall—place these prokaryotes squarely with other Gram-negative bacteria within the vast group of cyanobacteria.

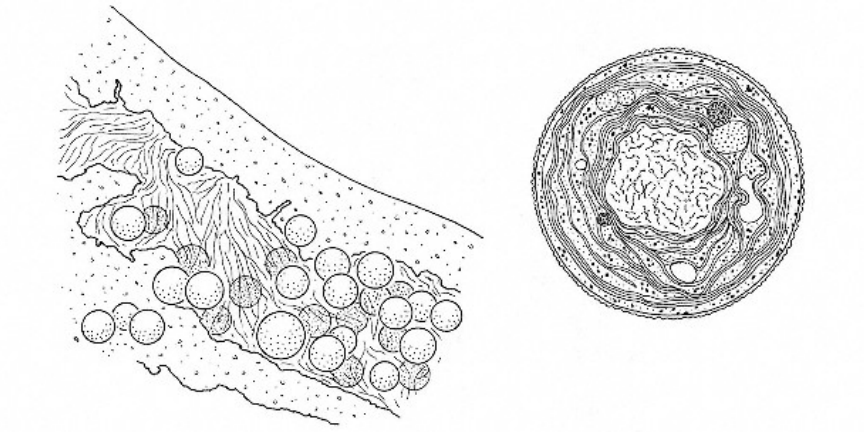
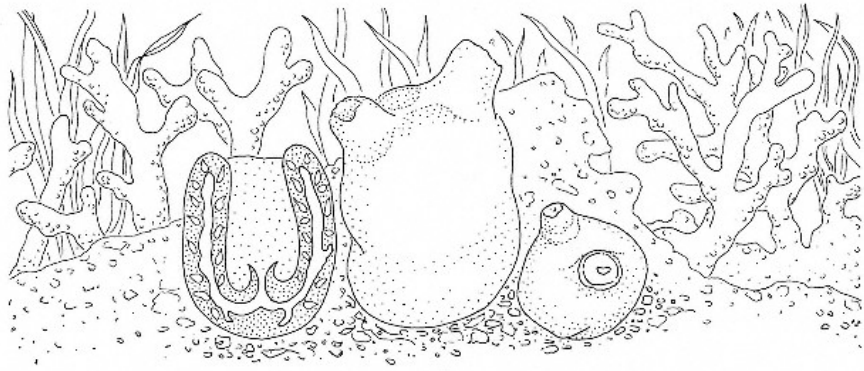
Prochloron (**A**) is a simple nonmotile coccoid that lives as a symbiont in the walls of the cloaca (the combined excretory and reproductive canal at the end of the intestine) of sessile chordates called tunicates (**B**; see page 148). Although first discovered in the South Pacific, *Prochloron* also grows in tunicates near the marine station of the University of Arizona on the Gulf of California (at Puerta Peñasco). The tunicate shown here, *Lissoclinum*, is in its natural habitat, a coral reef. In cross section, the cloacal cavity is visible (**C**). The cloacal wall (**D**) is embedded with bright green *Prochloron* symbionts.

Apparently *Prochloron* is an obligate symbiont because no one yet has been able to grow it separately. *Prochlorothrix*, however, is free-living; it grows easily in pure culture. Shaped like a filament, *Prochlorothrix* resembles the cyanobacterium *Oscillatoria* to the uninitiated. The only known species, which was discovered as a pollutant in a Dutch lake near Amsterdam, is called *P. hollandica*.



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Still another green chloroxybacterium is found in great abundance in the world ocean. At the bottom of the photic zone, as far down as 200 meters of clear water, tiny coccoid bacteria thrive. Many ocean-going research ships have discovered these productive phototrophic bacteria and called them "unidentified green coccoids."



Garden Soil

Phylum: Proteobacteria—Nitrogen-fixing Aerobic Bacteria

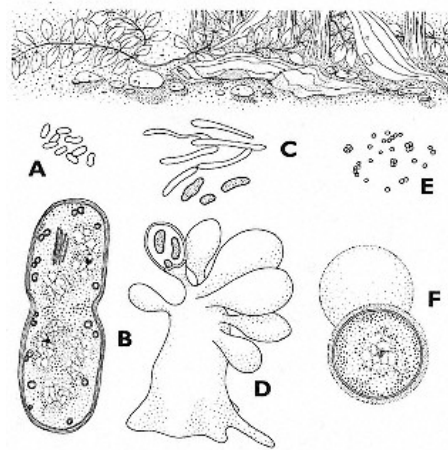
The best-known nitrogen fixer is *Rhizobium*, which forms a nitrogen-fixing symbiosis with the root hairs of plants from the pea family (Leguminosae), such as soybeans, alfalfa, clover, and lentils. These bacteria provide one of the crucial elements for plant growth, nitrogen, by fixing the inert gaseous nitrogen (N_2) of the air and transferring it to the carbon compounds of the bodies of organisms (i.e., converting it into organic nitrogen, $R-NH_2$; "R" represents the organic part of the molecule).

Nitrogen fixation requires the complicated enzyme complex nitrogenase. Composed of at least two different kinds of proteins that contain iron and molybdenum ions, nitrogenase is highly sensitive to oxygen. Without the oxygen-sensitive nitrogen-fixing capability of these bacteria, which must have an ancient and venerable history, we would all starve from protein deficiency because of the lack of available protein-forming nitrogen.

Other genera of nitrogen-fixing aerobic bacteria include *Azomonas* and *Azotobacter* (A). The cross section (B) shows tubules within *Azotobacter*, which are unusual in bacteria and may be involved in cell division. Respiratory membranes, ribosomes, cell membrane, cell wall, nucleoid, and division furrow can also be seen. Nitrogen fixers are motile, but *Rhizobium* transforms: The bacteria lose their flagella, and their enzyme systems swell up when they are inside the roots of legumes. They become permanently embedded in the plant cells, forming nodules on the root as the symbiosis matures. The nodules, often pink because of the presence of the oxygen carrier molecule leghemoglobin, stud the roots. They are seen easily with the unaided eye if the roots are removed carefully from the soil.

Phylum: Proteobacteria—Myxobacteria

In Greek *myxo* means "slimy." The myxobacteria, aerobic organisms that thrive in soil, are among the most morphologically complex of all bacteria. They glide by a poorly understood motion: Each cell moves slowly and is always in contact with a solid surface during movement. Individual cells come together to form colonies, and as water is depleted, they form differentiated, propagule-bearing stalks similar to those formed by the slime molds (see page 60).



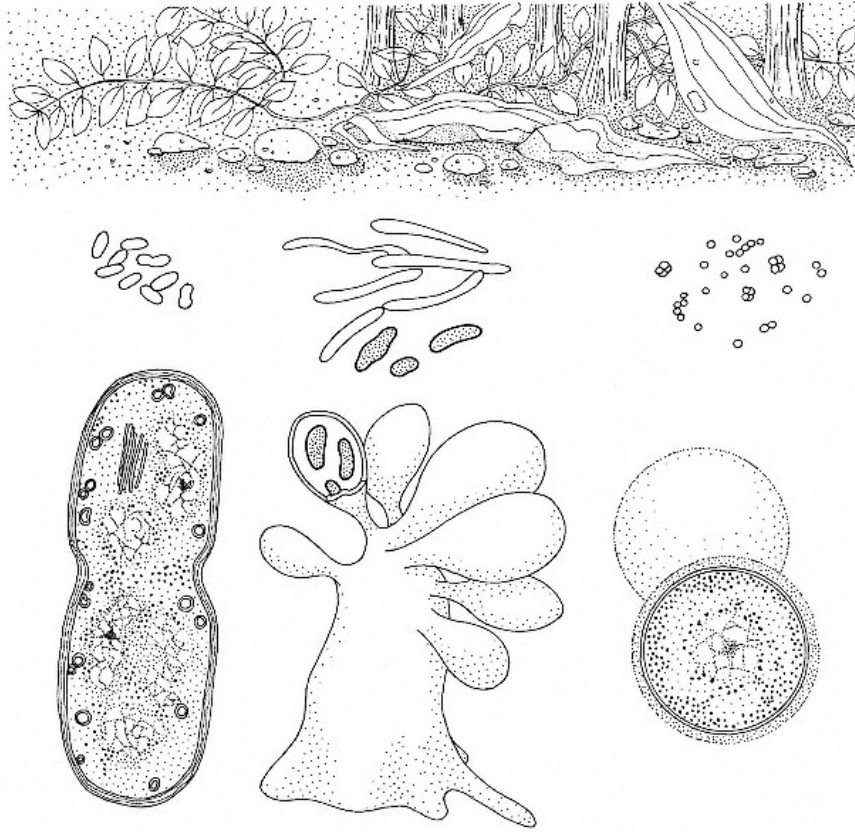
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Stigmatella aurantiaca (C) forms a distinctive tree-like structure with swellings (D), inside of which are bacterial myxospores. All myxobacteria are obligate aerobes with heterotrophic metabolism. They digest proteins and fatty-acid esters, and some probably can attack the lignin and cellulose of wood. They also digest the debris of other bacteria and of protists by secreting digestive enzymes into their surroundings and then absorbing the organic nutrients.

Phylum: *Deinococci*

The Gram-negative bacteria of the phylum Deinococci are spherical cells (*coccus* is the Greek for "berry") that characteristically divide to produce tetrads. They are either strictly or facultatively aerobic. Seven genera, distinguishable by morphology and arrangement of their cells, have been assigned to the phylum: *Micrococcus*, *Planococcus*, *Aerococcus*, *Sarcina*, *Gaffkya*, *Paracoccus*, and *Staphylococcus*.

Resistant to radiation, *Micrococcus* (E) grows in the coolant of nuclear reactors and resists ultraviolet and gamma rays. In a cross section of *Micrococcus* cells (F), the cell wall, membrane, ribosomes, and nucleoid are visible. Skin infections of humans and other animals are often associated with the growth of *Staphylococcus*. One strain in particular is found in prodigious numbers in women suffering from toxic shock syndrome.



Lake Shore

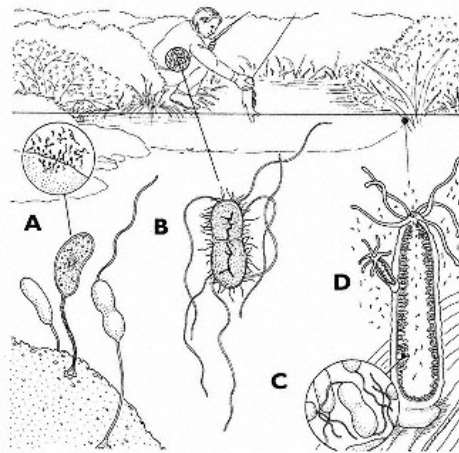
Phylum: *Proteobacteria*—*Omnibacteria*

Most organisms in the world are omnibacteria. This vast group includes all the facultatively aerobic, Gram-negative bacteria that cannot use carbon dioxide or other inorganic compounds as food. In other words, omnibacteria are heterotrophs. In the absence of oxygen these bacteria do not stop growing; rather they continue to respire without oxygen.

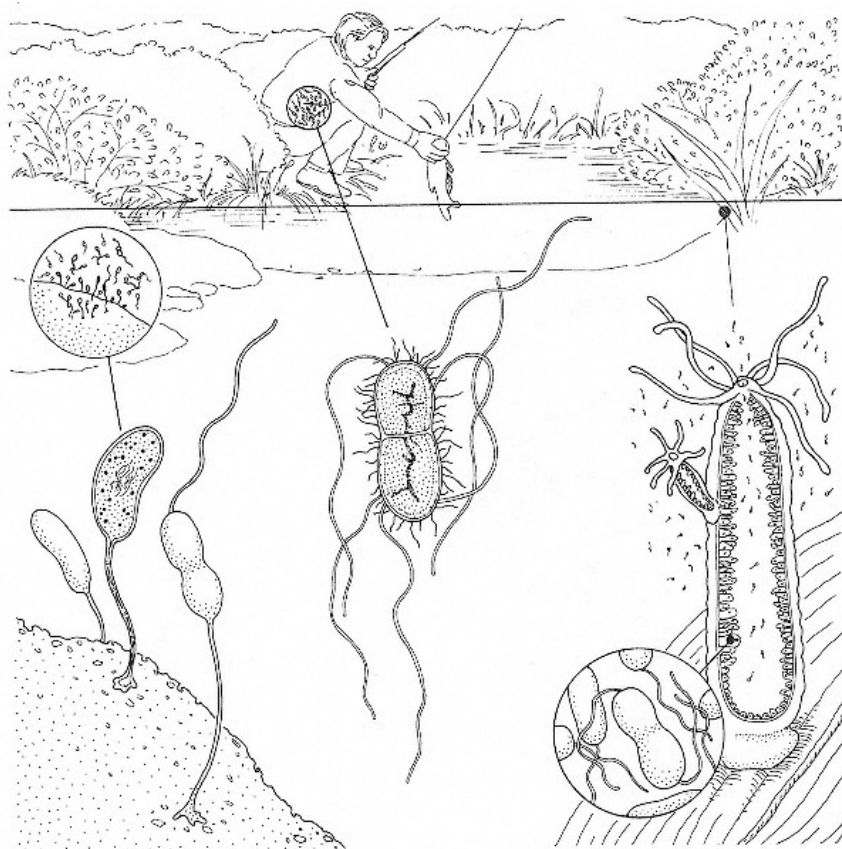
They take in ions such as nitrate (NO_3^-), which, when it receives hydrogen atoms, is called the terminal electron acceptor; and they produce nitrogen gas (N_2), nitrous oxide (NO_2 , also called laughing gas), or even ammonia (NH_3). Thus, omnibacteria are called facultative nitrate reducers, or denitrifiers. The latter expression comes from the disappointment of agriculturalists, who pay for added nitrate to fertilize their plants only to find that populations of omnibacteria have denitrified the useful nitrate (i.e., converted it to atmospheric gas) before the plants could take it up.

Examples of omnibacteria are *Caulobacter* (**A**, a swarmer cell and a cell with attached stalk); *Escherichia coli* (**B**), a resident of human large intestines and probably the most studied organism on Earth (shown here ready to divide); and *Aeromonas punctata* (**C**), pictured with *Hydra viridis* (**D**), a freshwater cnidarian (see page 126) with its many tentacles attached underwater to grass. This *Aeromonas* is a hydra symbiont that stays close to a good source of food: the algae-filled gastrodermal (digestive) cells of the green cnidarian in which it lives. Many types of aeromonads exist. They are abundant and common in ponds, lakes, and reservoirs.

The enterobacteria, a group of omnibacteria, are distinguished from one another by the carbohydrates that they can attack. Pathogens in this phylum include *Vibrio*, which induces diarrheal symptoms of cholera when it attaches to the intestinal linings of humans, and *Neisseria*, a bacterium found in great numbers in people suffering from gonorrhea or meningitis.



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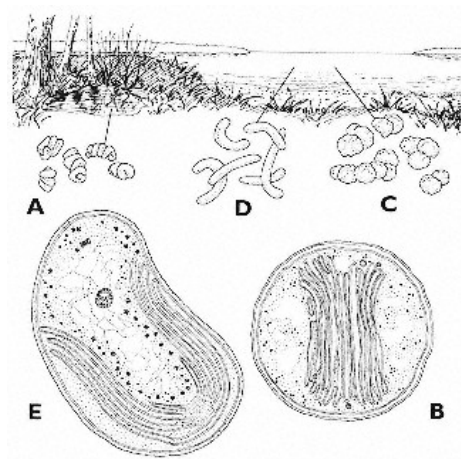
Ocean Edge

Phylum: Proteobacteria—Chemoautotrophic Bacteria

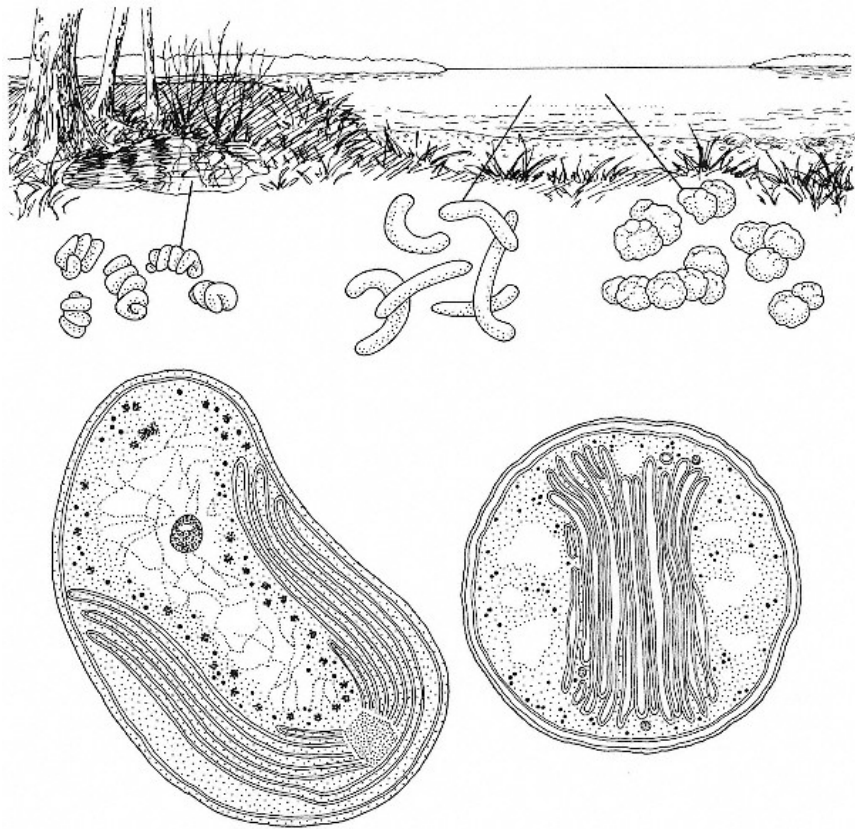
Chemoautotrophic bacteria are amazing because they live in water on inorganic chemicals alone. They need neither light nor food (organic compounds). There are several types of chemoautotrophs classified by the compounds that they oxidize to gain energy: nitrogen compounds, sulfur compounds, or methane.

Of the nitrogen oxidizers, *Nitrobacter*, *Nitrospina*, *Nitrocystis*, and *Nitrococcus* oxidize nitrite (NO_2^-) to nitrate (NO_3^-), whereas *Nitrosomonas*, *Nitrospira* (A), *Nitrosococcus* (B), *Nitrosolobus* (C), and *Nitrosovibrio* (D) oxidize ammonia (NH_3) to nitrite (NO_2^-). *Thiobacillus* oxidizes reduced sulfide compounds containing sulfide (S^{2-}), sulfite (SO_3^{2-}), thiosulfate ($\text{S}_2\text{O}_3^{2-}$), or polythionate (a larger, more complex sulfur compound) to sulfate (SO_4^{2-}). Because the resulting sulfate mixed with water makes sulfuric acid (H_2SO_4), *Thiobacillus* often greatly acidifies its environment. Methylomonads use methane (CH_4) or methanol (CH_3OH) as their sole source of energy and carbon. They cannot even grow on food (i.e., complex organic compounds).

The chemoautotrophic bacteria are ecologically significant because they cycle inorganic nitrogen and carbon compounds—elements critical to the growth and reproduction of living organisms. *Nitrobacter winogradskyi* (E) is a bacterium in the waters of the marine littoral zone. Its cell wall, respiratory membranes, nucleoid, ribosomes, and carboxysome (the storage granule of the CO_2 -fixing enzyme) can be seen. Out in the water, where photosynthetically produced oxygen from above meets ammonia from below, these bacteria thrive.



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Foods

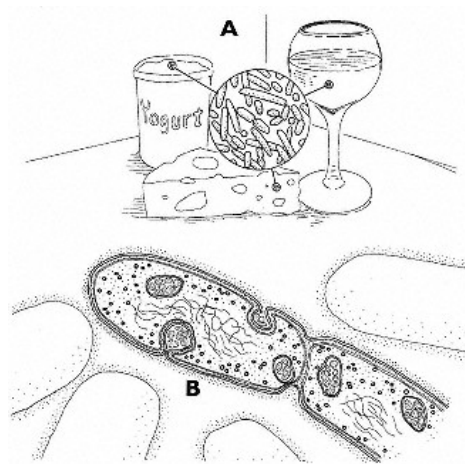
Phylum: Endospora—Fermenting Bacteria

"Ferment" means to convert from sugar (such as glucose or sucrose) or fibrous substances (such as cellulose fibers or starch) to other organic matter—most notably ethyl alcohol (ethanol), methanol, or even lactic or propionic acid. In short, fermentation is a process that occurs in the absence of oxygen in which carbohydrate is converted to an alcohol or acid. Even though the enzymes involved in fermentation can be extracted from the cell, large-scale fermentation requires metabolizing microbes to assure the quality and quantity of the products.

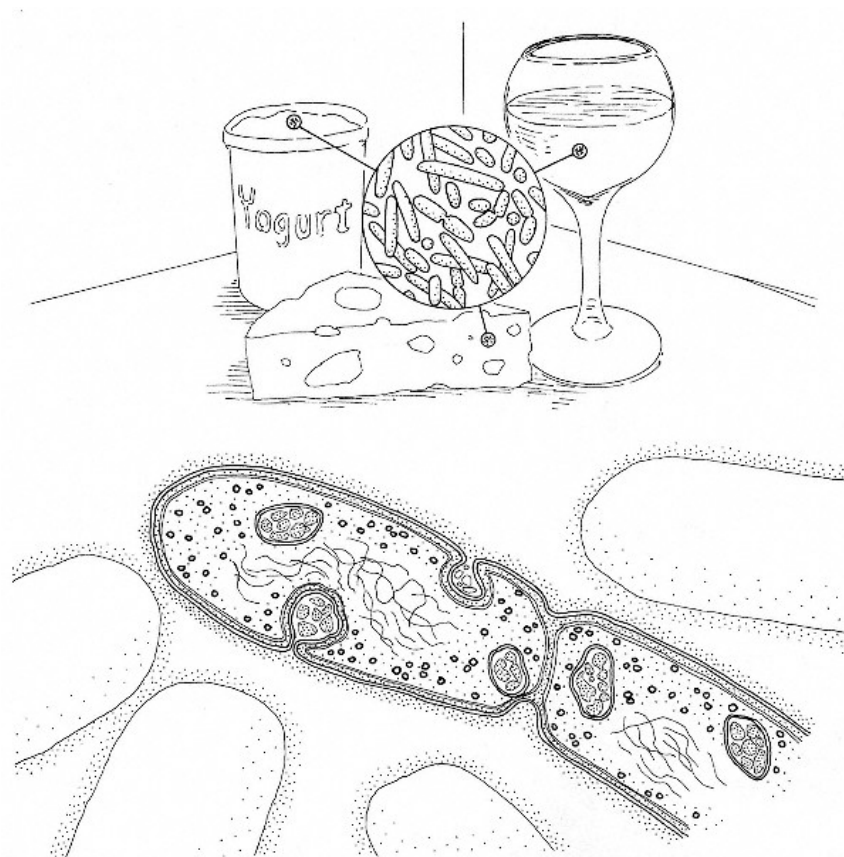
This phylum Endospora contains fermenting genera such as *Clostridium*, which is used in processing linen fibers, and *Lactobacillus* and *Streptococcus*, both crucial in the production of yogurt and other milk products. Some of these specialized fermenters are able to break down almost anything (except plastic) through their anaerobic, fermentative metabolism.

Lactobacillus (A) from yogurt, spoiled milk, and the human mouth is grown easily in culture. In this cross section (B) the sheath (capsule), outside cell wall, ribosomes, and DNA fibrils are visible. Different species of *Clostridium* cause gas gangrene and botulism. The lactic acid bacteria, such as *Lactobacillus*, *Streptococcus*, and *Leuconostoc*, are famous for their ability to ferment sugar (in particular that in milk) and to produce lactic acid, as well as formate, succinate, carbon dioxide, and ethanol. One product of this process is kefir, a carbonated yogurtlike drink that has been known in eastern Europe and western Asia for thousands of years.

Approximately twenty-five different bacteria and four yeasts are associated into a kefir curd (or granule) that acts as an individual, dividing and growing. The kefir curd, which looks like a granule of cottage cheese, is an example of "domesticated microbes."



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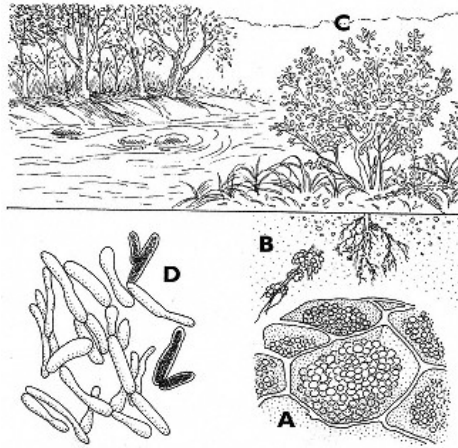
Woodland Stream

Phylum: Actinobacteria

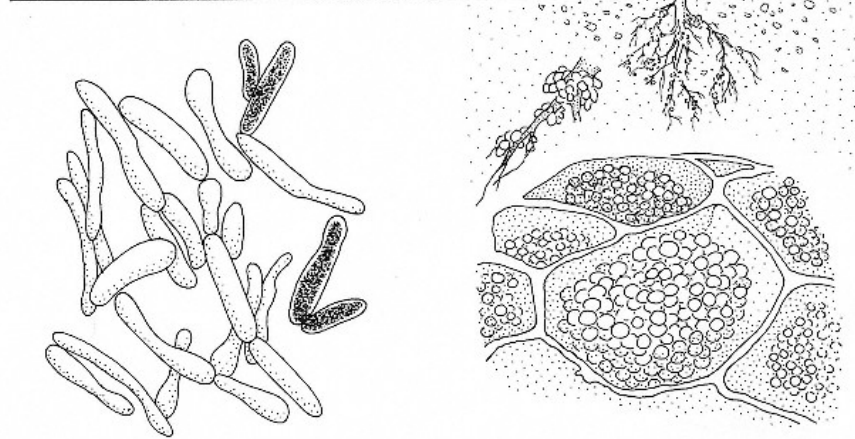
Many actinobacteria grow as stringy masses in colonies and appear fuzzy to the naked eye, so superficially they resemble fungi. They live mainly in the aerobic zone of the soil and traditionally have been called actinomycetes (literally "ray-shaped fungi"). Electron microscopic and other studies show unequivocally, however, that they are bacteria and are not related to fungi. Although some actinobacteria, such as *Streptomyces*, have given us as many as 4,000 different antibiotics, others are considered disease agents because they are associated with symptoms of diphtheria, tuberculosis, and Hansen's disease (leprosy).

One notable genus of phylum Actinobacteria is *Frankia* (A), which forms nitrogenfixing nodules on tree roots (B) similar to those found in *Rhizobium*-laden roots of legumes. Known as actinorrhizae, organisms such as *Frankia* are common in the roots of certain temperate forest trees, including the alder (*Alnus*, C). Another actinobacterium, *Cellulomonas* (D), is capable of breaking down cellulose from trees. In this picture, offspring cells are still attached to two cells that have divided, showing the Y and V configuration typical of many actinobacteria, especially those in the family Nocardiaceae.

The odor of fresh earth, whether from newly hoed compost or from a rotten log recently overturned, comes from thriving populations of actinobacteria in their favorite habitat: organic-rich soil.



Kathryn Delisle



Saline Habitats

Phylum: Chloroflexa

The group, Chloroflexa, of green nonsulfur phototrophs, comprises only three genera. It was found only recently to be distinct from the other anaerobic phototrophic bacteria. *Chloroflexus* (A) is a green filamentous photosynthetic bacterium in a benthic microbial mat. Its cells have chlorosomes with photosynthetic membranes (B). Yet, unlike in other green phototrophs, hydrogen sulfide is not the hydrogen donor in photosynthesis, so sulfur and sulfate are not deposited. Photosynthetic members of Chloroflexa are informally known as "green nonsulfur photosynthesizers."

Phylum: Chlorobia

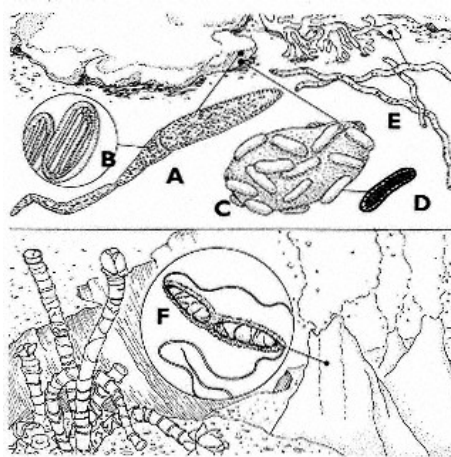
Photosynthetic organisms that cannot swim cover large heterotrophs to make aggregates called "bacterial consortia." *Chlorochromatium aggregatum* (C), in which the smaller cells on the outside are green sulfur photosynthesizers (D) (with chlorosomes as shown), bears a few dozen of such nonoxygen producing photosynthesizers on its surface.

Phylum: Saprospirae

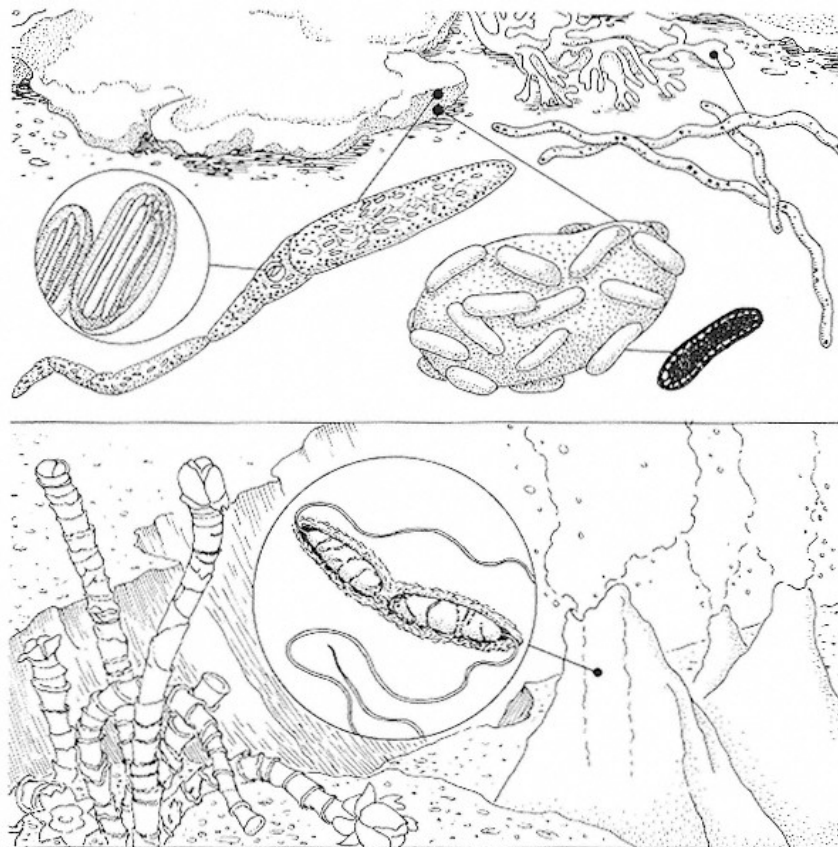
Saprospirae are Gram-negative fermenting, gliding bacteria and their oxygen-respiring relatives. *Saprospira* (E), a large gliding bacterium that moves by unknown means along the surface of sea weeds, is an osmotroph. Internal polyphosphate granules are visible in the gliding cells. These cells are typically embedded in slime and cannot swim, but require contact with a solid surface to glide.

Phylum: Thermotogae

Thermotoga is a genus of bacteria new to science. It bears a unique thick covering at its surface, known as a toga. This species *T. thermarum* (F) withstands hellish temperatures at great depths in the ocean's abyss. *Thermotoga subterranea* was taken from a deep continental oil well in the Paris basin in 1995. A strict anaerobe, this new bacterium grows optimally at 70°C, a very high temperature from our point of view. At least three other new genera belong to this group, again defined by rRNA sequences: *Aquifex*, *Fervidobacterium*, and *Thermosipho*.



Kathryn Delisle



Chapter 2— Protoctista

Kingdom Protoctista includes organisms whose cells originally formed by bacterial symbioses. Protoctists are defined by exclusion: Members of this kingdom are not animals (which develop from an embryo called a blastula), nor are they plants (which develop from an embryo that is not a blastula and that is retained in the mother's tissue). They also are not fungi (which lack undulipodia at all stages and develop from spores), nor are they bacteria (which have prokaryotic cell structure). All protoctists are nucleated and live in aquatic habitats. Eukaryotic microorganisms and their immediate descendants are protoctists: all algae (including the seaweeds), undulipodiated (motile) photoplankton and water molds, the slime molds, slime nets, and that misnamed miscellany, the protozoans. Most protoctists, but certainly not all, are also aerobes that respire oxygen in their mitochondria. Almost all of the swimming protoctists have $[9(2)+2]$ undulipodia (see page 4) at some stage of their life history. In all algal protoctists the chlorophylls inside the cells are contained within membrane-bounded structures called plastids.

Some protoctists are marine, some live primarily in freshwater, and many inhabit the watery tissues of other organisms. Nearly every animal, fungus, and plant has a protoctist associated with it at some time during its development. Some protoctist phyla—such as the Apicomplexa (see page 98), the Microspora (see page 58), and the Myxospora (see page 56)—include hundreds of species, all of which live necrotrophically on other organisms.

The protoctists show remarkable variation in cell organization, pattern of cell division, and life history. Like plants, some are photoautotrophs, which eliminate oxygen gas in the light; others ingest or absorb nutrients or living, swimming food heterotrophically. (Protoctists may be phagotrophs or osmotrophs or both at the same time.) In many species, the type of nutrition depends on environmental conditions: When light is plentiful, they photosynthesize; in the dark, they feed. Although protoctists are far more diverse in ecological niche and nutrition than are animals, fungi, or plants, they are far less diverse metabolically than are the bacteria. That the appearance of protoctists may have occurred about two billion years ago is suggested by well-dated fossils

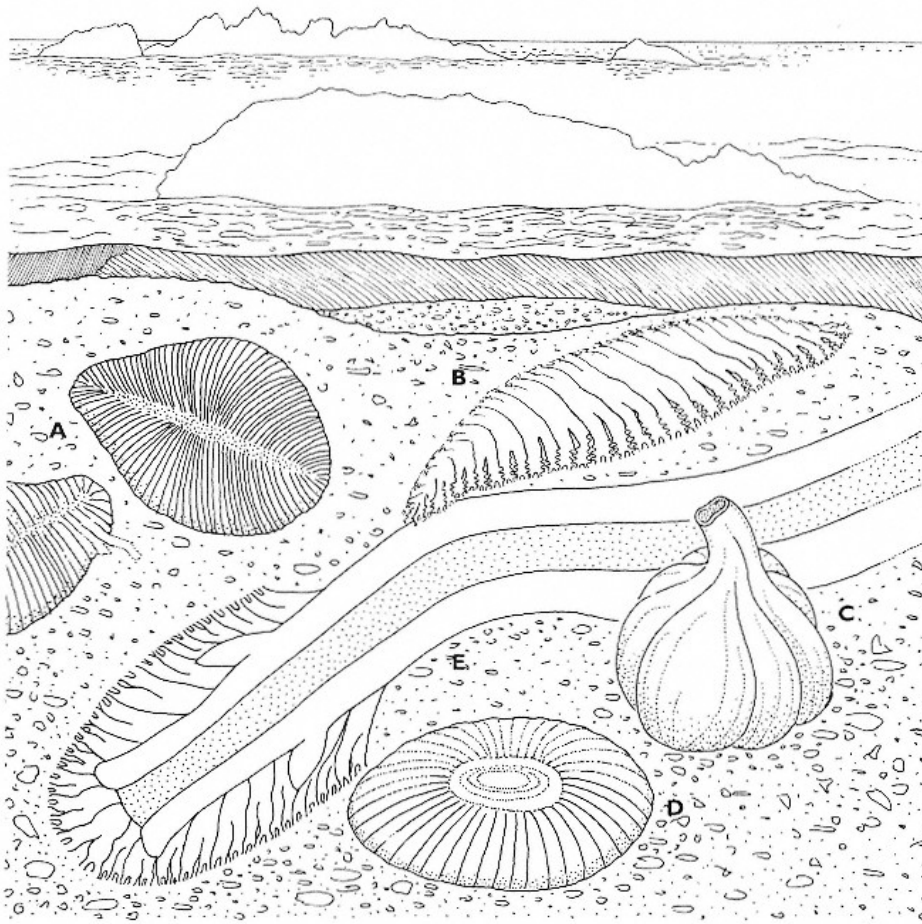


Figure 12

The fossil remains of the Ediacaran biota, first discovered in South Australia, date back to 600 million years ago. When first discovered, in the late 1950s and early 1960s, these organisms were called fauna and labeled as animals. Now some scientists believe that they were protists, some of which may have been ancestral to certain animal phyla. Pictured here in their shallow coastal habitat, at about half their natural size, are *Dickensonia* (A), an unnamed spindleshaped form (B), *Inaria* (C), *Cyclomedusa* (D), and an unnamed bloated being (E) that lived prostrate on the seafloor. Whatever they were, the organisms that made up the Ediacaran biota were unique. All are extinct. By about 530 million years ago they had been replaced by shelled Cambrian animals. Kathryn Delisle

such as *Grypania*, probably an alga. Protocists subsequently diversified into a variety of weird beings, most of which are probably extinct (Figure 12). Fossil protocists, especially thick-walled resting stages or cysts, can be extracted from shale rock treated with hydrofluoric acid.

Swamp

Phylum: Rhizopoda

Pictured here are three types of rhizopods drawn to relative scale: *Amoeba proteus* (A), shown engulfing a ciliate (B); *Arcella polyppora* (C), which lives in a hardened shell, or test; and *Mayorella penardi* (D), a polypodial ameba. Commonly called amebas, the rhizopods are single-celled, uninucleate, heterotrophic organisms that move by means of pseudopodia. The ameba protrudes a temporary foot (pseudopod) of cytoplasm, which is used for locomotion or for feeding. The moving, feeding form is called the trophozoite; the dormant stage (if there is one) is referred to as a cyst.

There are about two hundred species of amebas, including *Entamoeba histolytica*, the symbiont whose presence in large numbers is correlated with intestinal gas and diarrhea in humans. As a cyst, this microbe can tolerate the acidic gastric fluid that it encounters when entering the human intestinal lining. Its growth apparently causes symptoms of amebic dysentery. Ameba cysts are found in drinking water and on fruits and vegetables washed in water contaminated with human feces.

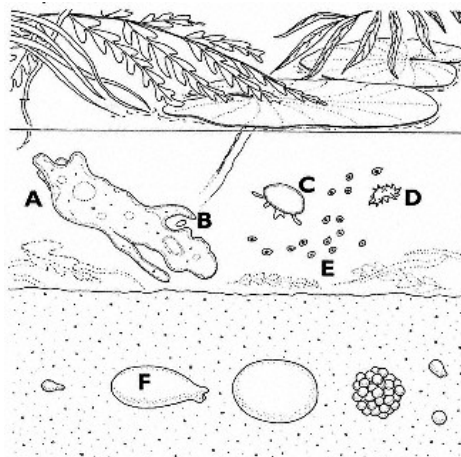
Amebas similar to those pictured here eat phototrophic organisms such as cyanobacteria (see page 32) and algae (e.g., chlorophytes, see page 84). Other rhizopods eat heterotrophic bacteria and protists. All amebas, however, ingest their food by an engulfing process called phagocytosis. Many consume other protocists (including other amebas), fungi, and bacteria. A mixture of amebas can be found in concentrations of 10^4 to 10^5 per gram of dry weight in sandy loam soil. Some amebas—like the uninucleate ones shown here (E)—are tiny, as small as 1 or 2 micrometers. In comparison, others are giant—up to 1,000 micrometers (1 millimeter).

In addition to these single-celled amebas, the phylum Rhizopoda includes the cellular slime molds, Acrasea and Dictyostelida (see page 60) and the phototrophic ameboid plasmodium *Chlorarachnion* (page 70).

Phylum: Archaeoprotista—Pelobiontae

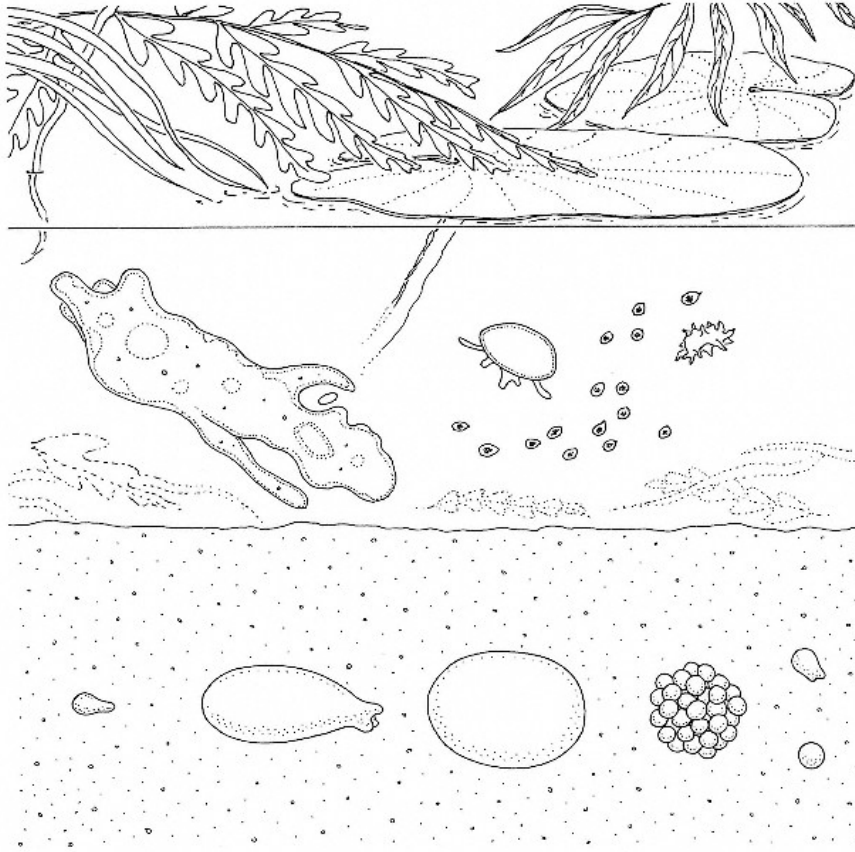
In the mud at the bottom of stagnant streams and ponds in temperate regions of the Northern Hemisphere is the curious unique microbe *Pelomyxa palustris* (F), a species of the phylum Archaeoprotista (see page 72). Individuals often move slowly, looking like tiny drops of water, over the surface of decaying leaves and other brownish vegetation. Because it can grow to 5 mm long, this organism can be seen by the observant naturalist's naked eye.

This giant ameba differs from other amebas, such as rhizopods (see this page), in many ways. It is multinucleate but lacks mitochondria, Golgi bodies, and other organelles usually found in eukaryotes. It harbors three types of endosymbiotic bacteria, at least one of which functions like mitochondria. The other two actually rid *Pelomyxa* cytoplasm of excess hydrogen, not combining it with oxygen as mitochondria do, but rather as methanogenic bacteria do (see page 20): The hydrogen from food is combined with carbon dioxide, and methane is given off as waste.



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Harboring two kinds of methanogenic symbionts allows *Pelomyxa* to live in microaerobic conditions. Although it does require some oxygen, *Pelomyxa* can survive lower concentrations of oxygen than exist in the atmosphere. Like all other amebas, pelobionts lack a sex life that involves meiosis or fertilization. They reproduce to form numerous binucleate cells or a few multinucleate ones. They consume algae and plant debris and were dubbed "exceedingly gluttonous animals," by Joseph Leidy, who in 1879 was the first to describe them.



Estuary with Oyster Bar

Phylum: *Haplospora*

Haplosporans are infamous because of their effect on the seafood industry. All haplosporans live in the tissues of freshwater or marine animals. Some, such as *Haplosporidium nelsoni* (A), which has caused serious epidemics in the American oyster, *Crassostrea virginica* (B), a mollusc (see page 148), are destructive. As symbiotrophs, these haplosporans may be benign or pathogenic, a state that is believed to be a function of salinity and probably temperature. They are not found north of Massachusetts nor south of Virginia, and most species can survive only symbiotically in mollusc tissue.

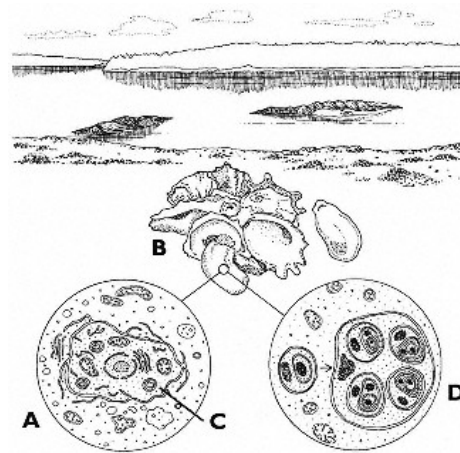
Unlike the superficially similar paramyxans (see this page), haplosporans typically form unicellular, uninucleate propagules, called spores. They live between the cells in animal tissue as uni- or multinucleate unwall cells called plasmodia, and they contain haplosporosomes (C), membrane-bounded organelles of unknown function.

Phylum: *Paramyxa*

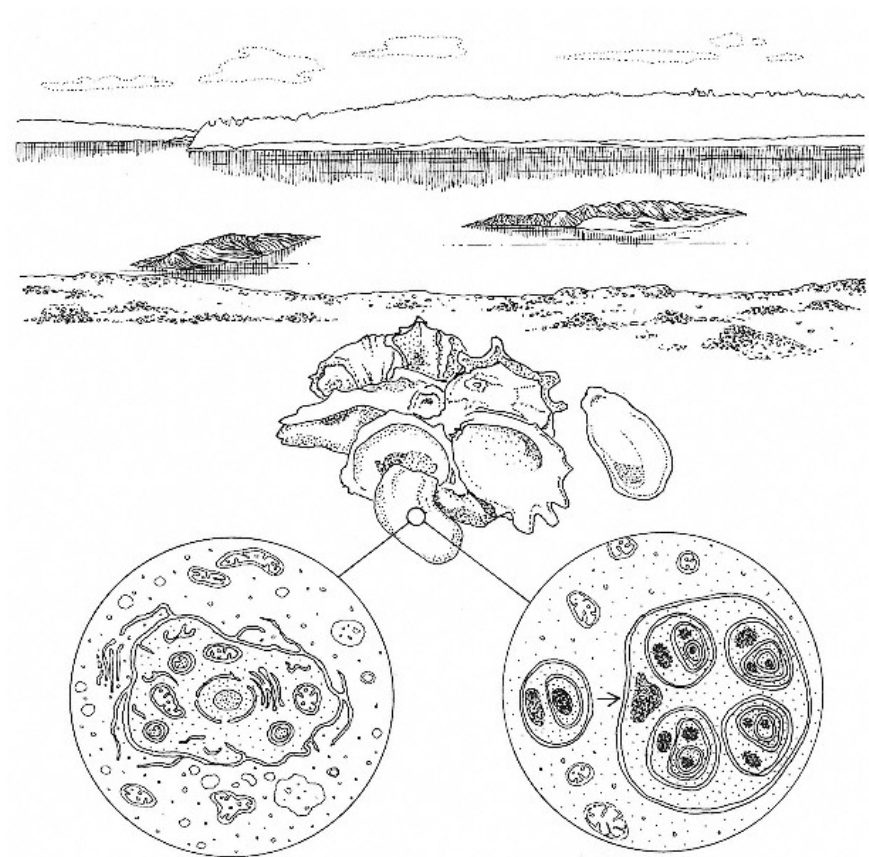
The paramyxans, all of which live in the tissue of animals, are unique because of the way they form propagules: Through a process of internal cleavage, cells called spores are enclosed inside one another like Russian dolls. Because paramyxans lack the attachment structures and apical complex, they are not apicomplexans (see page 98), and because they lack haplosporosomes, they are not haplosporans (see this page). Because of their internal cleavage—the formation of cells inside of cells—paramyxans are given their own phylum.

The three genera and six species of paramyxans are distinguished by the number of spore cells and by the taxon of the insect (see page 150) or mollusc (see page 148) in which they reside. The best-known paramyxans are troublesome pathogens that infect commercially important seafood—bivalve molluscs such as oysters and clams. *Paramyxa paradoxa* grows necrotrophically in the larval intestinal epithelium of annelid worms (see page 142) such as *Poecilochaetus serpens*.

Before electron microscopy helped clarify the distinctions between apicomplexans (see page 98), haplosporans (see this page), microsporans (see page 58), and paramyxans, all of these organisms were jumbled together and maligned as "parasites." Shown here is *Marteilia refringens* (D), a multicellular paramyxan with a small number of cells (fewer than twelve) per individual, which lives in large numbers in the European oyster, *Ostrea edulis*.



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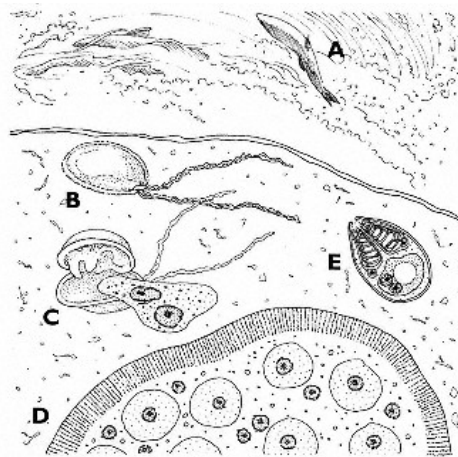
Salmon

Phylum: Myxospora

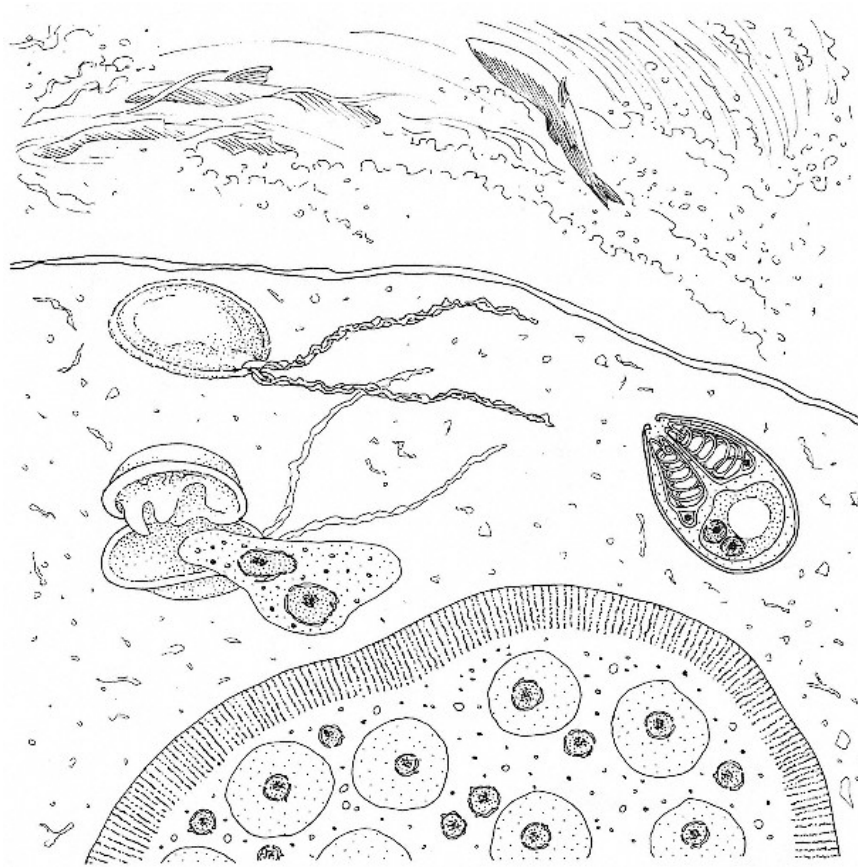
The myxosporans once were thought to belong to a broad grouping of protocists called sporozoans. Unlike other former sporozoans—now recognized to be apicomplexans (see page 98), microsporans (see page 58), or paramyxans (see page 54)—which are single-celled protists, myxosporans are multicellular. Each propagule has two nematocyst-like structures called polar capsules with filaments inside. These polar capsules release the filaments that, like a dog's leash, attach the myxosporans to the intestinal tissue of the animal in which it resides.

The phylum Myxospora is divided into two classes: the Myxosporae, with more than a thousand species, and the Actinosporae, with only thirty-seven species. Included in the phylum are important symbionts of fish, some of which cause serious diseases. *Myxobolus cerebralis*, for example, lives in sockeye salmon (*Oncorhynchus nerka*, **A**). Pictured here are the infection stages within the salmon. The sticky polar filaments are extruded (**B**), and the sporoplasm is released (**C**) with haploid nuclei that later fuse in a sexual event of fertilization, which occurs before development of the multinucleate plasmodium.

The plasmodium (**D**) has two types of nuclei: haploid nuclei with one set of chromosomes and diploid generative cells that form after karyogamy. A cross section (**E**) of a mature myxosporan propagule (still referred to by many as a spore) shows the two polar filaments inside the capsule.



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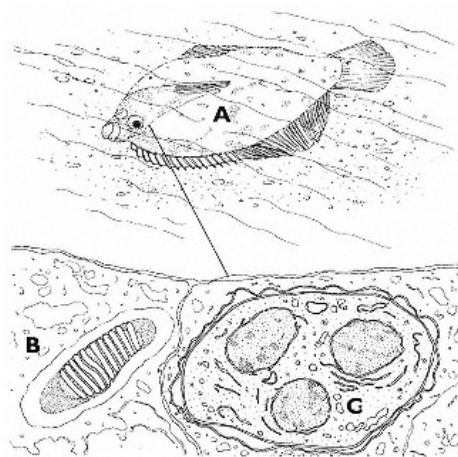
Continental Shelf with Flounder

Phylum: *Microspora*

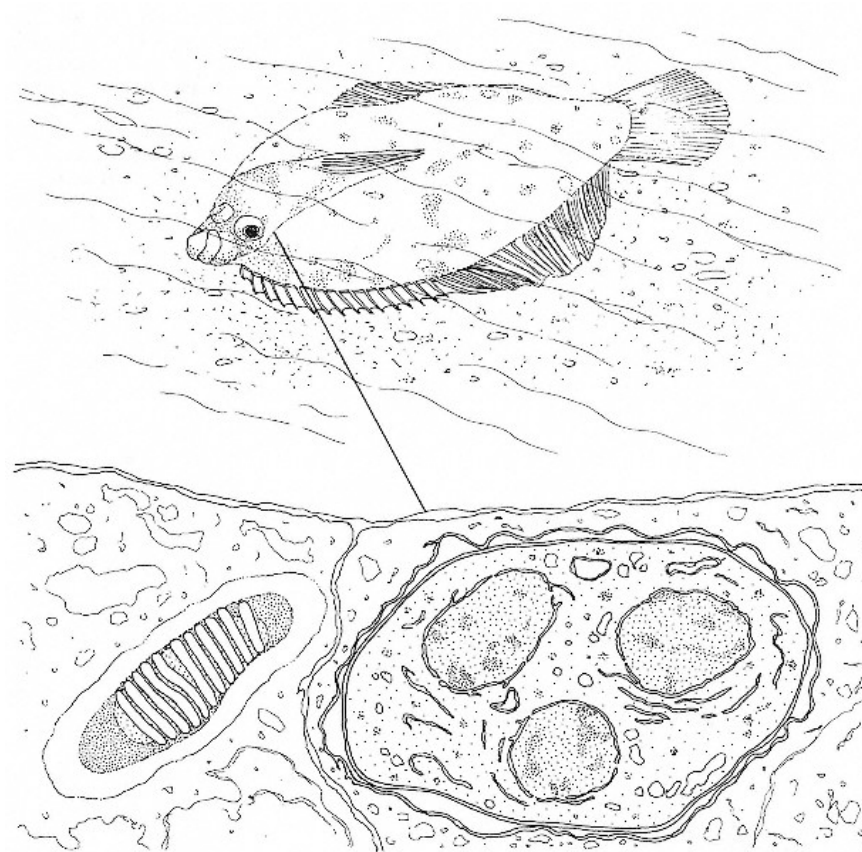
All microsporans (also called microsporidians) are small, unicellular symbiotrophs that must live inside the cells of animal tissues. Unlike most protists, these organisms lack mitochondria at all stages of their life history; microsporans may even be relicts of protist life before mitochondria evolved. Nearly all arthropods (see page 150) and chordates (see page 148) harbor microsporans unique to their species. Microsporans are found in all classes of vertebrates, especially fish. *Glugea stephani* (bottom, **(B)** and **(C)**), for example, lives in the starry flounder (*Platichthys stellatus*, **A**).

Microsporan bodies are modified as unique infection devices, which have been called spores because they appear as small, mysterious, dark propagules and are usually present in great quantity. These "spores" form the infective structure, called the polar tube (**B**), which is only 0.1 micrometer in diameter but is 100 micrometers long and is coiled up within the spore cell. When released, the tip of the tube jabs an animal cell, allowing the nucleus and cytoplasm of the microsporan cell to flow through the tube and inoculate the tissue cell of the animal. Once inside, the cell forms a multinucleate plasmodium (**C**), which then undergoes sporogony (that is, multiple fission) to form many offspring microsporans at one time.

In some cases the microsporan infection resembles a tumor because the infected animal cell survives, but it grows, accommodating more and more microsporans until it depletes the food supply from the surrounding tissue. The microsporan-induced, single-cell tumor (hypertrophied animal tissue cell) is such a unique structure that it has a special name: a xenoma.



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Birch Forest Floor

Phylum: Rhizopoda—Acrasea

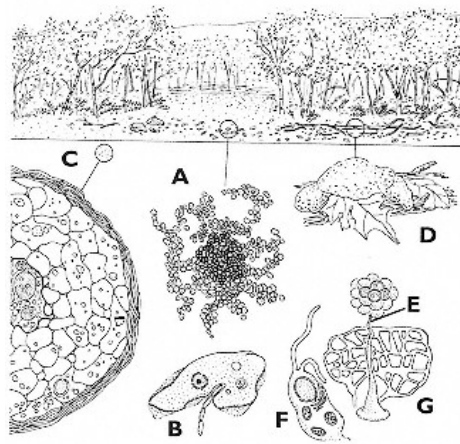
The acrasids are cellular slime molds of the phylum Rhizopoda (page 52). They live freely as bacteria-eating, heterotrophic protists in freshwater and rotting vegetation. They abound as slime on fallen logs in woodland settings. Although meiotic sexuality is rare, cellular slime molds display an elaborate sort of parasexuality: orgies in which hundreds of companions come together and fuse. Fusion leads to reproduction because propagules are formed that distribute the former amebas away from areas where they have exhausted the food supply.

Individual amebas of the cellular slime mold aggregate to form a structure called a pseudoplasmodium (because the ameba cells inside are still intact, so the structure is genuinely multicellular). The aggregate takes on the appearance of a slug. As conditions become drier, the slug differentiates into a sporophore with a sorus that contains dark, resistant propagules, which, except for being on the top of an erect sporophore, are virtually indistinguishable from ameboid cysts. These propagules are carried away by wind; some develop into amebas. Because of their unique differentiation from amebas to slugs to erect cyst-bearers, cellular slime molds are studied extensively by cell biologists. Two are shown here: *Copromyxa spicata* (A) and *Acrasis rosea* (B, ingesting bacteria).

Phylum: Rhizopoda—Dictyostelida

Dictyostelids are cellular slime molds with complex life-history stages: amebas, aggregation forms, and stalks that bear spores. Dictyostelids, also of the phylum Rhizopoda (page 52), are distinguished from their closest relatives, the acrasids, because of several differences: Dictyostelids have better-differentiated stalk and spore cells, form more distinct sorocarps (the spore-bearing structures), and align into throbbing streams during ameba aggregation.

Because morphogenesis is separate from differentiation in its life cycle, *Dictyostelium discoideum* is used in laboratory experiments to study development. Dictyostelid spores germinate into amebas, the feeding stage of the cellular slime mold. As food or sunlight diminishes, the amebas aggregate into a visible sluglike form called a grex. The aggregating ameba and shape-changing grex compose the morphogenetic phase; the sporophore differentiates as basal disc, stalk, and spore cells.



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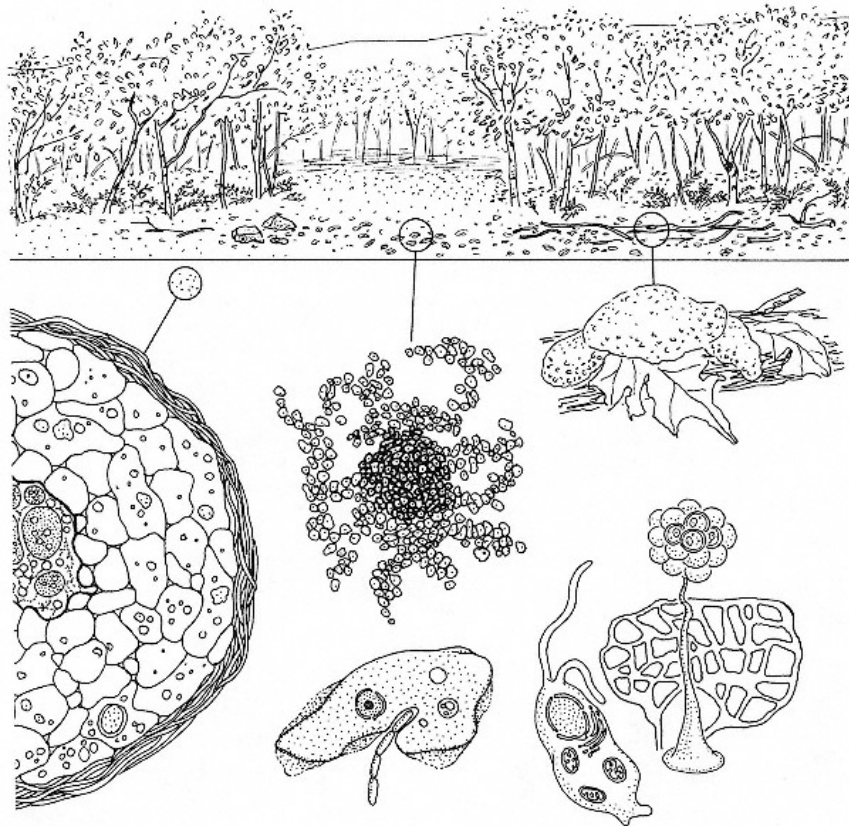
Amebas of different strains fuse to form a diploid zygote, called a giant cell, which then engulfs other amebas. As more amebas congregate near the giant cell, they become enclosed in a sheath and grow to form the macrocyst. Shown here (C) is the macrocyst of *Polysphondylium violaceum* with the giant cell in which meiosis is occurring, as seen in the center. This structure forms the grex, which migrates. Later it develops into the spore-bearing sorocarp.

Phylum: Myxomycota

The plasmodial slime molds are denizens of the forest floor and its decaying trees. Unlike cellular slime molds, these organisms are

composed of myriad nuclei not organized into cells; rather, the nuclei and other cell components move back and forth inside the multinucleate mass called the plasmodium. The movement is called intraplasmodial or cytoplasmic streaming.

Depicted here is the large yellow myxomycote *Fuligo septica* (**D**). Its sporophores (**E**) are 1 to 5 centimeters in diameter and can be seen on well-fertilized lawns and logs. The sporophore consists of a basal disc, a stalk, and a sporangium or sporocarp, the stage in the myxomycote life history that produces propagules. Diploid spores produce either haploid undulipodiated swarmer cells (**F**) or haploid amoebas, superficially like free-living amoebas, called "myxamoebas." Unlike other amoebas, myxamoebas can fuse with similar cells to produce a zygote that grows by nuclear division without cytoplasmic division to form the multinucleate plasmodium (**G**). The plasmodium in turn gives rise to stalked sporophores (**E**).



North Atlantic Coast

Phylum: Rhodophyta

Rhodophytes are red algae, a great marine group containing some of the largest multicellular prototists, including many common seaweeds. Because they do not form diploid embryos retained in maternal tissue, rhodophytes are not plants. Red algae differ from aquatic plants in many other ways as well. The two classes of rhodophytes are the Bangiales and the Florideae, such as *Polysiphonia harveyi* (A). The cells of Florideae interconnect by small holes in their walls through which cytoplasm can flow. Called pit connections, the holes are visible in this detail of a cell (B).

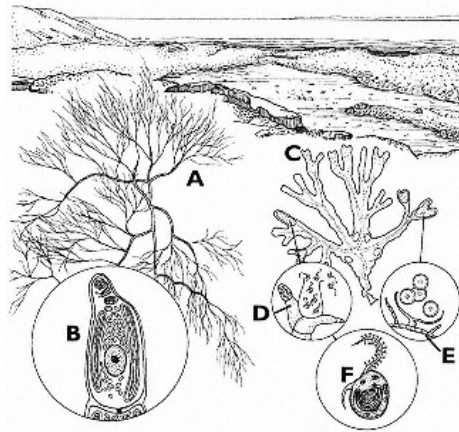
No rhodophytes have undulipodia, but many have sexual stages. Small, spherical, immotile male cells, carpospores, are shed in large numbers over female threads, which they penetrate by growth. The life histories of some Florideae are very complex, whereas some Bangiales reproduce only by binary fission, showing no evidence of sex or gender.

All rhodophytes have reddish plastids (called rhodoplasts) that contain chlorophyll *a* and phycobiliproteins, which color the algae red. This phylum includes 4,000 species, including the coralline algae, which form calcium carbonate in their cell walls. Red algae provide the material used in making agar, carrageenan, and other polysaccharides for the manufacture of ice cream and other food products and pharmaceuticals. The agar gels used in DNA biotechnology could not be made without the products of *Gracilaria*, a prolific red alga. Some red algae are consumed whole, such as *Porphyra*, which is eaten in *gim bob* (Korea) and *sushi* (Japan).

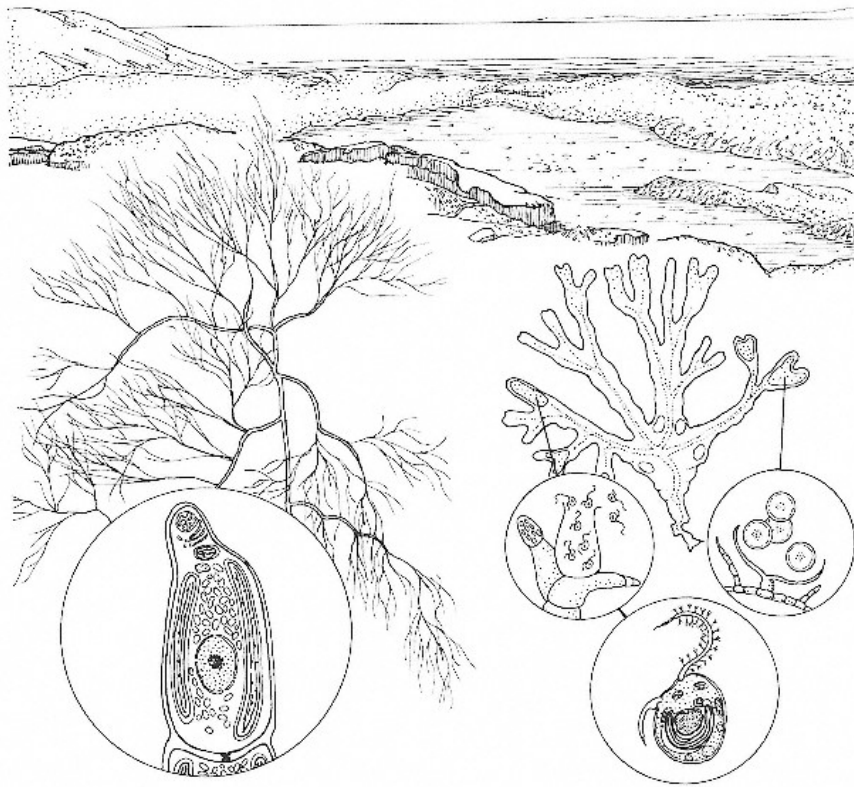
Phylum: Phaeophyta

Phaeophytes, or brown algae, are the largest prototists. Some forms, like the giant kelp, grow to up to 10 meters long. Marine biologists speak of kelp forests, where thick populations bob with the waves. The Sargasso Sea is named for its great *Sargassum* alga. Phaeophytes live on rocky coasts around the world, dominating the intertidal zone and shoals near the shore. They are the primary producers for many communities of marine animals and microbes.

Phaeophyte sexuality is depicted here in the species *Fucus vesiculosus*. The diploid form, or sporophyte, is the conspicuous seaweed itself (C). On its surface (the thallus) the sporophyte produces little bumps, which are sex organs: antheridia (D, shown releasing male gametes) and oogonia (E, shown releasing female eggs). The tiny male gametes (F) are motile sperm cells, each with two undulipodia. One undulipodium is long and has mastigonemes; the other is short and whiplike. The sperm swim to the oogonia and fertilize the eggs. The fertilized egg then germinates, grows rhizoids, and becomes the new sporophyte. Brown algae, such as *Laminaria*, are eaten and used in dyes and adhesives. Phaeophytes are also a source of vitamins, medicines, and minerals.



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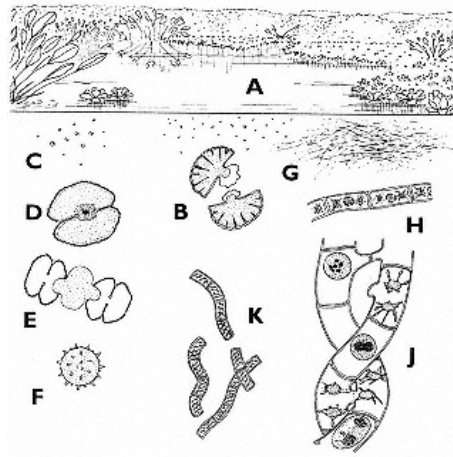
Shallow Pond

Phylum: Gamophyta

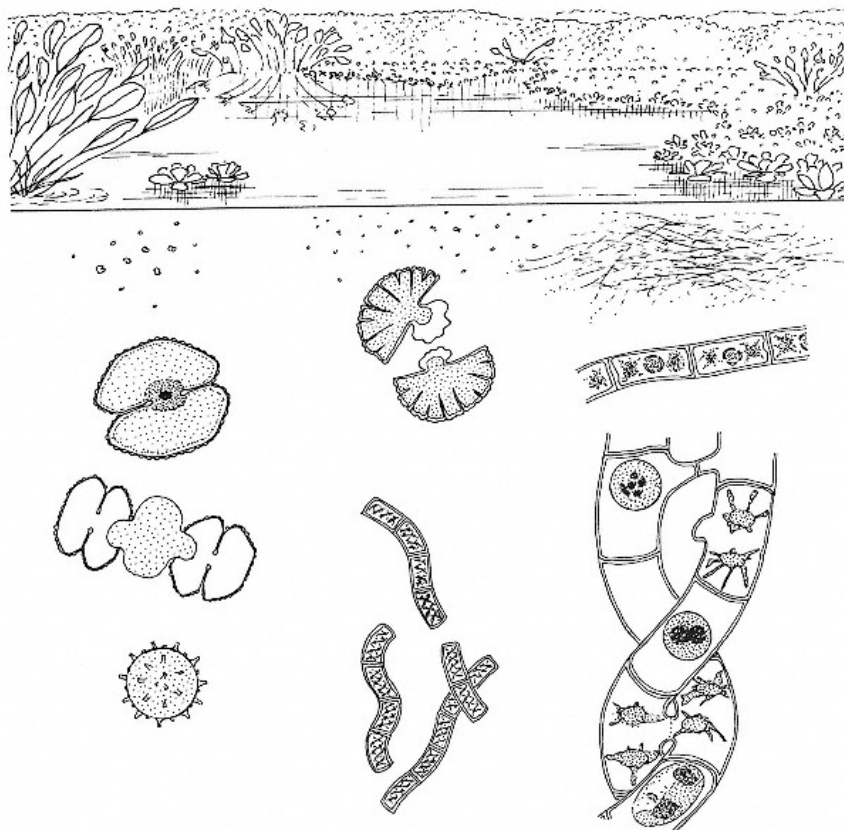
This phylum of freshwater green algae, called gamophytes, is distinguished from all other green algae by its sex life. Gamophytes conjugate: During the life cycle two bodies of more or less equal form come together to mate and fuse nuclei in the absence of any sperm or eggs. No undulipodia are ever formed by gamophytes. The group contains some of the most beautiful aquatic microorganisms known, although to the unaided eye and the unenlightened observer they appear mostly as floating pond scum (A). Many are green filaments; the others, such as *Micrasterias* (B) and *Cosmarium* (C–F), belong to a group that look like little jewels, called desmids.

Zygnema sp. (G) forms an algal mass. Individual cells of *Zygnema* (H) show the nuclei and stellar (star-shaped) chloroplasts with pyrenoids. The stellar chloroplasts are also visible in these two conjugating strands of *Zygnema* (J). *Micrasterias denticulata* reproduces asexually; shown here are two halves budding (B). Strands of *Spirogyra* (K) are recognizable by their characteristic helically wound chloroplasts.

Also shown are free-floating individuals of the desmid *Cosmarium* sp. (C). A single cell of *Cosmarium* (D) shows the nucleus and chloroplasts. In desmid sexuality the spiny ameoboid zygotes leave their tests (shells) to conjugate (E). The resulting spherical resistant body (F) falls to the bottom of the pond until spring, when it returns to an active growing stage.



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Marine Abyss

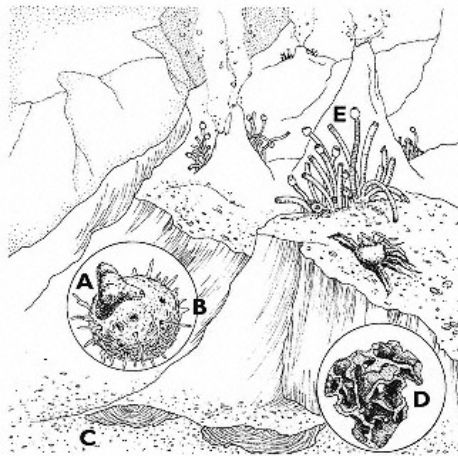
Phylum: *Xenophyophora*

From the most remote depths of the ocean, the abyss, come the rarely seen, strange protoctists known as xenophyophores (in Greek *xenos* means "foreign," and *phyo-* means "to produce"). These little-known heterotrophic organisms often have been mistaken for fecal pellets, mineral deposits, or foraminiferan tests because they cover themselves by cementing pieces of foreign material together.

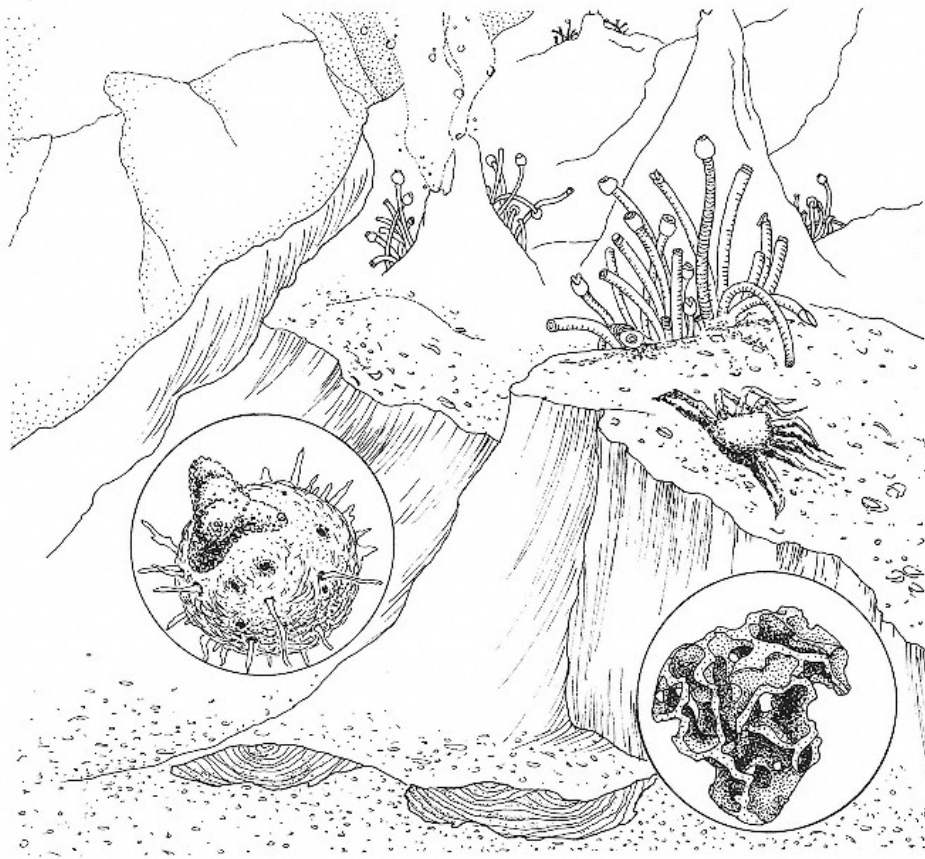
The traditional, rough sampling techniques used in investigating the abyss usually break these protoctists into pieces, increasing the confusion that surrounds them. Better understanding of the deep-sea vents, cold seeps, and other features of the seafloor, as well as gentler methods of sample collecting, now provide an abundant supply of xenophyophores for study. Thirteen genera and forty-two species have been described, but by only a few scientists.

The xenophyophores are plasmodial organisms—that is, they are formed of a multinucleate common cytoplasm that is inside a cemented, branched tube system called a granellare. The cytoplasm of many xenophyophores contains crystals of barite (barium sulfate). Several species are depicted here: *Galatheaamina tetradlea* (A); *Reticulammina lamellata* (B, with its pseudopods extended for phagocytotic feeding); the flat *Stannophyllum zonarium* (C, on the ocean bottom); and *Psammietta globosa* (D).

Stannophyllum can grow very long for a protoctist (up to 23 centimeters), but even at this length it remains only 1 millimeter thick. Almost no one has seen these protoctists alive. Fossils (e.g., *Paleodictyon*) in sedimentary rocks look much like xenophyophores; whether the modern and ancient beings are related, however, is still unknown. (See page 152 for a discussion of the tube worms, E.)



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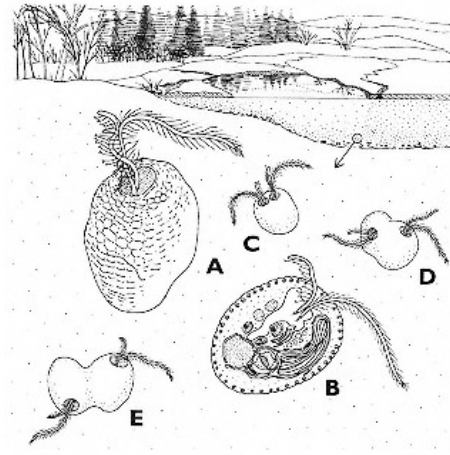


Ice-Covered Lake

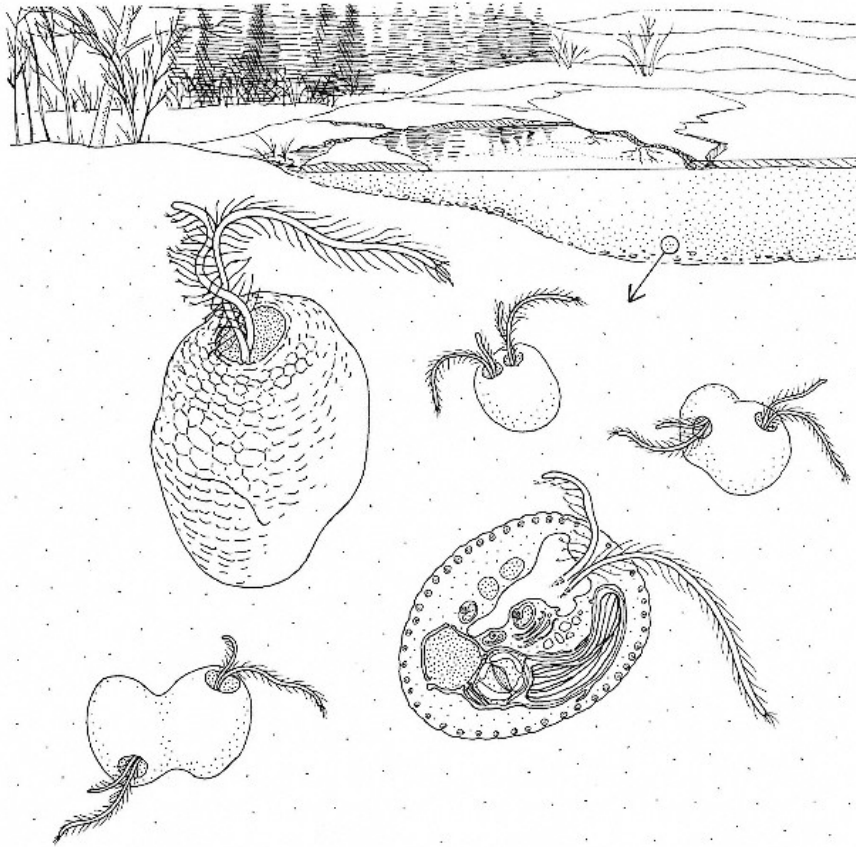
Phylum: Cryptomonada

Also known as cryptophytes or phytoflagellates, cryptomonads are ubiquitous and abundant photosynthetic, motile, aquatic protists. Some form colonies of mucilaginous sheaths. Cryptomonads are a major constituent of the microbiota in ponds in early spring. Like euglenids (see page 74), these organisms photosynthesize but also may eat. If cryptomonads have any sexual life, it has gone undetected. They are generally found in cold environments. The reddish brown color of the red-tide ciliate (see page 94), *Mesodinium rubrum*, in the ocean is due to cryptomonad endosymbionts that are partly photosynthetic. Hundreds of these photosynthetic cryptomonad symbionts reside in the cytoplasm of just one of these fastmoving ciliates.

The cryptomonads, such as *Cyathomonas truncata* (A), have two anteriorly directed undulipodia of unequal length inserted in a gullet, or crypt. This cross section of *Cyathomonas* (B) shows its organelles. Cryptomonads reproduce by a distinctive form of cell division: A second crypt forms (C), one of the two crypts migrates to the opposite end of the cell (D), and the cell divides (E). Many also have trichocysts, which are expelled to sting and capture small protists or bacteria. About sixty species are known; some, such as *Copromonas*, eat only bacteria, lack photosynthesis, and grow well in the dark in the laboratory. In nature, they dwell in dung.



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River Delta

Phylum: Cryptomonada—Glaucocystophyta

Glaucocystophytes are rare freshwater algae, part of the phylum Cryptomonada (page 68), that live photoautotrophically (producing their own carbon products by using sunlight) with the aid of bright bluish green, chloroplast-like bacterial symbionts called cyanelles. Lacking a cell wall, these symbionts are surrounded by membranes; they lie in a vesicle. Glaucocystophytes are either mastigote or coccoid algae. The motile forms have two undulipodia, both with brushlike mastigonemes. *Gloeochaete* sp. (A) produces stiff, hairlike extensions called pseudocilia arising from the apical depression (B).

Nine genera and thirteen species of glaucocystophytes are recognized. Although they have limited biochemical and genetic makeup, the cyanelles inside the cells of some species of glaucocystophytes, such as *Cyanophora paradoxa* and *Glaucocystis nostochinearum*, have been classified as symbiotic cyanobacteria.

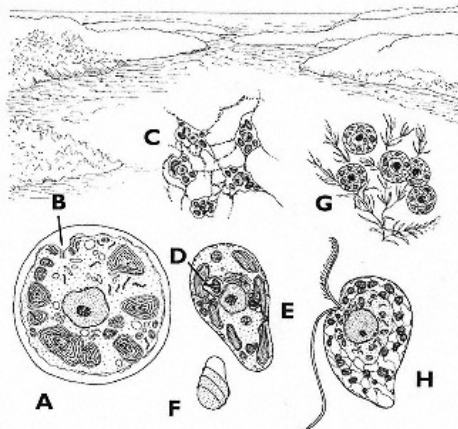
Phylum: Rhizopoda—Chlorarachnida

Although others are thought to exist, to date only one chlorarachnid—*Chlorarachnion reptans*, a phototrophic ameba that lives in a plasmodial reticulum network (C)—has been formally described. Each cell has several bright green plastids (chloroplasts), making the ameba capable of photosynthesis, although it eats protoctists phagotrophically. *Chlorarachnion* has a distinctive periplastidial compartment in the region near the base of the pyrenoid (D), where starch is formed. Distinctive zoospores (E) form and disperse *Chlorarachnion* cells through the sea water in which they live. A single undulipodium is wrapped helically around the body of the cell as it swims (F).

Once considered a xanthophyte (see page 78) or a foraminiferan rhizopod (see page 96), *Chlorarachnion* (whose name means "green spider web") is an extremely atypical alga. It is considered part of the phylum Rhizopoda (see page 52). Its plastids have chlorophyll *b*, and its mitochondria have tubular cristae (the folded membranes), whereas other algae with chlorophyll *b* have mitochondria with flat cristae.

Phylum: Chrysomonada—Raphidophyta

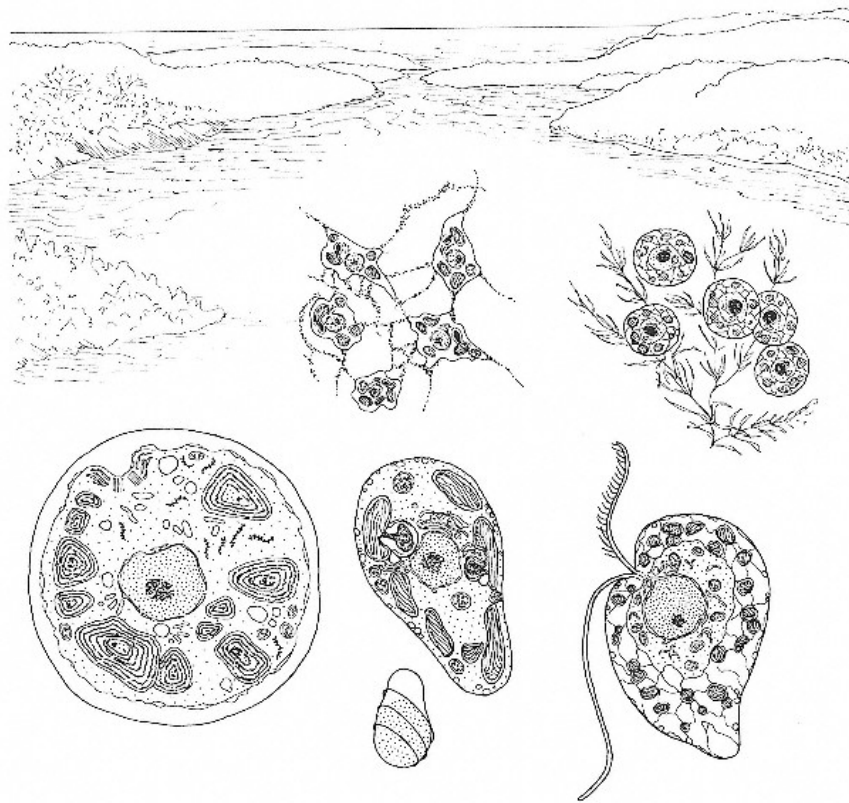
Raphidophytes are tiny, obscure algae that, even to specialists—phycologists and marine biologists—are not well known. Here they are placed in the phylum Chrysomonada (see page 90). Detailed structural analysis is required for proper identification of the genera. Raphidophytes are unicellular, wall-less algae that live, among aquatic plants or adjacent to the mud. They are heterokont (i.e., they have two different undulipodia), but only the forwardly directed undulipodium bears the tubular hairs called mastigonemes.



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At least one species, *Olisthodiscus luteus*, is quite prolific. Scientists have determined that the dominant planktonic organism in Narragansett Bay (Rhode Island) in summer is this raphidophyte, which has a large Golgi body (or dictyosome), used in secretions, adjacent to the central nucleus.

Only four genera and nine species of raphidophytes have been described. Shown here are *Vacuolaria* sp. (**G**, growing among water weeds) and the marine species *Chattonella* sp. (**H**, in cross section), which was named after the French marine biologist Edouard Chatton (1883–1947), the first person to recognize the difference between prokaryotic and eukaryotic microorganisms. Chatton lived at the marine station Laboratoire Aragon on the western French Mediterranean and worked tirelessly from approximately 1920 until his death in 1947 to make known the complex life histories of marine protoctists.



Fallen Log

Phylum: Archaeoprotista

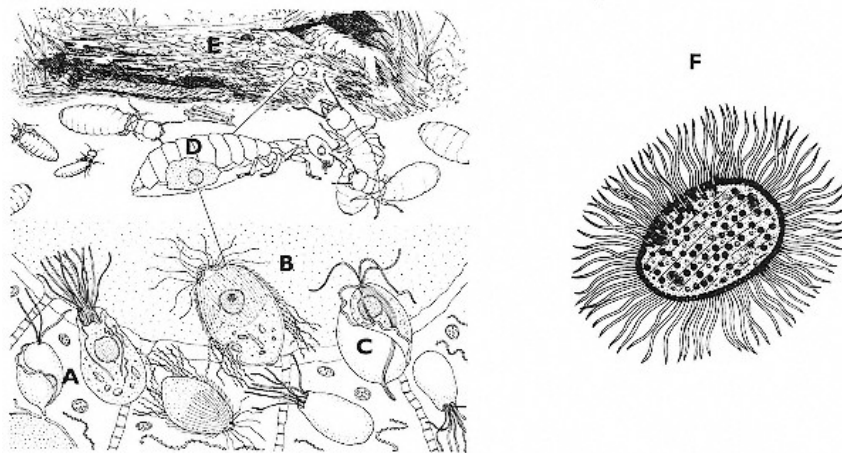
This phylum of amitochondriate protocists consists of three classes: the Archamoebae, such as *Pelomyxa* (see page 52); the Metamonada, which includes the diplomonads, retortamonads, and oxymonads, many of them symbionts of animal intestinal tracts; and the Parabasalia, such as the trichomonads and hypermastigotes shown here (A–C). These too are almost entirely symbionts of animal intestines and other tissues.

Most archaeoprotists are unicellular with at least one undulipodium; some have thousands of undulipodia. Three representative genera of parabasalians are shown here: *Lophomonas* (A), *Trichonympha* (B), and *Trichomonas* (C). None have mitochondria, but many harbor bacterial symbionts.

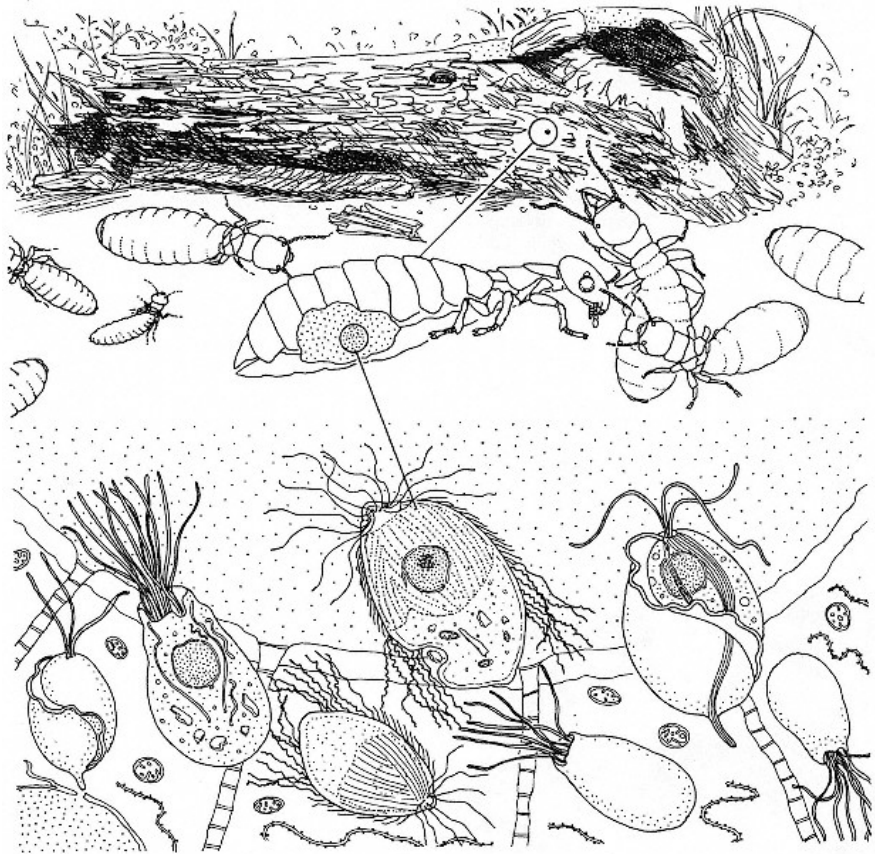
In this scene of termites is a hidden component. Dry-wood-eating termites, *Pterotermes occidentis* (D), eat and nest in the logs of *Cercidium* (E)—paloverde, a leguminous tree—but actually the microorganisms in the gut of the termite digest the wood. The termite itself ingests but cannot digest any wood. In this symbiosis, the parabasalian protists digest the cellulose from the wood into sugars for themselves and form acetate, which enters the cells of the termite intestines, thus nourishing these colonial insects.

Phylum Zoomastigota

The zoomastigotes are a miscellany of small heterotrophic unicells, most of whom derive their food osmotically. This phylum likely contains the ancestors of animals. It includes free swimming forms such as *Reclinomonas*, the opalinids (F), which are symbiotrophs in the rectum of frogs, and the choanomastigotes, which are thought to be direct ancestors of sponges (see page 124).



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Outfall Pipe

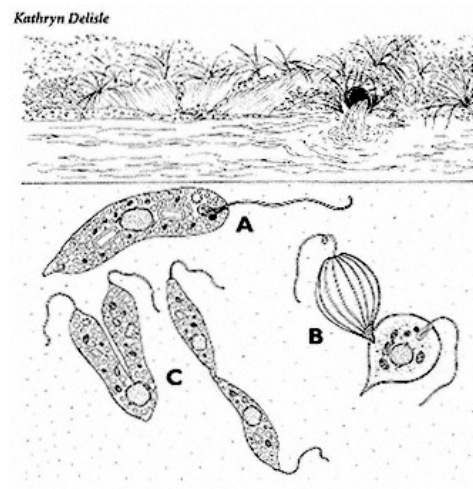
Phylum: Discomitochondria

This new phylum includes the euglenids and kinetoplastids, such as *Trypanosoma*, the protist associated with African sleeping sickness, as well as the amebomastigotes. They all have similarly shaped mitochondria.

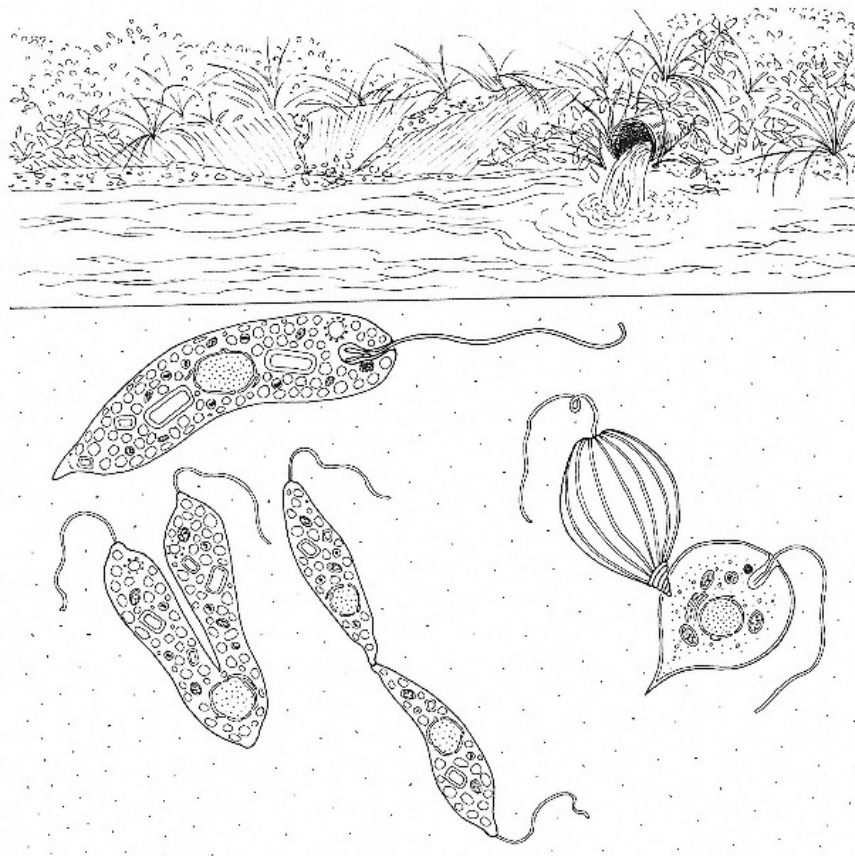
Because they exhibit the classic characteristics of both animals and plants, euglenids are the perfect example of why the two-kingdom classification is archaic. Like animals, euglenids are motile because they have anteriorly directed undulipodia. Like plants, they are packed with chloroplasts for photosynthesis. Euglenids differ from green algae (chlorophytes, see page 84) because they have a different combination of colored compounds in their plastids and their cytoplasm, and they lack a cellulosic cell wall. Instead they have a proteinaceous pellicle—a ridged, flexible, highly characteristic cell covering.

Euglenids differ from the conjugating green algae (see page 64) because they have no sex. Of the approximately 800 species of euglenids that have been reported in the literature—even those that are colonial, multicellular forms—not one has been seen engaging in sexual activity. All euglenids reproduce by binary fission, starting at the undulipodiated end of the cell. Some species, such as *Euglena gracilis*, have been useful for analyzing cell organelles. For example, the cell can lose its chloroplasts and, if well fed, survive and reproduce without them. *Euglena gracilis* has been used as an indicator in water-quality studies and in bioassays for vitamin B₁₂.

Pictured here are *Euglena spirogyra* (A) and *Phacus* sp. with its ribbed pellicle (B, external and internal views). Two stages of division during the reproduction of *Euglena gracilis* are shown in longitudinal cross section (C).



Kathryn Delisle



Marine Chalk Cliffs

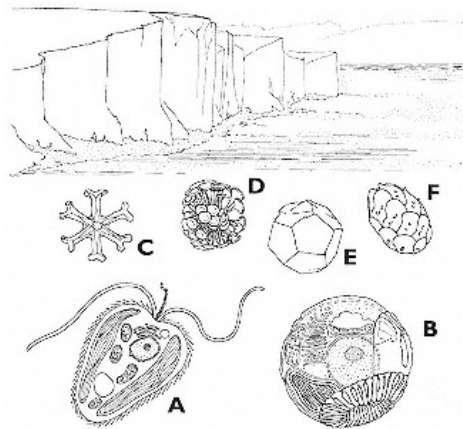
Phylum: Haptomonada

Organisms that float with the waves are called plankton by ecologists. If capable of photosynthesis, they are called phytoplankton. Because *phyto-* means "plant," however, this term should be replaced by "photoplankton." Prymnosiophytes (also called haptophytes or haptomonads) are typical of "cosmopolitan" photoplankton. Mostly single-celled algae, prymnesiophytes have chrysoplasts, just as the chrysophytes do (see page 90), but are mainly marine.

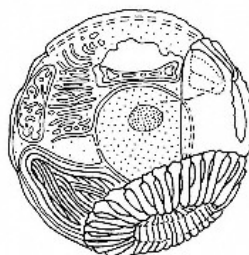
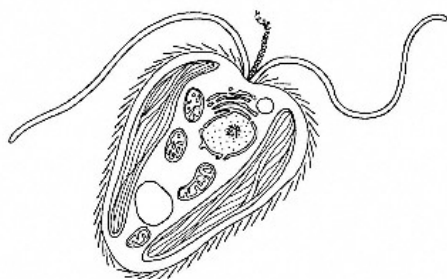
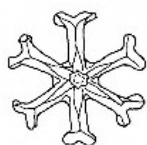
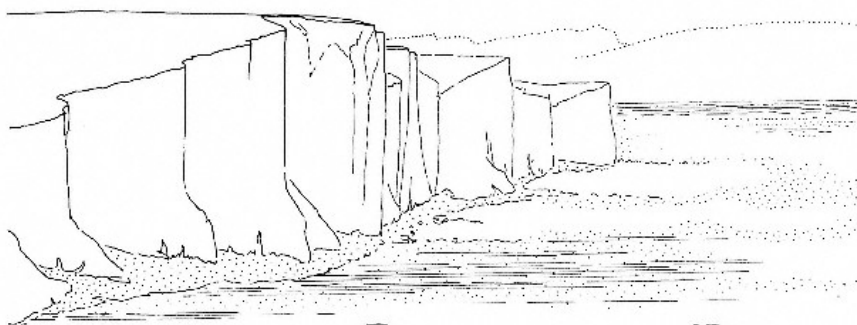
Some prymnesiophytes also form the distinctive resting stage called the coccolithophorid, a single cell covered with little calcium carbonate buttons or plates called coccoliths, which means "berry stones." Fossilized coccolithophorids and forams (shelled granuloreticulosans; see page 96) make up the famous chalk cliffs of England. The prymnesiophyte *Phaeocystis poucheti* contributes a significant amount of the gas dimethyl sulfide to the atmosphere as a byproduct of manufacturing a substance that maintains its salt balance. (Compounds made by cells that regulate internal salt concentrations are called osmolytes.)

For many years scientists were not aware that the free-swimming stage of prymnesiophytes (e.g., *Prymnesium parvum*, **A**) and the coccolithophorid (such as *Emiliania huxleyi*, **B**) are two different stages of the same group of organisms. Coccoliths are distinguished by their shapes; some examples of coccoliths include discoasters (**C**), rhabdoliths (**D**), pentoliths (**E**), and helicoid placoliths (**F**). No one knows what these scales do, but they may act as a sort of venetian blind that modulates the sunlight reaching the plastids.

How do these tiny algae construct their elegantly patterned covering? Within the motile stage, organic scales form inside an organelle called the Golgi apparatus. Calcium carbonate crystallizes on the scales in species-specific patterns. As these microscopic coccoliths assemble, microtubules move them out to the surface of the algal cell.



Kathryn Delisle



Lake Surface

Phylum: Eustigmatophyta

Eustigmatophytes are obscure, tiny, "eyespot" algae. They are yellowish green and contain a single, long xanthoplast like that of the xanthophytes (see this page). Their cell organization is completely different from that of the yellow-green xanthophytes, however.

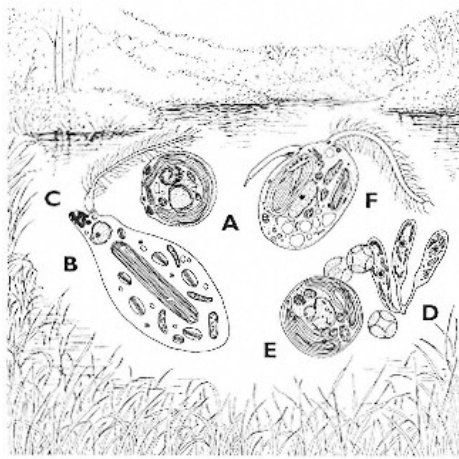
The name Eustigmatophyta is derived from the presence in all of these organisms of eyespots with stigmas. Informally called eustigs, these inconspicuous protists tend to be known only to professional botanists and pond-water enthusiasts.

Generally found in freshwater, eustigs such as the representative genus *Vischeria* sp. form immotile, coccoid growing cells (A). Not known to engage in any type of sexuality, they reproduce by binary fission. The zoospore of *Vischeria* sp. (B) has a single, mastigonemate undulipodium with an undulipodial swelling at the base. An adjacent swelling, filled with drops of carotenoids, forms the eyespot (C). This organization of the cell probably assures that undulipodial movement directs the cell to optimally lighted environments because the plastid absorbs visible light, which excites the carotenoid pigment.

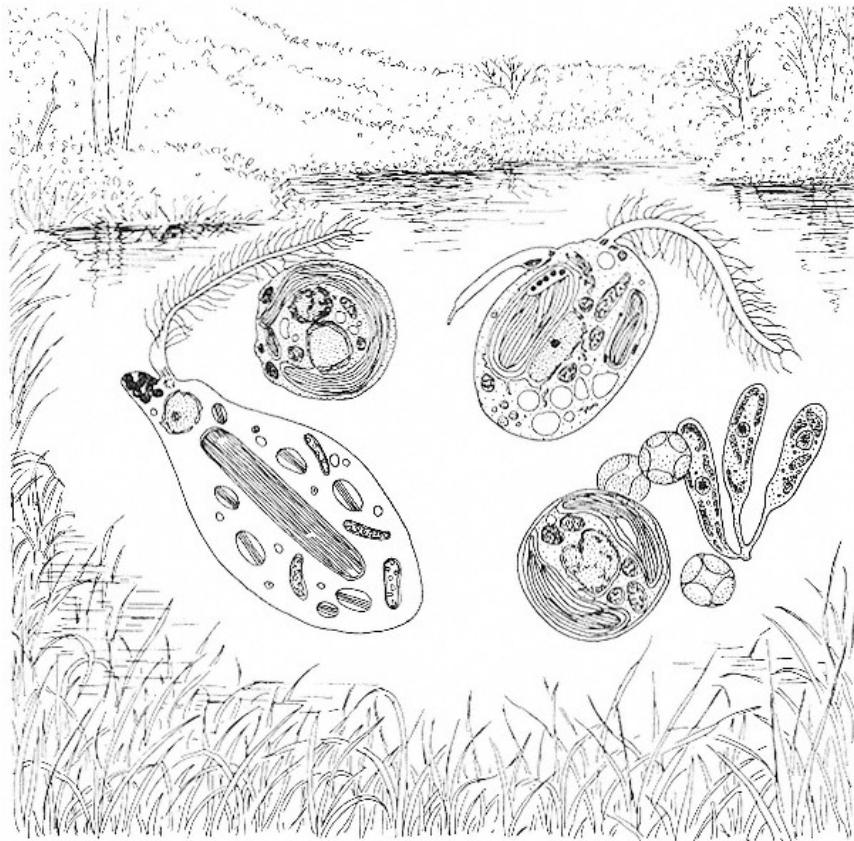
Phylum: Xanthophyta

People tend to think of xanthophytes, often called yellow-green algae, as pond scum. Most xanthophytes are freshwater algae with photosynthetic pigments, including xanthins, which make them yellow-green. Many xanthophytes have been seen only rarely, probably because they exist in small numbers. Pictured are the colonial genera *Ophiocytium* (D) and *Botrydiopsis* (E), which resembles a bunch of grapes.

Xanthophytes overwinter as cysts. In the spring they germinate, changing shape as they become motile zoospores (F). The zoospore, a spermlike cell that swims but is capable of reproducing without fertilizing an egg, loses its undulipodia and begins to grow into the alga itself. Xanthophyte zoospores are heterokont: One undulipodium is longer than and different from the other: It is covered with mastigonemes. Most xanthophytes have yellow-green, disc-shaped plastids (photosynthetic organelles) that are situated against the cell wall.



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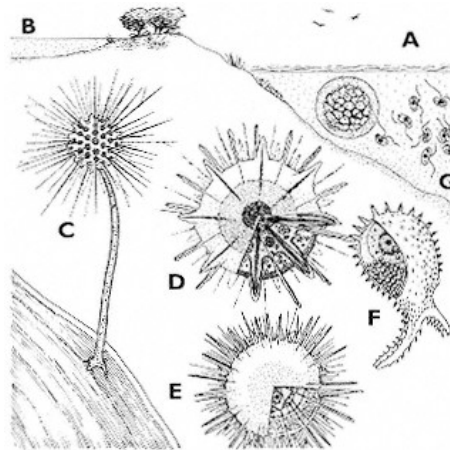
Ocean Water Column

Phylum: Actinopoda

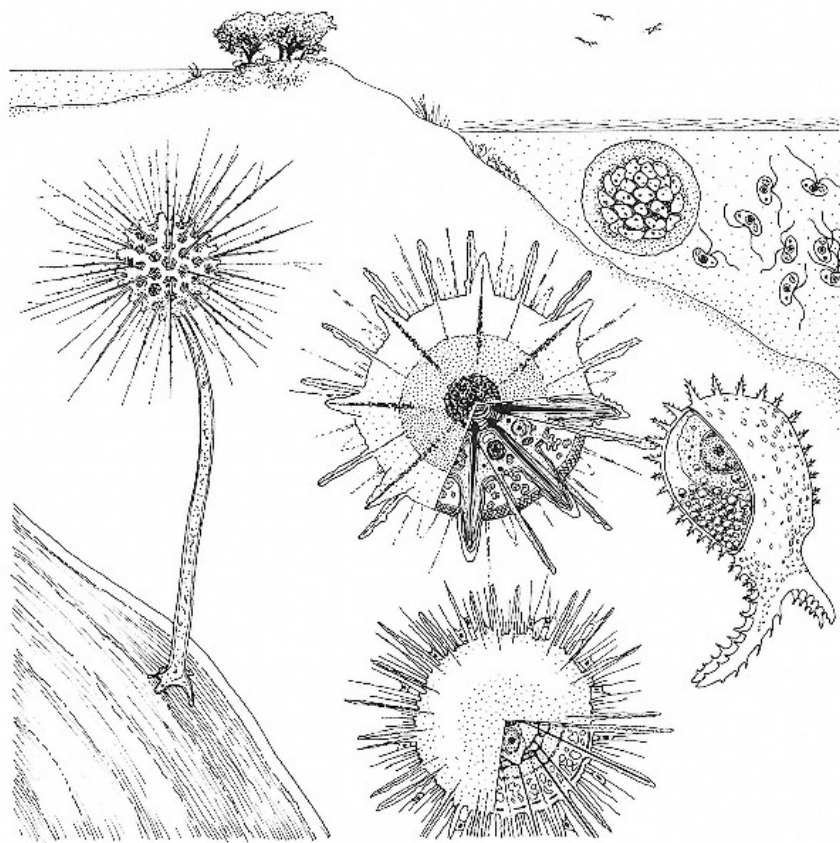
Known to microscopists for three centuries as sun animalcules because of the rays that project from their cells, actinopods are distinctive, heterotrophic protocists. Microtubules and filaments called axopods underlie their long, slender, projecting cytoplasmic organelles. In the plankton literature they are called radiolarians (in marine environments, **A**) or heliozoans (in freshwater, **B**), but ultrastructural studies have revealed their relationship to other protocists.

The particular arrangement of the microtubules along the axis of the ray (called the axoneme, which means "axis thread") is what classifies the actinopods. Four groups are recognized: (1) Heliozoa, such as *Clathrulina fragilis* (**C**), shown here attached to a submerged leaf in a stream; (2) Acantharia from the sea, such as *Phyllostaurus siculus* (**D**), shown here with a cutaway section that reveals the spicule, cytoplasm-coated axopods (which are used to capture food), and capsular wall made of microfilaments; (3) Polycystina, such as *Spongosphaera polyacantha* (**E**), shown here with a cutaway section that reveals the silica skeletal spine, axopods, and plates of the capsular wall; and (4) Phaeodaria, including *Challengeron wyvillei* (**F**), shown here with a cutaway section that reveals the endoplasm, nucleus, and a ball of waste product called the phaeodium.

Ameboid cells of phaeodarians are contained within plasmodial spheres, from which they are released as undulipodiated swarmer cells (**G**). These aquatic propagules develop without any sexuality and metamorphose into adults. Polycystines, phaeodarians, and acantharians traditionally have been called radiolarians because of their marine habitat. Only electron microscopy and chemical analysis reveal the great differences among these floaters. The acantharian skeleton, unlike that of the others, is made of barium sulfate. Heliozoans covered with siliceous scales are common in freshwater streams and ponds.



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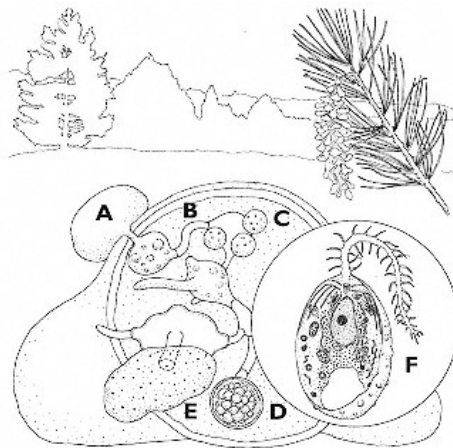


Pine Pollen

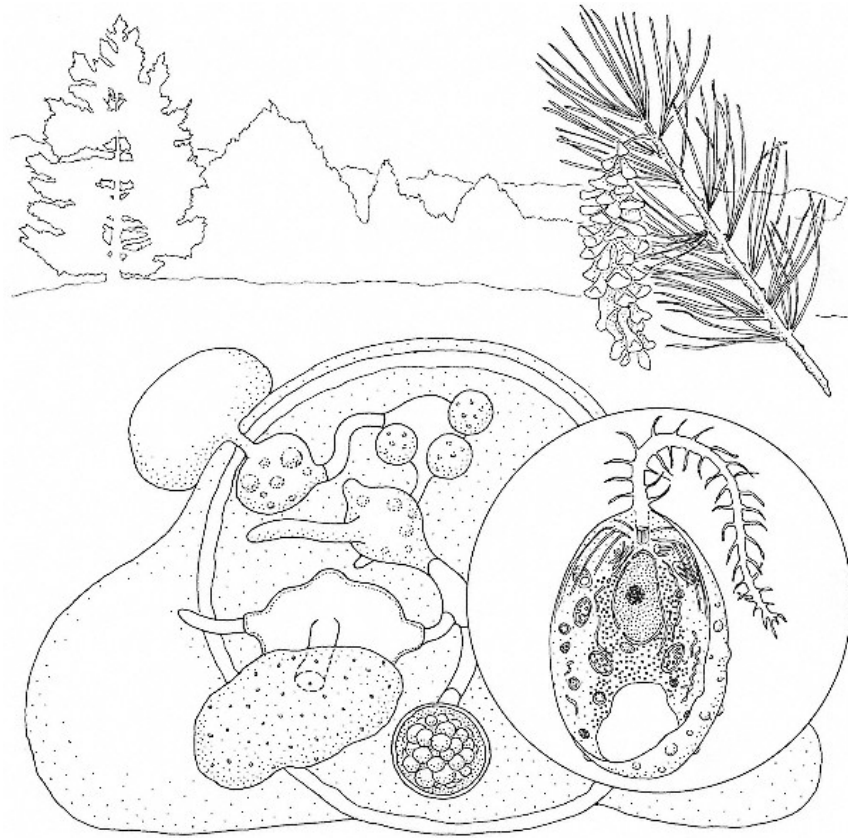
Phylum: *Hyphochytriomycota*

Because they look like white fuzz at a particular stage of their life history—just as plasmodiophorids (see page 86), chytridiomycotes (see page 92), and oomycotes (see page 102) do—hyphochytrids traditionally have been classified as fungi. They are more appropriately classified as protocists, however, because they produce undulipodiated cells and lack the spores and life-cycle details of the ascomycote (see page 110) and basidiomycote (see page 112) fungi.

Hyphochytrids form swimming cells called zoospores that are capable of further development without fertilization. Each zoospore has a single, anteriorly directed undulipodium that bears mastigonemes. The species shown here, *Hyphochytrium catenoides*, grows on shed pine-pollen grains. The hyphochytrid cell produces a germ tube (A), which it uses to penetrate the cell wall of the shed pollen. Inside the pollen grain, the developing thallus (B), differentiating zoospores (C), sporangium (D), and protoplasm being discharged from the sporangium (E) of *Hyphochytrium* are visible. The magnified view of a hyphochytrid zoospore (F) shows the mastigonemes on its anterior undulipodium, as well as the nucleus, mitochondria, microtubules, and Golgi apparatus. To date, five genera and twenty-three species of hyphochytrids have been described in the professional (mostly mycological) literature.



Kathryn Delisle



Atlantic Sheltered Bay

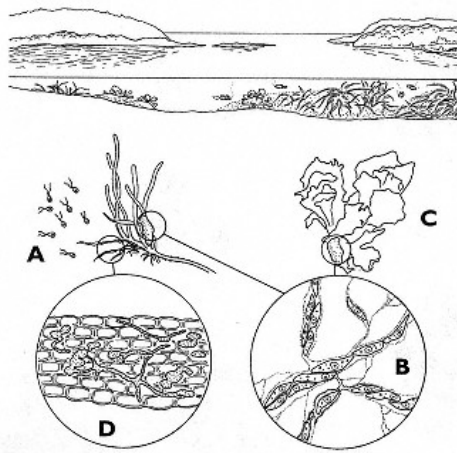
Phylum: *Labyrinthulata*

The labyrinthulids, or slime nets, are colonial protocists that form membrane-bounded ectoplasmic networks devoid of cytoplasmic constituents. Labyrinthulid cells produce these transparent networks from specialized organelles, called sagenogens or bothrosomes, at the cell surface. How cells within the colony move is unknown, but movement requires contact between the cell and the slime network and does not involve undulipodia.

Labyrinthulids are heterotrophic, absorptive organisms that spend most of their lives moving back and forth inside the network, absorbing food osmotrophically. Some disperse via heterokont zoospores with two undulipodia. Labyrinthulids are found mainly in shallow marine benthic environments associated with algae, with sea grasses such as *Zostera marina* (A), or with organic-rich sediments.

The representative genus, *Labyrinthula* (B), contains eight species. Careful studies of obscure marine protocists called thraustochytrids unexpectedly revealed a relationship between them and the labyrinthulid slime nets. Now included in this phylum, therefore, are seven genera and thirty species of thraustochytrids. The cells of this arcane group of encysting protocists also produce bothrosomes. Because they are clearly related to labyrinthulids and they produce undulipodiated cells, thraustochytrids are no longer classified as fungi.

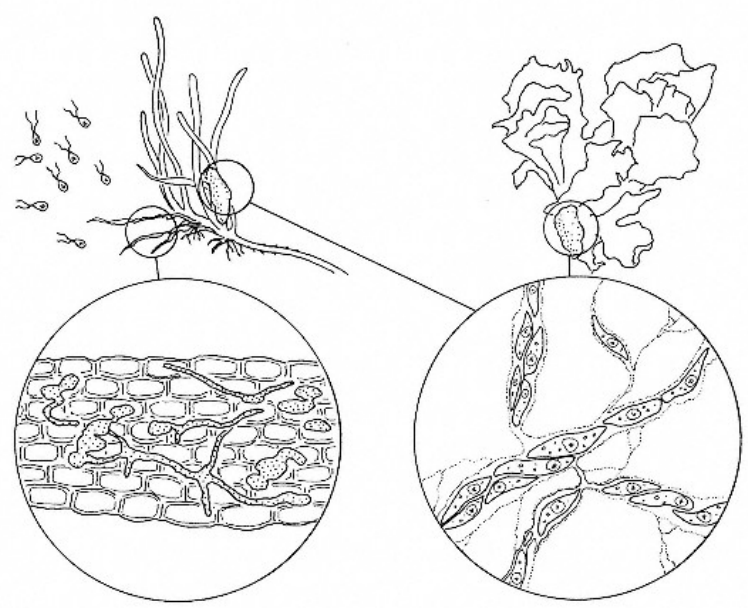
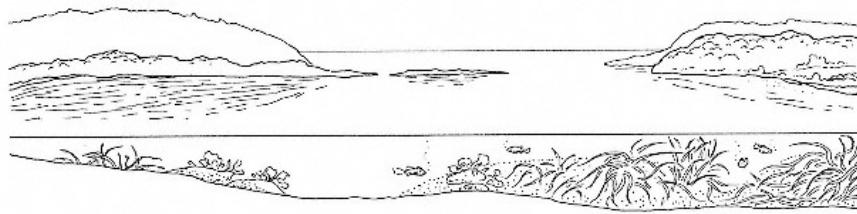
Phylum: Chlorophyta. Most green seaweeds and other green algae belong to the huge group of fascinating organisms known as chlorophytes. Many form zoospores, propagules that are capable of developing without a mate. Many also make very similar motile cells that are called gametes because, to develop, they must find a mate and fuse with it. Each zoospore or gamete has cup-shaped, grass-green chloroplasts and at least two anterior undulipodia of equal length. These are organisms of great translucent beauty and cosmopolitan distribution.



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The 16,000 species of chlorophytes range in size from the 12-micrometer single cell of *Chlamydomonas*, invisible to the naked eye, to the conspicuous sea lettuce *Ulva lactuca* (C). The endobiotic chlorophyte *Chaetosiphon moniliformis* (D) grows in the decaying leaves of eelgrass (*Zostera marina*, A). Although many are marine, chlorophytes are a major component of the freshwater photoplankton. Some live permanently on the bark of trees, others live in tree holes, and still others live chasmolithically—that is, in the crevices of rocks. Chlorophytes are estimated to fix more than one billion tons of carbon in oceans and freshwater lakes each year.

Because of the structure of their walled cells and the way the cells divide, certain genera of chlorophytes, such as *Klebsormidium*, are believed to be the closest relatives of plants. Sexuality, followed by the formation of overwintering zygospores—hard-walled, resistant structures—is common in the phylum.



Cabbage Field

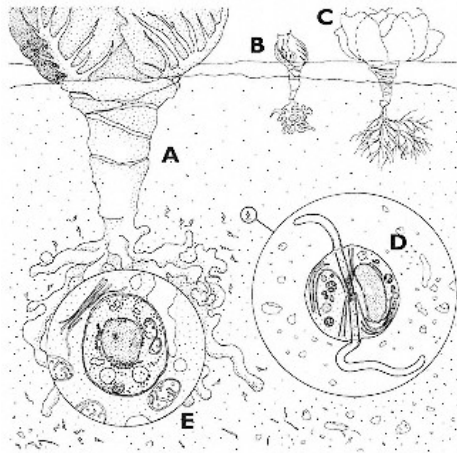
Phylum: *Plasmodiophora*

The plasmodiophorids comprise another group of protoctists infamous for the disease-forming ability of a few of their members. Plasmodiophorids are obligate symbiotrophs; some grow on algae and fungi, whereas others grow on plants. The plasmodia, the multinucleate structures, are much smaller than those of the plasmodial slime molds (see page 60), and they live inside the cells of the organisms with which they are symbiotically associated.

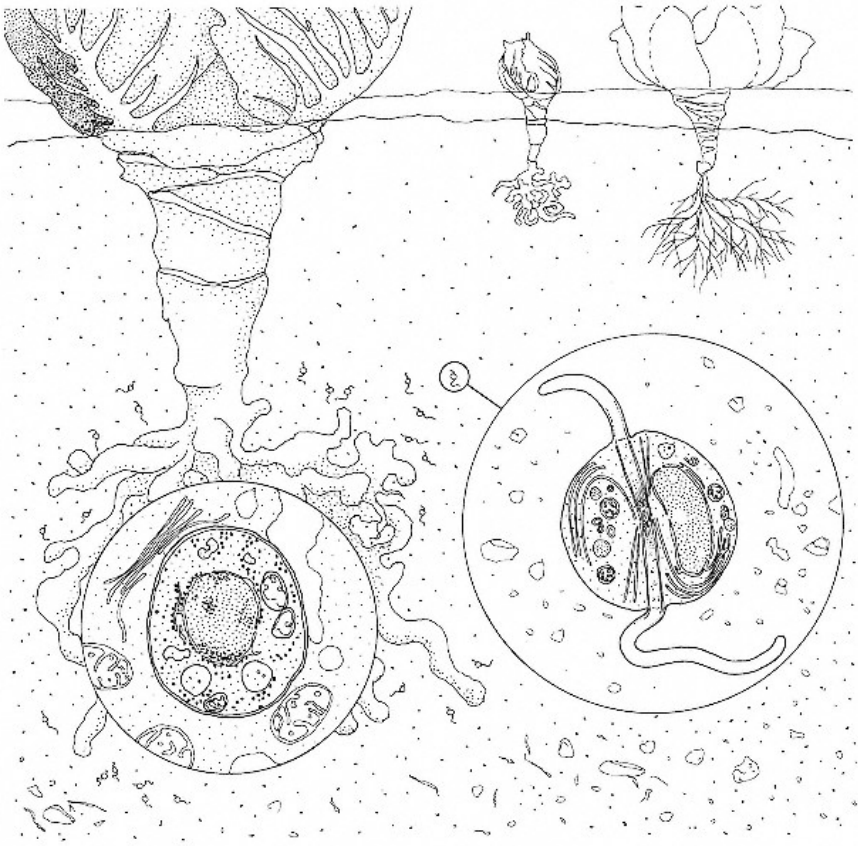
Although the trophic stage is a multinucleate plasmodium, the life cycles and cell structures of plasmodiophorids are completely different from those of the plasmodial slime molds. For example, *Plasmodiophora brassicae* (**A**), which infects cabbage via the damp soil around the plant roots, requires two sets of zoospores and plasmodia to complete its life history. The infected cabbage plant (*Brassica oleracea*, **B**) appears much different from a healthy plant (**C**), whose fine root networks are free of infection.

This detail of a zoospore (**D**) of *P. brassicae* shows its two undulipodia—one directed forward, the other backward—as well as the nucleus, Golgi apparatus, microtubules, and mitochondria. The detail of the secondary sporangium (**E**) in a cabbage root hair shows the nucleus within the protoctist (denoted by the bold line), surrounded by the organelles (Golgi apparatus, mitochondria, and cytoplasm) of the plant cell.

Plasmodiophorids are studied primarily by scientists concerned about the destruction of important food plants—that is, plant pathologists in schools of agriculture. Much more needs to be known about the details of the structure of the plasmodium, sexuality, cell behavior (the way the chromosomes clump and the nucleolus persists in mitosis), and many other aspects of the life of these obscure, often necrotrophic organisms.



Kathryn Delisle



Coastal Red Tide

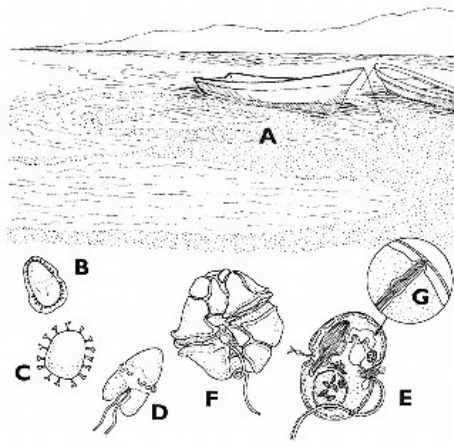
Phylum: Dinomastigota

Some people have estimated that there are 20,000 species of dinomastigotes. Even if you have never heard of them, you probably know what some of them can do. Dinomastigotes (also called dinoflagellates) are remarkably sculptured and diverse organisms. They are known mainly because some of them form the toxic red tides (A) that poison fish and shellfish. Some dinomastigotes are bioluminescent and cause a phosphorescent light on the sea at night. Others live inside the cells of cnidarians (see page 126) such as reef-forming corals and sea anemones. Most dinomastigotes are covered with armored plates, which helped them fossilize well during the Phanerozoic eon.

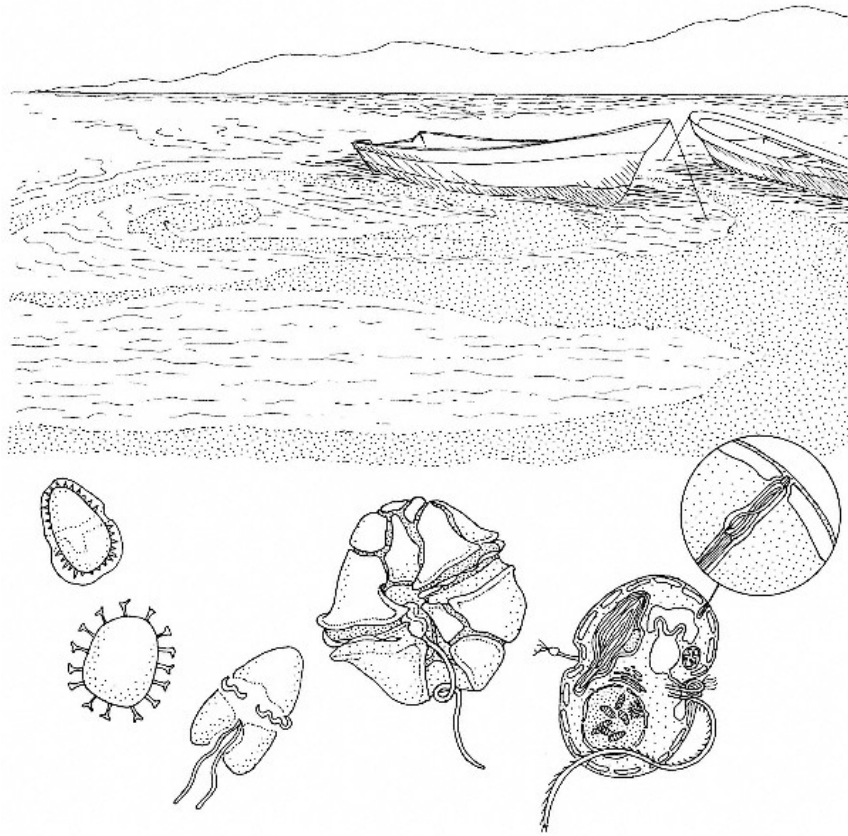
The life history of the dinomastigote *Pyrocystis* has several stages, including the resting cyst (hypnocyst, B), the dormant spiny cyst (C), and the planozygote (D). This cross section (E) of the adult *Gonyaulax tamarensis* (F) shows its organelles, with a detail of the trichocyst (G), an organelle that discharges suddenly to sting prey. The arrangement of the two undulipodia—one longitudinal and one transverse—in a characteristic groove is distinctive for the entire phylum.

Dinomastigote DNA is referred to as mesokaryotic (literally, between prokaryotic and eukaryotic). Whereas chromatin is organized in fine fibrils like that of bacteria, it is clumped into chromosomes that can be seen (with a microscope) before, during, and after cell division. The complex coverings, or tests, of some dinomastigotes have robust walls and permit the cells to overwinter in sediment. The tests bear exit pores through which the cells emerge in the spring. These cell features are unique to the 4,000 known species of dinomastigotes.

Typical cells of the colonial dinomastigote *Polykrikos* pile one atop the other like building blocks. Some dinomastigotes are necrotrophs on marine animals. Only detailed cell-structure studies, however, make their dinomastigote affinities unequivocal. Fossil evidence dates dinomastigotes to at least the earliest times of the Cambrian period, 580 million years ago.



Kathryn Delisle



Farm Pond

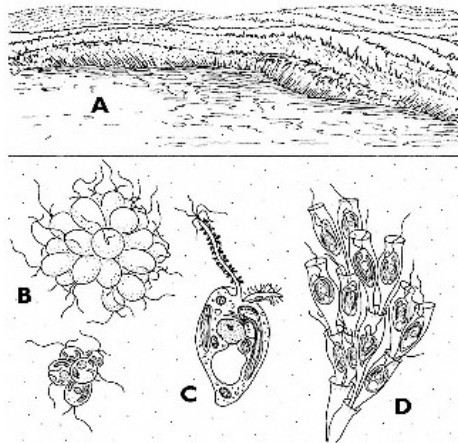
Phylum: Chrysomonada

Also known as golden-yellow algae or chrysomonads, the chrysophytes are algae that look like brownish or yellowish scum to the naked eye. The group includes single-celled, individual plankton protists, including the Raphidophyta (see page 70) and larger forms. In the larger masses, the colonial forms, as well as the single cells, each cell has chrysoplasts—organelles in which photosynthesis is based on chlorophylls *a* and *c*. Fucoxanthin is the most important accessory pigment. Chrysophyte swarmer cells or mastigotes are heterokont: Each has two undulipodia of unequal length, the longer of which has brushlike mastigonemes.

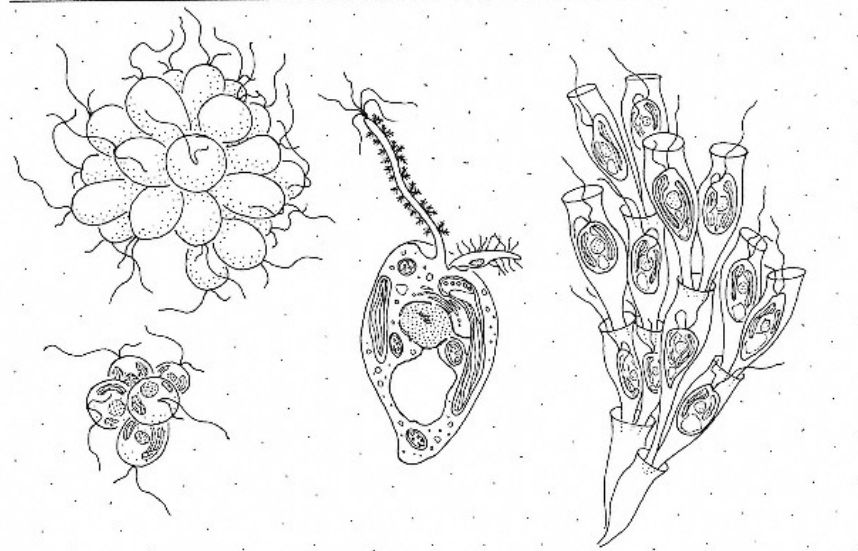
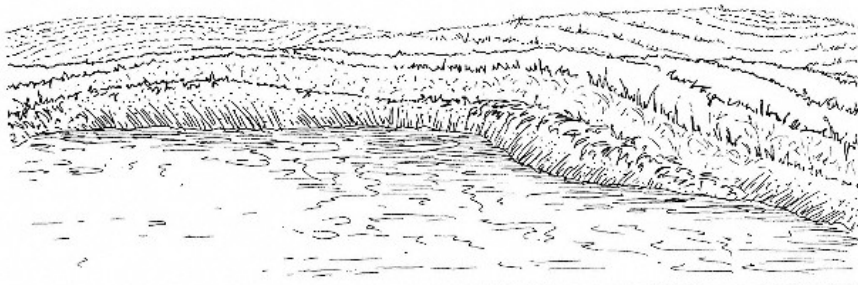
Chrysophytes are more common in freshwater, such as this farm pond (A), than in salt water. Yet one group, the silicomastigotes, which incorporate silica from sea water in their tests, is exclusively marine. Chrysophytes are useful to ecologists and geologists who reconstruct the past history of the environment. Many chrysophytes form beautiful sculptured silica scales that are resistant to decay. The scales of *Mallomonas* and other genera of Mallomonadaceae, for example, are entirely distinctive. They make useful paleoecological indicators of lakes because each species grows under specific conditions of temperature, light, phosphate concentration, organic content, and other ecological factors.

Shown here are the colonial chrysophytes *Synura* sp. (B, with a clump of cells breaking away to form a new colony) and the single-celled *Ochromonas* sp. (C), an organism used by cell biologists to study morphogenesis (the appearance of new form and other cell functions).

In the chrysophyte *Dinobryon* (D), typical chrysophyte cells are surrounded by vase-shaped loricas in a colony. These protocists are relatively common and can be collected by students wishing to study the golden yellowish pond scum.



Karthryn Delisle



Decaying Pond Vegetation

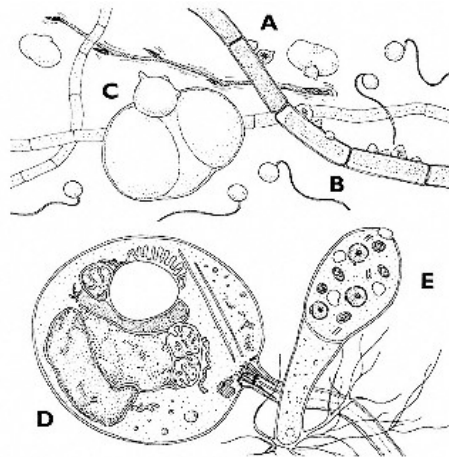
Phylum: Chytridiomycota

Of all the funguslike prototists, chytridiomycotes bear the closest resemblance to fungi. Some scientists argue that filamentous fungi were derived from these organisms by loss of undulipodia; others believe that chytridiomycotes are undeniably prototists and that the earliest fungi were yeasts. Like fungi, chytridiomycotes contain a nitrogen-rich polymer of glucose called chitin in their cell walls and have absorptive nutrition. In most cases, they form a motile zoospore (which bears a single posteriorly directed undulipodium), as well as the chytrid body, a visible, cup-shaped structure in which the zoospores form.

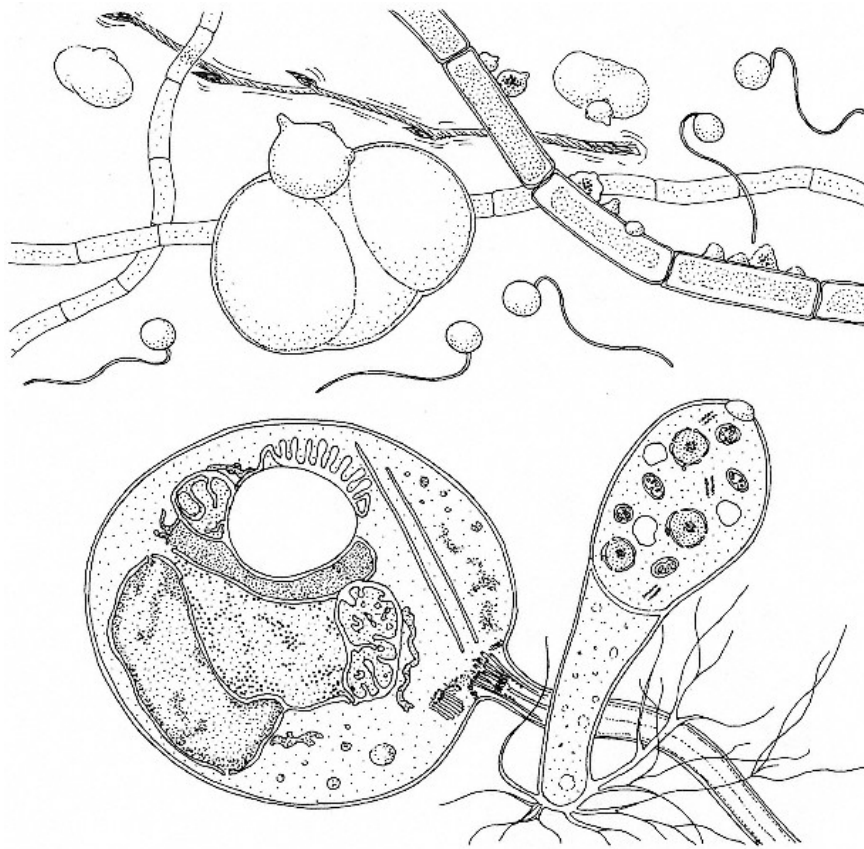
Chytridiomycotes live on plant debris in lakes, such as decaying leaves, fruits, pollen, or seeds swept into the water. Some are symbiotrophic. The phylum contains a thousand species, divided into four orders: Chytridiales (chytrids in the strict sense), Blastocladales, Monoblepharidales, and Spizellomycetales. Pictured here is *Rhizophydium granulosporum* (A) on the green alga *Oedogonium* (B), the chlorophyte (see page 84) from which *Rhizophydium* derives all its food. Here too is *Spizellomyces* sp. (C, with its discharge papillae), inhabiting a pine-pollen grain. The chytridiomycote eats out the plant material from inside. This detail of a generalized chytridiomycote zoospore (D) shows its organelles. Also shown is a close-up of the thallus of *Blastocladiella emersonii* (E), in which the rhizoids, basal cell, and apical sporangium, from which zoospores can be released in profusion, are visible.

At least five genera of chytridiomycotes—*Neocallimastix*, *Piromyces*, *Caecomyces*, *Orpinomyces*, and *Ruminomyces*—are obligate anaerobes. All of these grow inside the fermentation tanks (rumen or other modified digestive organs) of animals that have fibrous cellulose diets, such as cattle and elephants. Chytridiomycotes are thought to have lost their mitochondria and aerobic way of life after years of dwelling in the dark anoxic zones of animal intestines. Some of these prototists engage in sex as spermlike swimming cells that find themselves attracted to female filaments.

Decaying pond vegetation provides a habitat for myriad microorganisms besides chytridiomycotes, such as algae, euglenids, filamentous bacteria, and many others. In the professional literature the habitat is called aufwuchs (from German) or periphyton (literally, "around the plants"). These aufwuchs or periphyton communities are home for many prototists besides certain aerobic members of the Chytridiomycota. The soft, thick film of microorganisms that make up the periphyton community is easily observed on underwater stems of plants that grow in Florida's Everglades National Park and similar warm, sunny sites.



Karthyry Delisle



Pond Rocks

Phylum: Ciliophora

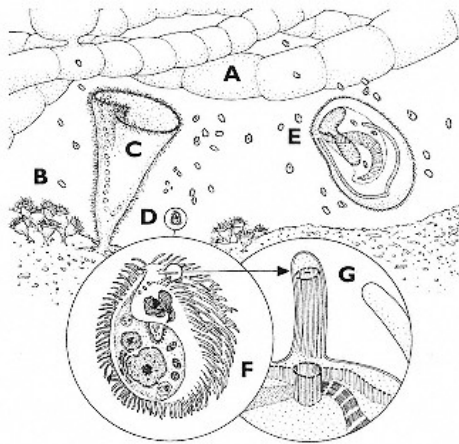
In brackish water, the open ocean, a small pond or puddle, the intestines of mammals, or even the sulfide-charged hot vents of the abyss, ciliates abound. Most ciliates are phagotrophic or osmotrophic microbes, but some, having acquired algal symbionts or borrowed chloroplasts, are secondarily photosynthetic.

Ciliates are a clearly distinguishable phylum of Protoctista. They have rows of cilia called kineties, a cytostome (or cell mouth), and pronounced nuclear dualism (the diploid micronucleus is the germ nucleus whose meiotic products are exchanged during conjugation, whereas the larger macronucleus is the control center of the cell for protein synthesis and differentiation). The micronucleus does not divide by mitosis and has large quantities of uniquely organized DNA, as well as its own style of amitotic division.

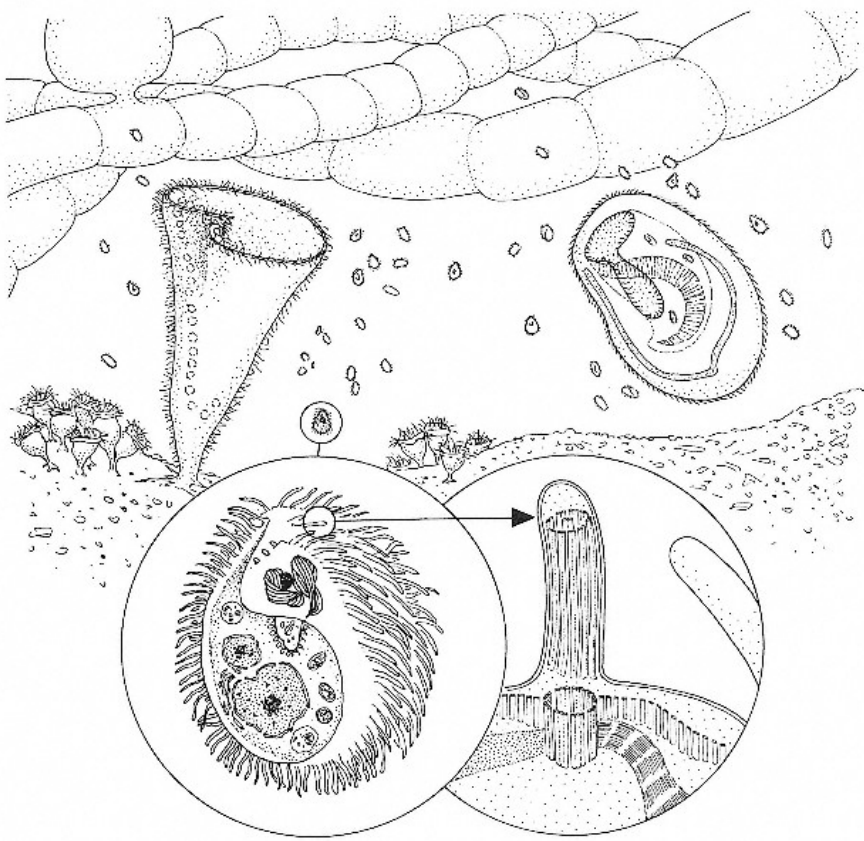
Some 1,100 genera and 7,500 species of ciliates have been discovered. Most scientists estimate that at least 10,000 species are extant. Shown here beneath strands of the bladderwort *Utricularia* sp. (A)—which traps ciliates—are *Vorticella* (B) and *Stentor* (C) attached to rocks, free-swimming *Tetrahymena* (D), and *Bursaria* sp. (E) containing prey *Paramecium*. The detail of *Tetrahymena* (F) shows the cytostome with specialized cilia, the locomotive cilia, the micronucleus and macronucleus, and the mitochondria.

Although some ciliates lack cilia (the shafts are so short that they are virtually nonexistent), none are without the underlying kinetosome. This detail of a ciliate kinetosome and cilium (G) shows the kinetosomal fibers and microtubular ribbons. Nearly all ciliates are single-celled, but some, such as the sessile *Acineta*, give rise to swimming forms, and others, such as *Sorogena*, form spore stalks and are genuinely multicellular.

The huge (one meter wide) freshwater colonial ciliate *Ophrydium* looks like a mass of green algae, but it is a complex, light-loving ciliate formed by thousands of attached cells, each packed with single-celled green algae. If forced for more than two days to live in darkness, the colony throws off small green swimming cells that invade new well-lit habitats and begin to grow again into a colony. Tintinnids, a family of marine ciliates, form tests, hard parts that permit them to be recovered as fossils, even from Mesozoic sediments.



Karthyri Delisle



Tropical Coast

Phylum: *Granuloreticulosa*

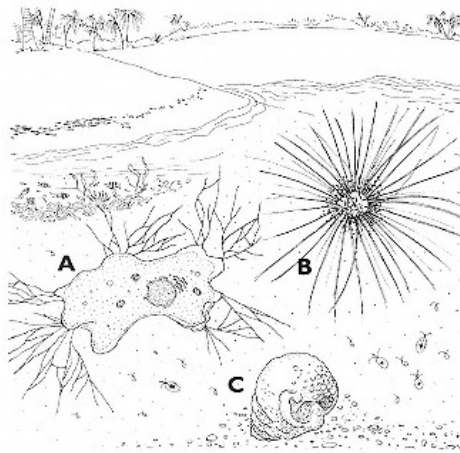
Most granuloreticulans are foraminiferans (called forams for short). Forams form a diverse group of marine organisms known for their elaborate tests (shells) of calcium carbonate or sand grains. Their fossil remains are useful to geologists, not only for oil exploration, but also in the reconstruction of ancient climates (paleoclimatology).

The largest forams are sometimes mistaken for snails, and even geologists who work with them refer to them as animals, as part of the fauna. They are clearly protists, however, entirely unlike animals in their sexuality, reproduction, development, and cell structure. Either naked (e.g., reticulomyxids) or pore-bearing and shelled (foraminiferans), granuloreticulans extend highly active leglike cell projections called reticulipodia. When these thin reticulipodia contact each other, they fuse to form the foram network.

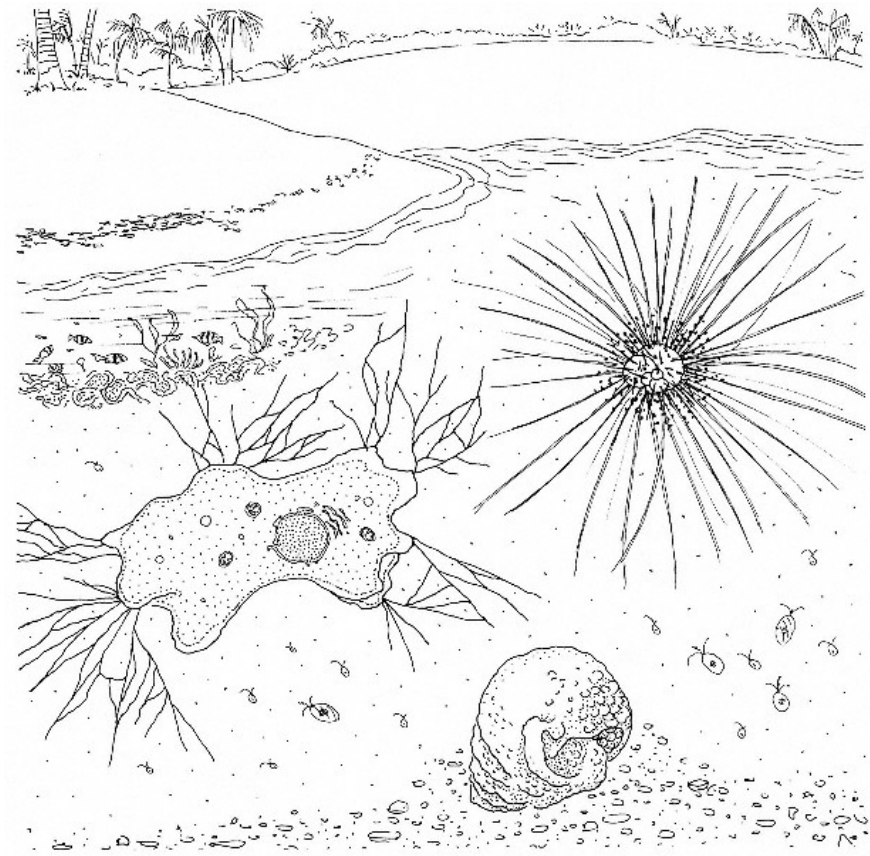
Three representative genera of forams are shown here on a coral reef. *Heterothecalobata* (A), with its anastomosing granular reticulopodia displaying two-way streaming motion, is shown in its diploid agamont form, which is capable of reproducing without sex (i.e., it is a stage in the life cycle that does not form gametes). The planktonic *Globigerinoides* sp. (B) has dinomastigote symbionts (see page 88) on its spines and rhizopodial network. The benthic foram *Textularia* sp. (C) has an agglutinated test made from surrounding sand grains.

These forams are pictured with their food organisms: green algae (see page 84), diatoms (see page 100), and ciliates (see page 94). Although most are predacious heterotrophs, many forams harbor symbiotrophic algae, or even foreign chloroplasts, and thus supplement their predatory food habits with photosynthesis.

Even though the forams are exceedingly diverse and show complex sex lives and developmental patterns (e.g., some burst to form hundreds of swimming cells at one time), the details of their biology are still poorly known. Attempts to grow forams in laboratory cultures tend to fail, in spite of the great abundance of these organisms in marine and estuarine waters (in the open sea about forty living planktonic species are known). Forams are especially abundant in coastal sediments, where most of the thousands of living species reside. Some 4,000 living species have been identified, and the fossil record boasts of 35,000 to 40,000 species.



Karthryn Delisle



Mosquito and Blood

Phylum: Apicomplexa

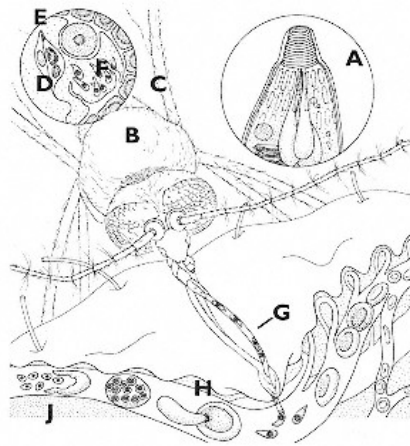
Traditionally, people, domestic animals, or fish that were sick with or died of diseases that could be correlated with little dark bodies in the tissues and with cysts excreted in their feces were described as having sporozoan parasites. We now know that many unrelated protists form little dark spots in tissues as obligate symbiotrophs. They derive their nutrition from the blood of the chordate (see page 148) and in some cases are necrotrophic, causing serious disease. Most live nearly invisibly, however, having developed astounding ways to insure a stable food supply.

One great group of what were once called sporozoans contains the thousands of kinds of apicomplexans. Apicomplexans derive their name from a cell structure, the entirely modified anterior portion of the cell called the apical complex (A). These organisms live in the tissues of animals, notably arthropods (see page 150) and chordates (see page 148). The distinctive arrangement of fibrils, microtubules, vacuoles, and other organelles assures the forced entry of apicomplexans into the living bodies from which they derive their food.

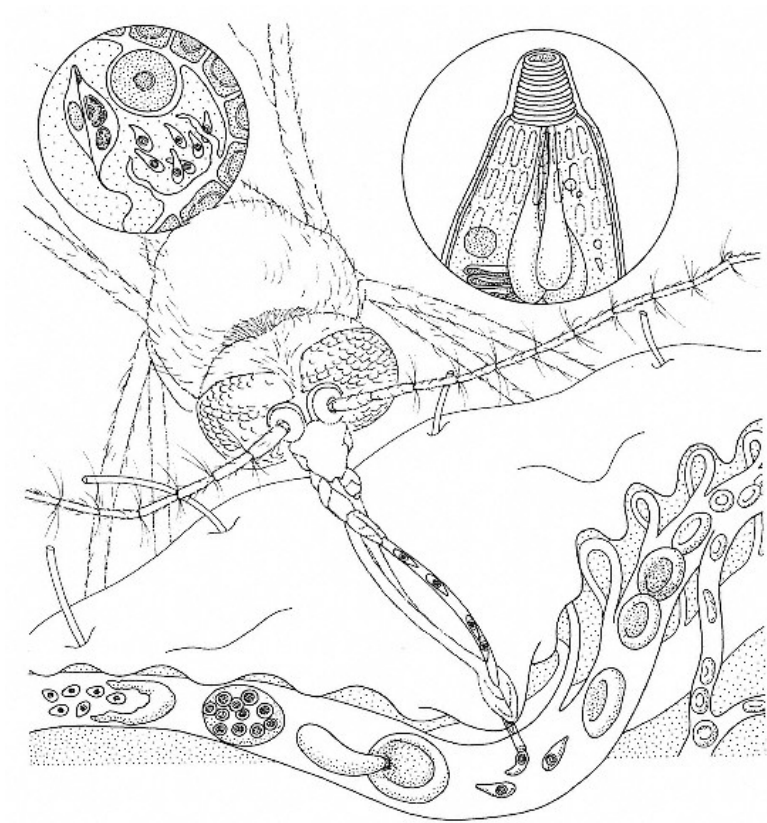
Plasmodium sp., which is associated with malaria, is the most infamous apicomplexan. The life cycle of *Plasmodium* involves its forced entry into two animal species: humans and the *Anopheles* mosquito (B). The life-cycle stages of *Plasmodium* shown here in the intestinal lining of the mosquito (C) are the undulipodiated zygote (D), the unsporulated oocyst (E), and sporozoites excysting from the oocyst (F).

Once excysted, the sporozoites enter the mosquito's saliva and pass through its proboscis (G) into the human bloodstream. In the human vein, the sporozoite attaches to a red blood cell (H), which grows into the vegetative stage called the trophozoite. The trophozoite then breaks up, releasing merozoites (J), which are taken up with the blood by the mosquito. Not shown here is meiosis, the process of cell division that reduces the number of chromosomes from the diploid (double set) to the haploid (single set) form. Meiosis in *Plasmodium* occurs in the mosquito.

Other well-known apicomplexans include *Toxoplasma*, which infects people via their cats, and *Eimeria* (as well as other coccidians), which lives in farm animals and pigeons.



Karthryn Delisle



Oceanside

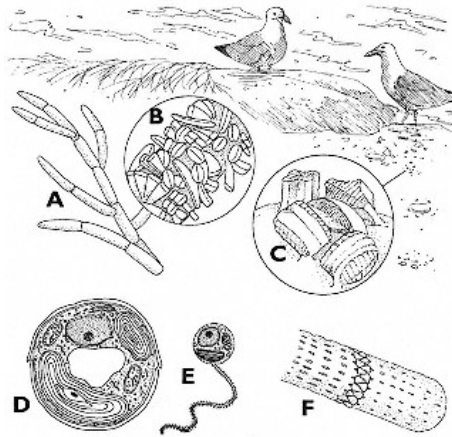
Phylum: Diatoms

Diatoms are sexual prototists. Primarily single-celled, aquatic, photosynthetic organisms, all of them form elaborate and beautiful tests (shells) of silica. Some form complex colonies. Diatoms live most of their life cycle in the diploid state; then they produce haploid gametes. In one group (the centric diatoms), motile male sperm is undulipodiated and fertilizes an immotile, naked, female ameboid cell called a protoplast. In the other group (the pennate diatoms) both sex cells are ameboid; neither has undulipodia. They shed their silica walls as they emerge and fuse.

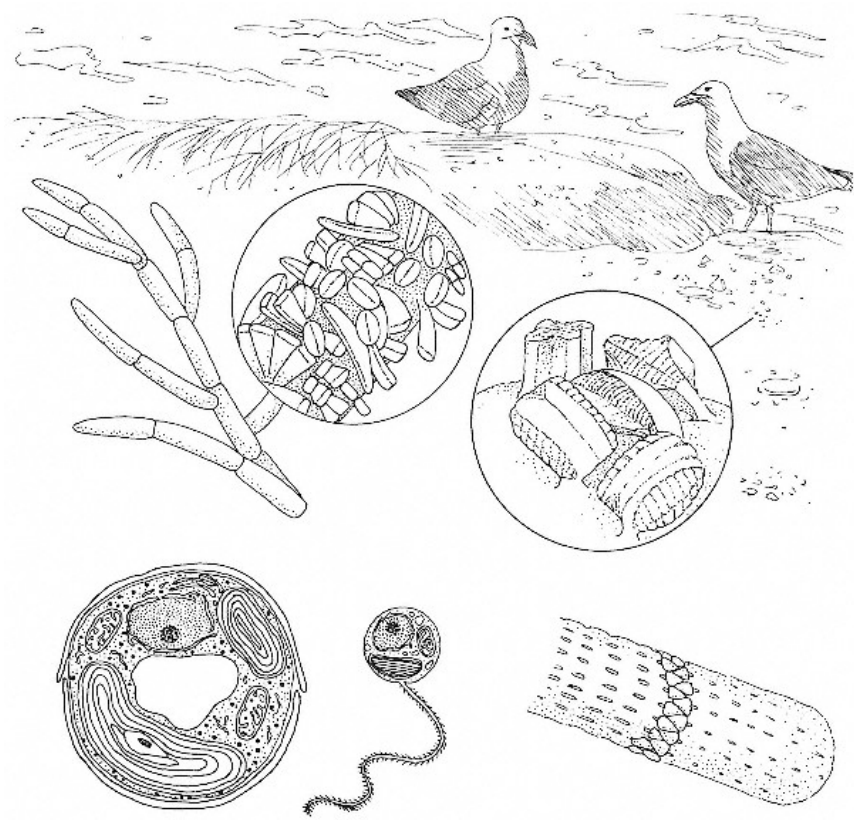
Diatoms have greenish brown chrysoplasts and are masters of biomineralization, depositing silica in gorgeous patterns in their cell walls. Their empty tests, mostly as fossils, are called diatomaceous earth. Diatoms are used extensively in water filtration. They also display a distinctive form of actin/protein-based locomotion from secretions through slits in their cell walls.

Pictured in this marine habitat is the green alga (a chlorophyte) *Cladophora* (A), with attached diatoms (*Rhoicosphenia*, *Gomphonema*, and *Cocconeis*, B); the diatoms *Opephora*, *Amphora*, and *Fragilaria*, attached to a sand grain (C); and the centric diatom *Melosira* sp., with a cross section showing its plastids, nucleus, and mitochondria (D), its sperm (E), and a detail of the spines lining its two valves (F).

Some diatoms are colonial, living stacked on top of each other. Others are internal symbionts of foraminiferans (see page 96). About 250 genera and some 100,000 species of diatoms have been described and named, of which 10,000 are living. Diatoms are said to be the second most abundant type of organism worldwide. Bacteria, of course, are the most numerous.



Karthyri Delisle



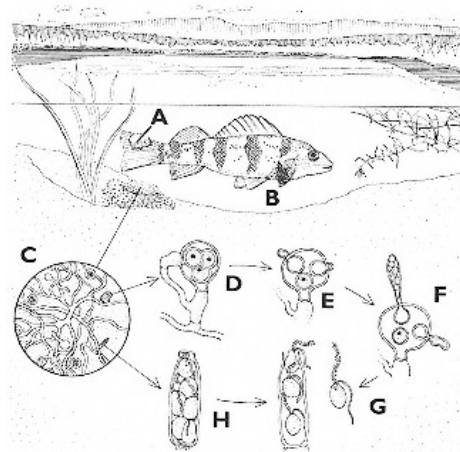
Pond Bottom

Phylum: Oomycota

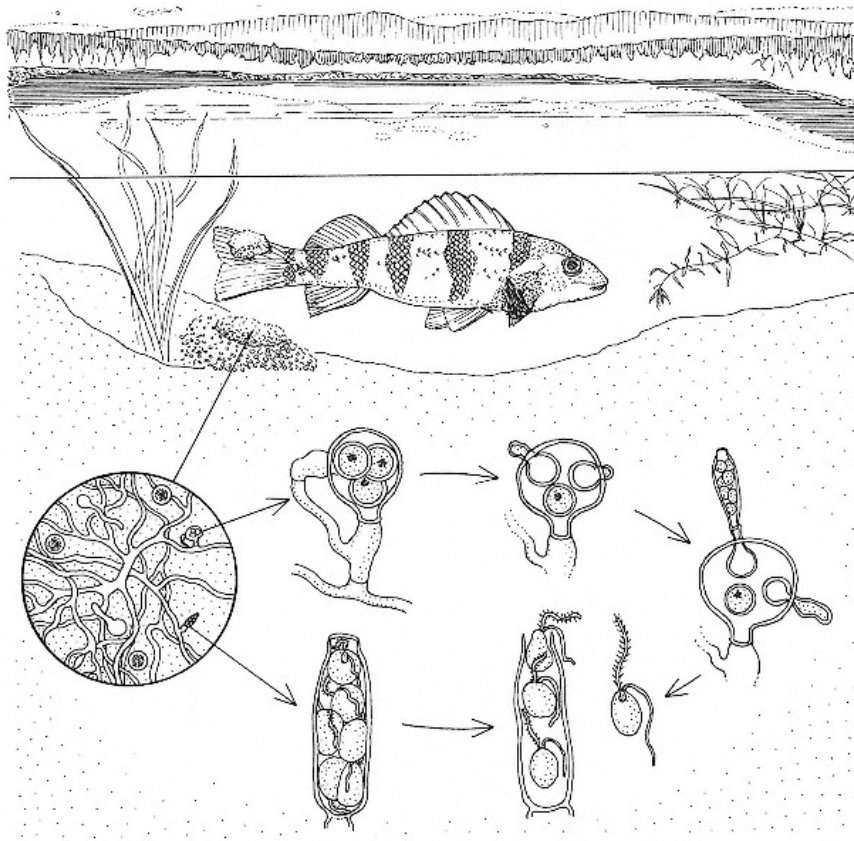
The oomycotes, another funguslike group of protocists, are often referred to as water molds. A better name might be "egg protoctists" or "egg molds." They differ from chytridiomycotes (see page 92) and hyphochytrids (see page 82) in many ways. Traditionally, oomycotes have been classified as fungi because in damp places they form visible, fuzzy, white masses. Their cell walls are made of cellulose, and their zoospores have two undulipodia. One undulipodium is directed forward during swimming and has mastigonemes; the other is smooth and trails behind.

Sexuality in oomycotes is unique, complicated, and distinctive. *Saprolegnia parasitica* (A)—which lives osmotrophically on the yellow perch, *Perca flavescens* (B), and its eggs—displays a typical oomycote sexual cycle (C). The ends of the filaments, specialized hyphal tips, develop into female oogonia and male antheridia (D). The antheridia and oogonia fuse; then the male nuclei can migrate. The male nuclei enter and fertilize the oosphere, or egg (E). This large cell resembles an animal egg. The fusion results in the formation of oospores (F), which divide mitotically. Their products are diploid zoospores (G), which swim away and propagate the water mold. Oospores also undergo meiosis and form haploid nuclei that then differentiate into haploid zoospores, which are released. Alternatively, zoospores are produced by direct mitotic division in a sporangium (H).

Oomycotes usually live necrotrophically on plants or freely in freshwater on plant debris. The group includes such infamous plant pathogens as *Phytophthora infestans*, associated with late blight of potato, and *Plasmopara viticola*, associated with grape mildew.



Karthryn Delisle



Pacific Nearshore Waters

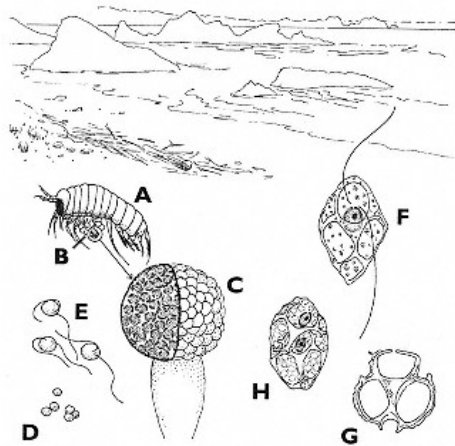
Phylum: Ellobiopsida

The ellobiopsids are obscure but important symbiotrophs of planktonic animals—shrimp, copepods, amphipods, and euphasids (all arthropods, see page 150). Although their life history is not fully known, observed behavior of one of the well-known species, *Thalassomyces marsupii*, a symbiotroph with the amphipod *Parathemisto* (A), is shown here.

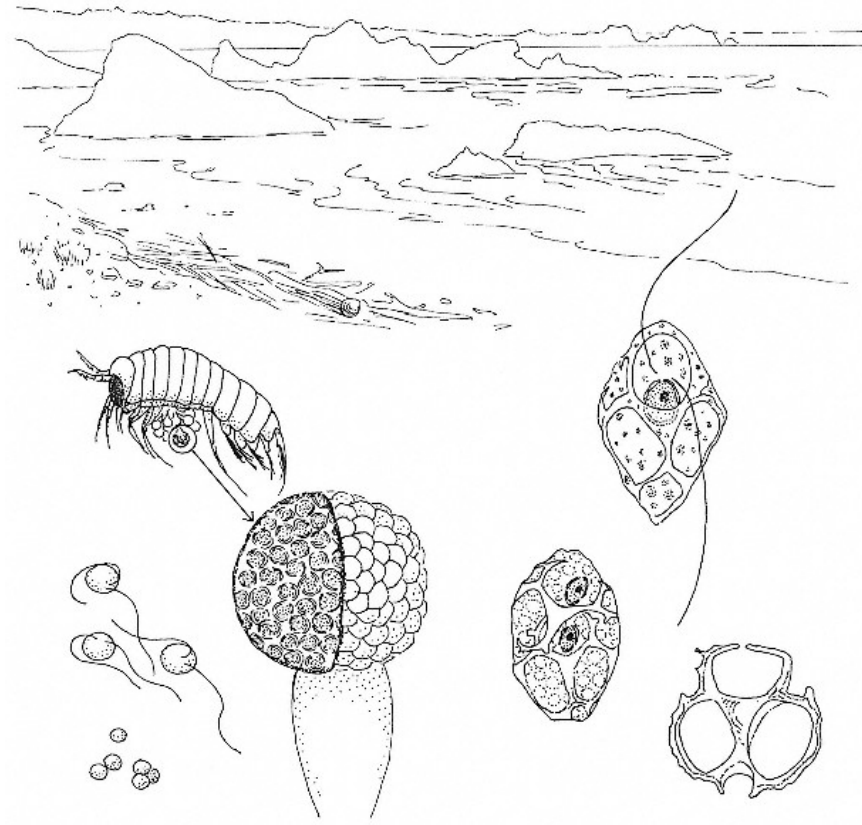
The ellobiopsid attaches to the reproductive organs—the ovaries or egg masses—of the amphipod and grows out of the animal's body, forming numerous branches, or trophomeres (B). These branches then develop into coenocytic (multinucleate), reproductive structures called gonomeres (C). This detail shows the outside of the gonomere and a cross section with the many nuclei inside. The gonomere facets, or breaks into many faces, which open and release unicellular spores (D). These spores develop two undulipodia—one posterior and one circumferential (E). It is suspected that these motile "zoospores" then enter another animal to establish the symbiosis again. This second invasion by undulipodial zoospores has not yet been observed or confirmed experimentally, however. Further research is needed to determine to which protocyst phylum these organisms are most closely related. Until that time, this group is considered *incertae sedis* (literally, "without a seat").

Phylum: Ebridians

Because of their skeletons, ebridians are known better to marine paleontologists than to biologists. Ebridians are a small group of protocysts with internal skeletons composed of siliceous rods. They live in coastal marine environments and form periodic "blooms" following the blooms of their food organisms: diatoms (see page 100) and dinomastigotes (see page 88). *Ebria*, a common genus, is shown here. *Ebria tripartita* (F) displays the two distinctive anterior undulipodia of the phylum. Also shown is the siliceous skeleton (G) and cell division (H). The name *Ebria* comes from the Latin word *ebrius*, which means "drunken"—a reference to the movement of this organism when it is swimming.



Karthryn Delisle



Chapter 3— Fungi

Kingdom Fungi includes molds, mushrooms, yeasts, and other eukaryotes that form fungal spores (Figure 13). Fungi lack undulipodia at all stages of their lives. If fungi indulge in sex, they conjugate—their threadlike or spherical bodies fuse to form recombinant haploid (or dikaryotic) new bodies. These fascinating eukaryotic organisms can produce huge numbers of hardy propagules called spores without engaging in sex at all.

Fungal spores germinate to grow into slender tubes called hyphae. Crosswalls called septa divide hyphae into cell-like units in some fungi. In other fungal species, walls are not formed. Each cell-like unit usually contains more than one nucleus and many mitochondria (the number depends on the species of fungus). Septa seldom completely separate the cells; thus, cytoplasm flows more or less freely through the hyphae.

The growing form of most fungi is a large mass of hyphae called a mycelium. Reproductive structures, which are also made of hyphae, form in response to seasonal changes in weather, such as rain or desiccation. Some fungal reproductive structures include puffballs, morels, mushrooms, and shelf fungi. Among the largest and most complex fungal reproductive structures are the immense shelf fungi on trees, some of which arise from mycelia that are up to two meters in diameter. Most fungi, however, are microscopic.

All fungi are heterotrophs that absorb food through their chitinous cell walls, rather than ingesting (eating) it. Nearly all are aerobes. Fungi secrete powerful enzymes that break down live or dead materials into a solution of molecules outside the fungus body. These sugar, protein, and other molecules are transported into the fungus through its cell walls. The stiff cell walls of fungi and the exoskeletons (shells) of lobsters both contain chitin, which is a tough, nitrogenous, long-chain polysaccharide. Fungi are tenacious, resisting cold and hot weather, severe desiccation, and other environmental insults. Their cell walls resist water loss. Some even grow in strong acid. Others survive in clean tap water and other environments that contain nearly no nitrogen. Still other fungi are capable of etching glass lenses as they grow on minute quantities of organic compounds, and yet others contaminate jam and even strong chemicals with their fuzzy growth. Often the least conspicuous of the eukaryotes, fungi are among the most resilient, living in every ecosystem from Antarctic rocks to human skin.

Truffles and chanterelles are prized edible fungi. Fungi are employed to ripen Camembert, Roquefort, and other blue cheeses. Fungi are treasured as the original source of the antibiotic penicillin. Fungi are also the source of the medicine ergot, which constricts smooth muscle. In small doses ergot derivatives constrict arteries and are given to relieve migraines and after childbirth to prevent hemorrhaging. In large doses, however, ergot is toxic.

The human body harbors mold- and yeast-like fungi; some normally cause no problems. Suppression of the immune system, by certain medications, organ and tissue transplant procedures, radiation, malnutrition, debilitating illness, AIDS, or leukemia, can allow fungi to invade human tissue. Artificial body parts from hips to heart valves provide growth sites for fungal colonies, thereby increasing the risk of fungal infections. Fungi harbored within "sterile" urinary catheters are a common source of nosocomial (hospital-acquired) infection. Thus, the prevention and treatment of fungal infestations in humans continue to be important concerns.

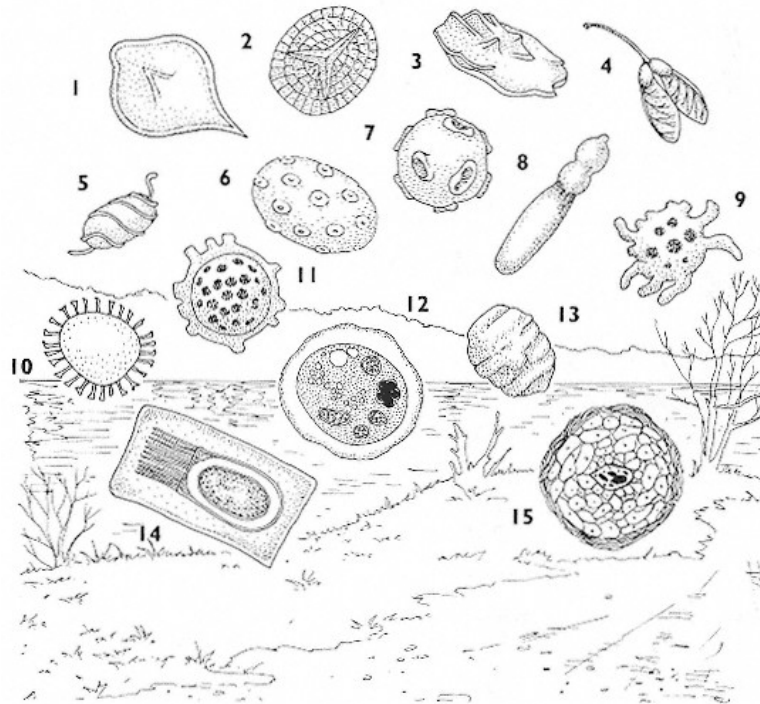


Figure 13

Pictured here are several types of spores and seeds, both of which are resistant propagules: (1) ascospore (mold), (2) fern spore (nonflowering plant), (3) deuteromycote spore (fungus), (4) red maple samara, *Acer rubrum* (seed of flowering plant lies within), (5) horsetail spore, *Equisetum arvense* (nonflowering plant), (6) ascospore (fungus), (7) moss spore, *Polytrichum* sp., (8) basidiospore (fungus), (9) lichen soredia (propagule consisting of algal cells surrounded by fungal hyphae), (10) dinomastigote cyst (protoctist), (11) basidiospore (fungus), (12) amebacyst, *Paratetramitus* (protoctist), (13) tardigrade tun (animal, see page 140), (14) *Arthromitus* parent cell with walled spore with attached spore filaments (bacterium), and (15) macrocyst (giant cell of cellular dictyostelid slime mold, protoctist). Spores are small, usually microscopic, propagules containing at least one genome. At some time, spores can mature into the growing form of the organism. Spores often resist starvation or heat. "Spore" is a general term that has been applied to spherical propagules from the moneran, protoctist, fungal, and plant kingdoms. A spore from an ameba of a cellular slime mold and a cyst (a eukaryotic propagule formed by many protoctists in response to starvation or desiccation) from the same species may appear identical in external structure. Two spores, on the other hand—one from an apicomplexan and the other from a basidiomycote, for example—will differ entirely from each other in genetic information. Seeds are fertilized ovules of seed plants (Ginkgophyta, Cycadophyta, Coniferophyta, Gnetophyta, and flowering plants, such as the maple shown here, 4) that usually include a food supply such as endosperm. Seeds propagate seed plants. *Karthyryn Delisle*

Orchard

Phylum: Zygomycota

The zygomycetes, or mating molds, are mostly filamentous organisms that live off of substances rich in organic compounds dissolved in the water or tissues of animals, plants, or prototists. The fungal filaments (hyphae) clumped together as a visible mass—a fungal body—are called the mycelium. Some zygomycetes are predatory. Shown here are *Dactylaria* sp. (A) attacking nematodes (see page 140) and *Dactylella tylopaga* (B) attacking amebas (see page 52) in the soil.

After the sexual fusion of hyphae that are of complementary mating types, the fused hyphae form resting structures called zygospores. They result from the fusion of two swollen structures and are multinucleate. Mature zygospores are visible to the naked eye as tiny dark dots. Zygomycetes also produce sporangia, which are raised on stalks called sporangiophores, without any mating or fusing. These sporangia are visible as black fuzz on bread (e.g., black bread mold, *Rhizopus*).

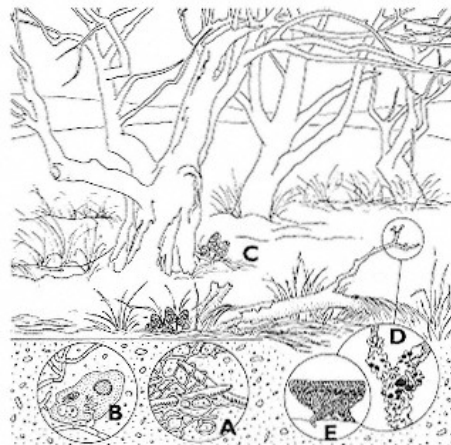
A small group of cosmopolitan or widely distributed zygomycete genera are crucial to establishing healthy environments for plant roots. The fungi provide the plants with phosphorus from rocks and soil. Unable to photosynthesize, the fungi feed osmotrophically on carbohydrates derived from the photosynthesis of the plants in which they reside. The zygomycetes are the fungal symbionts of the endomycorrhizae and reside within plant roots. Fungi such as *Glomus* and *Endosporella* live symbiotically with 80 percent of all vascular plants. Some have thousands of nuclei, which in synchrony fuse in pairs in what looks like an incredible orgy. Mucormycosis occurs when the zygomycete *Mucor* infects people with leukemia or AIDS.

Phylum: Ascomycota

The most familiar molds are ascomycetes, and the parts we usually notice are the clumps of sexual reproductive organs, such as the delicious morel, *Morchella esculenta* (C). The ascomycetes get their name from the ascus, a saclike structure containing haploid ascospores, which are not found alone but are often bundled together. Ascospores are found in all ascomycetes, whether they are the filamentous forms or the subvisible single-celled yeasts.

The morels, which are among the choicest edible fungi, are in the class Euascomycetae, which also includes the fungal partners of lichen symbioses. The yeasts ferment sugar or starch as nutrients and are used in the production of bread, beer, wine, and a yogurtlike beverage popular in eastern Europe and western Asia called kefir.

Ascomycetes produce propagules in prodigious numbers; many survive cold and dryness very well. These propagules form asexually (they have only one parent) and are called conidia. Conidia are primarily responsible for the propagation of these widespread fungi. Unlike bacterial spores, fungal spores cannot survive boiling, but some can be dry for years and then grow vigorously if organic-rich water comes their way. More than 30,000 species of ascomycetes have been

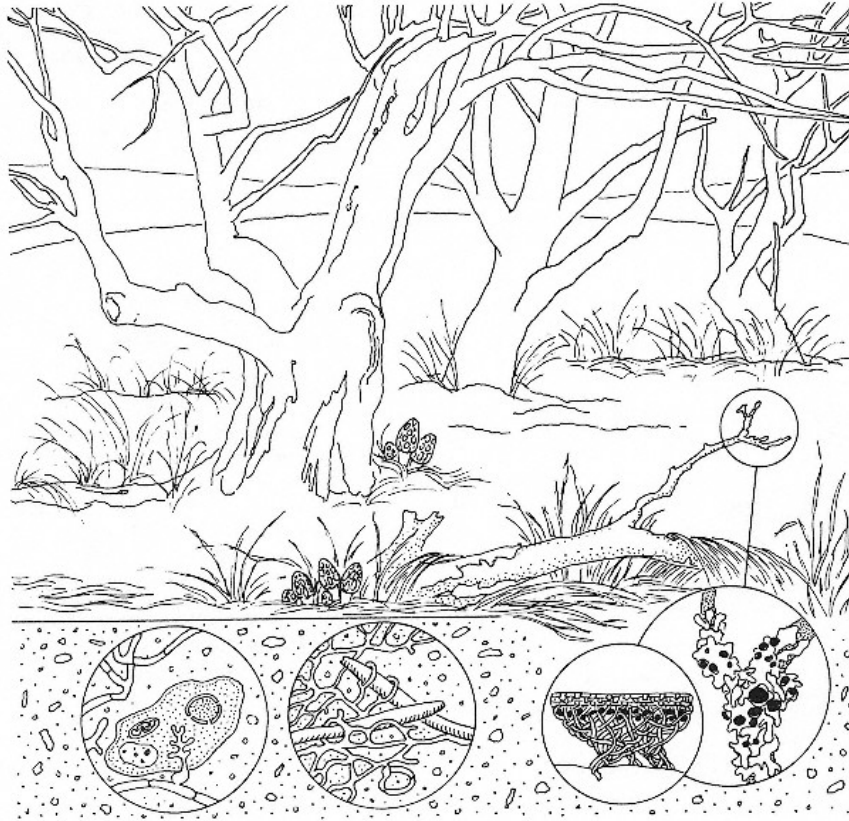


Karthryn Delisle

described, including the necrotrophs such as the fungi associated with certain diseases of trees, for example, chestnut blight (*Endothia parasitica*) and Dutch elm disease (*Ceratocystis ulmi*).

Phylum: Ascomycota—Lichens

Lichens are symbiotic associations of ascomycotes (see page 110) and green algae (see page 84) or cyanobacteria (see page 32). There are about 20,000 species of lichen fungi, almost all of which are ascomycotes that differ in appearance from the 30,000 ascomycotes described above. The lichen shown here is *Parmelia conspersa* (**D**). In cross section (**E**), the algal and fungal partners are visible. The photosynthetic algal component provides the fungus with organic nutrients; the fungus retains water from the symbiotic complex, dissolves mineral nutrients, and modulates the sensitivity of the partnership to environmental change. Lichens reproduce by soredia (see Figure 13, page 108). Lichens also disseminate via bits blown by wind to new locations.



Forest Clearing

Phylum: Basidiomycota

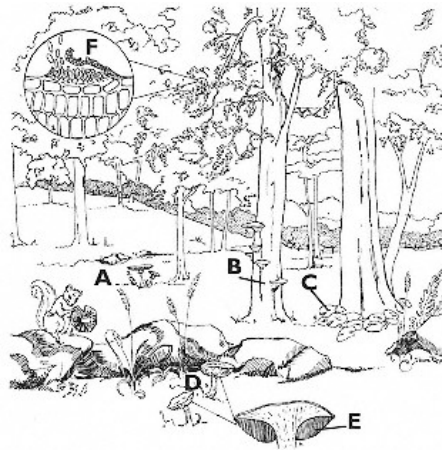
Included in the basidiomycotes are many of the most familiar larger fungi, including the mushrooms, puffballs, coral fungi, and the rust and smut plant pathogens. All make basidia, microscopic clublike structures tucked away in gills or pores. The basidia release haploid basidiospores, which are the end products of a complex cycle of fused hyphae. In the heterokaryotic mycelium (one with several different genetically distinguishable nuclei in the same hypha), the nuclei finally fuse (mate), and immediately after, they divide to form spores for the next generation.

The two classes of basidiomycotes are the Heterobasidiomycetae (the necrotrophic rusts and smuts) and the Homobasidiomycetae (which include most of the mushrooms). Pictured here are *Amanita* (A and cover art), a gilled mushroom, some species of which are among the most poisonous mushrooms; *Fomes* (B), whose mycelium extends around the roots and covers the small rootlets of trees with a fuzzy sheath; *Armillaria* (C), the honey mushroom; and *Boletus* (D), whose edible mushroom contains pores rather than gills (E).

Thousands of basidiomycote species form ectomycorrhizae, symbioses that provide phosphorus to the plants and carbohydrates to the fungi. The nearly ubiquitous zygomycote-based endomycorrhizae (see page 110) grow well on most plants but especially well on broadleaf trees and herbs. Ectomycorrhizae, by contrast, are found mainly on trees and shrubs.

Phylum: Ascomycota and Basidiomycota—Deuteromycotes

Deuteromycotes are molds that produce single-parent spores (conidia), usually in great profusion. No sexual act has ever been witnessed in the deuteromycotes, but they are thought to be ascomycotes (see page 110) or basidiomycotes (see this page) that have lost their potential to differentiate asci or basidia. Traditionally, deuteromycotes have been called the Fungi Imperfecti because they do not form sexual structures—i.e., botanically speaking their life cycle is not "complete." Some deuteromycotes have exhibited a parasexual cycle in which unspecialized hyphae fuse and their nuclei recombine.



Donna Reppard

Pictured here (F) is *Titaosporina* forming an acervulus on a leaf surface. Other deuteromycotes include the famous antibiotic producer *Penicillium*; *Aspergillus*, the fermenter used in making soy sauce and also the fungus responsible for aspergillosis, a form of pneumonia; *Candida albicans*, associated with a common vaginal infection and found in immunosuppressed adults; and *Trichophyton*, which lives in skin infected with athlete's foot and groins afflicted with jockstrap itch. Cryptococcosis and histoplasmosis are other infections caused in immunosuppressed humans by deuteromycotes.



Chapter 4— Animalia

Animals run the gamut of biodiversity from velvet worms (p. 150), which prowl the rain forest floor, to longfin char, which swim in one of the iciest, most remote continental lakes on Earth. Among the microscopic animals are aquatic rotifers (p. 140), 0.04 millimeters in length. The immense whales are the largest present-day animals. The giants of Kingdom Animalia are the great blue whale and the giant squid. The great blue, *Balaenoptera musculus*, weighs up to 135,000 kilograms (150 tons)—more than the greatest ancient dinosaur—and measures more than 35 meters in length. The giant squid, *Architeuthis*, is up to twenty meters in length with a four-meter-long body and sixteen-meter-long tentacles and is estimated to weigh 900 kilograms (1 ton). Sperm whales feed on giant squid at 200- to 700-meter depths off the New Zealand shore in the South Pacific. The largest dinosaur known from a complete skeleton is *Brachiosaurus* (*Ultrasaurus*), twenty to twenty-five meters in length and estimated to weigh 27,000 to 45,000 kilograms (30 to 50 tons).

Animal habitats are diverse: air, freshwater, salt water, deserts, and hot springs, as well as the tissues of other animals, fungi, and plants. Many animal species are aquatic; of these, most dwell in shallow waters. Nearly all major groups of invertebrate animals and some members of our own phylum, Craniata—whales, dolphins, sea otters, seals—inhabit the seas. The smallest aquatic animals are the zooplankton, which—along with plankton that photosynthesize—comprise the base of freshwater and marine food webs. Insects are the most numerous animals in terms of number of species, and because most insects are terrestrial, most animal species are terrestrial. However, the overwhelming number of Animalia phyla are marine.

Cold, deep waters are some of the most recently explored ecosystems, and their animal inhabitants are some of the most recently described. An example is the longfin char (*Salvelinus svetovidovi*), a fish discovered in 1985 in a three-million-year-old freshwater ecosystem in a Siberian meteorite impact crater. Tube worms taken from a

depth of 2,500 meters in the Pacific off the Galapagos Islands belong to one of the most recently described animal phyla—Pogonophora (p. 152).

Soil-inhabiting animals such as some annelid worms (p. 142) and nematode worms (p. 140) depend on an aqueous environment—the thin water film that coats a soil grain. Animal species that inhabit Earth's land surface include terrestrial arthropods (p. 150)—crickets, spiders, and butterflies—and terrestrial chordates (p. 148)—birds, reptiles, and mammals. The biological diversity of these terrestrial animals extends to every imaginable land habitat. For example, one tiny bat species makes its home in the spaces between nodes on a hollow stem of bamboo.

Most animals take food into their bodies and have elaborate modes for ingesting food. Hunting devices evolved by various animal species that pre-date our own species include poison darts, paralytic toxins, sticky hunting nets, harpoons, woven traps, sonar, and fishing lures. The longfin char ingests other members of its ecological community of Lake L'gygytgun ("ice lake"), such as amphipods (crustaceans) and zooplankton. Sponges engulf food particles in cells called phagocytes. Leeches usually prey on turtles, fish, frogs, and invertebrates, but are known to suck blood from unfortunate swimmers who venture into warm ponds or vertebrates walking through certain kinds of forests. Arboreal mice of tropical forests lap flower nectar; butterflies uncoil a long tube through which they suck in sugar-rich nectar. Some aquatic animals absorb food molecules across their cell membranes directly from the nutritious broth of sea water (pogonophorans, p. 152), from the urine of their host animals (Rhombzoa, p. 130), and from tissues of other animals (tapeworms, p. 132). Some animals ingest fungi and plants: buffalo graze on prairie grasses, reindeer (caribou) feed on lichens, moose browse on tree saplings, Japanese beetles ingest garden vegetables, box turtles munch wild strawberries, red squirrels nibble forest mushrooms. Humans consume an enormous variety of foods, such as pizza, grapefruit juice, and sweet corn. Remains of dead organisms would litter Earth were they not consumed by animals such as the dermestid beetle, certain bacteria, and fungi.

Not all animal species depend directly on sunlight and nutrients that plants photosynthesize. Pogonophorans, crabs, and fellow species of the deep-ocean hydrothermal vent communities derive their nutrients from methane and sulfides emitted from seafloor vents. Pogonophorans harbor symbiotic bacteria within their bodies and either absorb organic compounds synthesized by their bacterial partners or digest the bacteria directly.

In our five-kingdom classification system—plants, animals, fungi, protocists, and bacteria—animals are eukaryotic, heterotrophic, multicellular, diploid organisms that develop from two different gametes, sperm and egg. These gametes—haploid cells—join in the process of fertilization and produce a diploid zygote that divides to form an embryo called a blastula (p. 122). The blastula is a liquid-filled sphere of cells that is exclusive to members of the animal kingdom. Common patterns of development reflect what is probably the common ancestry of members of different phyla. Embryos of some animals develop directly into miniature adults (direct development). Dogs, for example, develop directly from embryo to adult. Embryos of other animals pass through a series of larval stages toward adulthood (indirect development). Molluscs, (p. 148) for example, have a larval swimming stage (p. 120). Sipunculans (p. 146), depending on species, have three patterns of development. Some sipunculans develop

directly. Some sipunculans form trochophore larvae and then metamorphose to adults. Other sipunculan species form trochophores, succeeded by pelagosphera larvae, and then adults. Larvae (Figure 14) facilitate the dispersal of young and then metamorphose into adults. By definition, adults produce sex cells—sperm and eggs—that fuse to carry on the endless life cycle of an animal species.

Like all other animal cells, those of the blastula lack the cellulose-containing walls that characterize cells of plants. Moreover, animal cells have complex connections—elaborate gap junctions and desmosomes—that ensure and regulate the flow of nutritive and waste materials and information. Some animal cells, but by no means all, communicate via nervous systems. Behavior—defined as response to light, response to touch, response to chemicals such as airborne hormones, sensing of dissolved gases, and response to temperature—exists in animals, plants, protocists, fungi, and bacteria, but is most diverse in animals. Only certain animals have nervous systems; fewer have brains; and even fewer possess sight. Multicellularity exists in all five kingdoms and is most diverse in animals. Animal cells are further linked into tissues—the eye of a cat, muscle of a char, epithelium of a pentastome, or nerve cord of an echiuran. Only placozoans (p. 122) and sponges (p. 124) lack tissues. Cells of many animals synthesize supporting skeletons, shells, plates, and spines; other animals maintain their body shape by hydraulic pressure.

Animals traditionally have been subdivided into two large groups: invertebrates (those lacking backbones) and vertebrates (those with backbones). Vertebrates include all chordates (birds, amphibians, reptiles, fish, sharks, mammals; p. 148). A chordate is an animal having a notochord; dorsal, hollow nerve cord; and pharyngeal gill slits. The chordates that lack a bony skull—acraniate chordates—include urochordates such as the sea squirt (p. 34), and cephalochordates such as *Branchiostoma*, a small group of fishlike marine animals (p. 133). The sea squirt and *Branchiostoma* lack vertebrae but do possess gill slits, notochord, and hollow, dorsal nerve cord during at least some portion of their lives.

Some animals are also classified as radially symmetric, such as jellyfish and comb jellies. Most of the rest are bilaterally symmetric, such as chimpanzees and arrow worms. Animals that lack left/right and dorsal/ventral symmetry include placozoans and sponges.

Contemporary classification schemes of animals are based on evidence derived from fossils and from extant organisms: molecular biology, chromosomal cytology, pattern of embryonic development, behavior, and morphology. Unambiguous animal fossils first appear in Precambrian rocks; the most likely animal ancestors common to living animals probably evolved during Ediacaran time more than 600 million years ago (see Figure 12, p. 50). Perhaps 99 percent of all of the species that ever lived are now extinct, and from this rich heritage have arisen the diversity of living animal species.

Most biologists agree that sponges evolved from the microscopic protocists known as choanomastigotes (choanomomads, p. 72). This protocist/animal connection is deduced from the fine structure of sponge and choanomastigote cells and confirmed by molecular evidence (ribosomal nucleotide sequence similarities). Sponges (p. 124) and comb jellies (p. 128) diverged deep in the past from other animal phyla.

The relationships among animals, plants, fungi, and other eukaryotes are inferred from the comparison of ribosomal RNA (rRNA) sequences. Most animal phyla likely

had ancestors different from the choanomonad ancestors of sponges and comb jellies. Molecular evidence implies that fungi and animals are more closely related than are animals and plants. Fungi and animals share a more recent ancestor in common. The origin and diversity of animals and their relation to other kingdoms will be explored vigorously as new phylogenies emerge.

This book groups animals into thirty-seven phyla. Animals are not distributed evenly among these phyla either in number of species or total number of individuals. In sexually reproducing organisms, a species is defined as a population of organisms that interbreed readily with one another but not with members of other species under natural conditions. Tigers will breed with other tigers under natural conditions. Lions will breed with tigers in captivity, but we have not observed that tigers and lions interbreed in the wild. How, then, is the enormous diversity of animal species distributed among the phyla? Insect species currently described number about 751,000. Other animal species total 281,000. Crustaceans, chelicerates, and other noninsect arthropod species total about 123,400. Highly diverse molluscan species total about 50,000. Mammals (4,000), birds (9,000), reptiles (6,300), amphibians (4,200), and fish and lower chordates (18,000) add up to 41,500 species of chordates. Add to these the species of sponges (5,000), cnidarians and ctenophorans (9,000), flatworms (12,200), nematodes (80,000), annelids (15,000), echinoderms (7,000), and those of smaller phyla (e.g., phylum Placozoa with only a single species described) to get a rough total of 1,032,000 currently described animal species—and those are only the ones that have been collected and named.

How, then, does this currently described total of animal species—1,032,000—compare with the number of species of all organisms? E. O. Wilson (*Diversity of Life*, 1992) reported that the total number of living species now on Earth is estimated to be between ten million and 100 million. (For comparison, about 4,800 bacteria, 69,000 fungi, 270,000 seed plants, and 57,700 protocists species are currently known.)

Forces that generate and maintain animal diversity include direct and indirect effects among predators, prey, and plants in their food web. One case study at Cocha Cashu in the Peruvian Amazon observed the role of top predators—the harpy eagle, puma (mountain lion), and jaguar—in this ecosystem. The two big cats annually consume eight percent of the crop of land mammals that weigh one kilogram or more as adults—peccary, capybara, agouti, and paca. These four prey species are consumed in the same proportions as their relative abundances at Cocha Cashu.

One result of this nonselective prey harvest is that the peccary and capybara, which may have a litter of three or more, produce more consumable material than prey such as agouti, which may have one or two young. Peccaries and capybaras, because they produce more, mainly determine the abundance of big cat predators. As a result of the abundance of puma and jaguar, the population of agouti—a prey animal that has few young—is indirectly depressed. Observations at Barro Colorado, Panama, an island having a habitat similar to that of Cocha Cashu, confirms this. Following construction of the Panama Canal, the biodiversity of Barro Colorado dropped; puma and jaguar that formerly inhabited Barro Colorado now are absent. Agouti and paca populations are more than ten times greater in Barro Colorado—now missing top predators—than in Cocha Cashu.

Animal diversity is linked to plant diversity in turn. The abundance of pacas, agoutis, and peccaries—animals that feed on seeds of large trees—may determine the

tree species diversity and abundance in the tropical forest. Perpetuation of diversity in tropical forests involves the maintenance of dynamic equilibrium between predators, prey, and their food plants.

The Barro Colorado ecosystem has additional links: small- and large-seeded trees contribute to the diversity of this Panamanian forest. The large seeds are consumed by pacas, agoutis, and peccaries. The small seeds are consumed by mice, rats, and tinamous (birds). The small-seed predators are prey for ocelots and raptors. Removal of the larger predators, either directly by hunting or indirectly by fragmenting the forest into patches too small to support the forest in its entire diversity, results in reduction of animal and plant diversity.

Geographic isolation may also generate and maintain animal diversity. The geographically isolated Hawaiian Islands, for example, and the island of Madagascar support extraordinary numbers of species. Animal species on these islands are geographically isolated from populations of closely related species. As a result, Madagascar and the Hawaiian Islands have high levels of endemism, that is, organisms that are found nowhere else. Charles Darwin's observations of finch and tortoise diversity in the Galapagos islands provided clues to the evolution of animal species. A closer analysis of areas having biodiversity as exceptional as Hawaii's reveals that they support 49,955 endemic plant species, or 20 percent of all plant species on Earth, as well as at least 500,000 endemic animal species, all confined to 0.5 percent of Earth's land surface (Myers, 1990).

Genetic isolation—separation of one animal population from another such that the two populations cannot interbreed—may also generate and maintain animal diversity. Siberian tigers are cut off from other tiger populations in southeast Asia by distances that bar the two from breeding (i.e., from exchange of genetic information). About 150 Siberian tigers are isolated in Korea and the former Soviet Union (Oldfield, 1989b). Tigers of the island of Bali are extinct and those of nearby Java are near extinction. Habitat islands—patches of an ecosystem such as the present range of Siberian tigers—resemble geographic islands in isolation of members of a species physically and, therefore, genetically. Populations so isolated may persist to become a new species via natural selection, may disappear rapidly, or may linger in populations too small to maintain the species. Tigers matter to our own species not only for their beauty but because tigers and other wild cats have many genes similar to those of our species. These cats experience many hereditary diseases (hemophilia) and other afflictions that resemble those of humans, including feline leukemia (FeLV, similar to HIV), seizures, and certain cancers. Understanding cat genes therefore may provide clues to human genetic disease and maladies.

How is it, then, with the enormous diversity of wild animal species, that humans have domesticated only a handful—horses, donkeys, camels, cattle, goats, sheep, pigs, llamas, water buffalo, chickens, ducks, geese, turkeys, guinea fowl, carp and about 300 other fish species, silkworms, and a scattering of others? This is puzzling, considering that an agricultural system based on multiple species is more stable than agriculture based on fewer species. Wild animals could be raised sustainably for animal protein without loss of biodiversity (Vietmeyer, 1991). Among these animals are the capybara (*Hydrochoerus hydrochoeris*), native to South American grasslands near water. The capybara weighs fifty kilograms, thrives on ranches in marginal habitat, and is a delica-

cy to native populations from Panama to the Amazon basin. Other potential protein sources include the green iguana (*Iguana iguana*), a large lizard of the American tropics; the chickenlike chachalaca (*Ortalis* sp.), a potential domesticated tropical fowl; and the babirusa (*Babirusa babirusa*), a forest pig of the southeast Asian Molucca and Celebes islands. Animals also provide pharmaceuticals and medical devices, such as pig heart valves. One of the newest medical materials derived from a non-human animal is the coral used for skull bone grafts. This porous coral skeleton acts as a substrate for new bone formation by the human recipient. Wild animal species bear a library of genes, potentially transferable to presently domesticated species. Such genes might contribute traits such as tolerance of high and low temperature, ability to thrive in

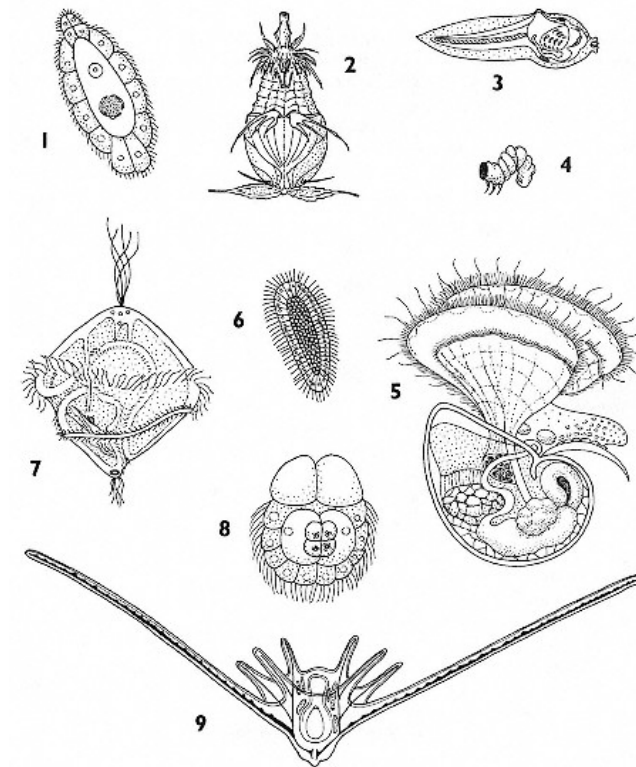


Figure 14

A larva is an immature or resistant stage intermediate between the embryo and adult stage of an animal. Larvae differ from their corresponding adult stages in form, function, and habitat. Most larvae are aquatic; often they swim, dispersing the species. The similarities of larvae of many classes of animals may have more to do with the power of dispersal of their larval developmental stages—trochophore, pluteus, or veliger—than with their ancestry. Some larvae resist environmental stresses such as desiccation, heat, and cold. Several types of larva are shown here with their associated phyla: (1) vermiform (Rhombzoa), (2) Higgins larva (Loricifera), (3) tunicate tadpole (Urochordata), (4) beetle grub (Mandibulata), (5) veliger (Mollusca), (6) planula (Cnidaria), (7) trochophore (Annelida), (8) infusoriform (Rhombzoa), and (9) pluteus (Echinodermata). The tun of the water bear (tardigrade) (see Figure 13, p. 108) is not a larva, but an extremely resistant stage that develops in response to low environmental temperature. *Kathryn Delisle*

habitats marginal for conventional agriculture, and resistance to disease. An agriculture based on multiple species is more stable than one based on fewer species.

Incentives for maintenance of animal biodiversity are abundant. Wild animals may be used directly for meat, hides, wool, ivory, oils and waxes, and medicines. Cross-breeding between wild and domesticated species can transfer desirable genes, rendering domesticated animals more vigorous. Localized animal varieties presently domesticated, such as banteng ("Bali cattle"), which thrive in hot, humid Indonesian lowlands, graze on poorer pasture than cattle, can drink salty water, produce low-fat-content meat, can work as draft animals, and can be more widely utilized to reduce conversion of wild lands to range and farm land. Deer that formerly were exclusively wild are now being farmed in New Zealand and the United States for their meat and antlers, reducing hunting and poaching pressures on wild populations. Wild animals such as the African chimpanzees and the Dominican parrot may be maintained in preserves and parks for educational and cultural values, tourism, and as a reservoir for their genetic potential. This last incentive to save biodiversity is particularly urgent because preservation of wild animals can conserve medicinal resources against species loss by habitat destruction and overharvesting. For example, horseshoe crabs cannot yet be induced to reproduce in captivity; their amebocytes—blood cells used to screen intravenous solutions for presence of a toxin produced by bacteria that is potentially fatal to recipients of IVs—must be harvested from wild horseshoe crabs. Preservation of wild animals from habitat destruction and overharvesting is especially urgent in the tropics, which is the habitat of medicinal fauna close to extinction and home to indigenous people who have a fragile hold on a priceless store of medicinal wisdom. The majority of animal species have not yet been examined for medicinal compounds.

The steps to save biodiversity are set forth succinctly by expert tropical biologist Daniel H. Janzen (1991): "Save it, come to know what it is, and put it to work sustainably."

Pebbled Sea Bottom

Phylum: Placozoa

Among the simplest animals alive today, placozoans change shape as they creep. They look like large, lumpy amebas (**A**) with neither head nor tail, neither left side nor right side. Only one placozoan species, *Trichoplax*, is known. By contrast, the insects (p. 150) encompass at least 751,000 species. Lacking distinct organs such as kidneys or hearts and tissues such as nerve and muscle, *Trichoplax* (along with sponges, see p. 124) is probably not ancestral to other animal phyla.

Why then is this tiny (0.2 to one millimeter across), multicellular, marine organism classified as an animal? The embryo of *Trichoplax* develops from a hollow, fluid-filled ball of cells called a blastula that is characteristic of all animals. The blastula (**D**) results from an egg cell fertilized by a sperm, that is, sexual reproduction. In addition, *Trichoplax* can split into two amebalike individuals, each containing about a thousand cells. Like many sea animals, young placozoans can swim, dispersing the species. Large adults crawl using their ventral cilia.

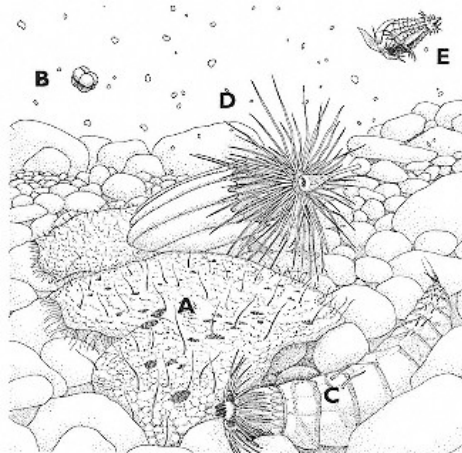
Phylum: Kinorhyncha

Kinorhynchs (from the Greek words *kinein*, meaning "to move," and *rhynchos*, meaning "snout"), such as *Echinoderes kozloffii* (**C**), are free-living marine worms with spiny heads. A kinorhynch moves forward by forcing fluid into its head and thereby everting its head, then anchoring the spines on its head, hauling itself forward, and finally retracting its head. Kinorhynchs do not swim. About 150 species inhabit muddy ocean floors and abrasive, coarse sediments as far north as Greenland and south to Antarctica. Some are commensal, living in sponges (p. 124) and attached to members of other marine phyla. Kinorhynchs usually are brownish yellow. The segmented cuticle differentiates into plates and spines common to kinorhynchs and loriciferans (see this page) and priapulid larvae (p. 130); these shared features indicate that these phyla may be related, even though no fossils of kinorhynchs are known.

Individual kinorhynchs are male or female, but usually no external features distinguish the sexes. The male deposits a packet of sperm called a spermatophore in females of some species. The fertilized eggs develop externally. As young kinorhynchs develop into adults, the juveniles molt their cuticles at least six times to accommodate their growing bodies.

Phylum: Loricifera

Like all other animals, the loriciferan shown here, *Pliciloricus enigmaticus* (**B**), probably develops from a blastula (**D**), although a loriciferan blastula has not yet been documented. *P. enigmaticus* can telescope its mouth cone, head, and neck into the sculptured, spiny plates called the lorica ("corset"). A lorica bristling with spines sheaths its abdomen. Loriciferans anchor themselves to submarine rocks and to other animals among the sand grains. Loriciferan larvae, such as the *Nanaloricus mysticus* larva shown here (**E**), paddle through the sea with their leafy toes. The toes are hollow and may

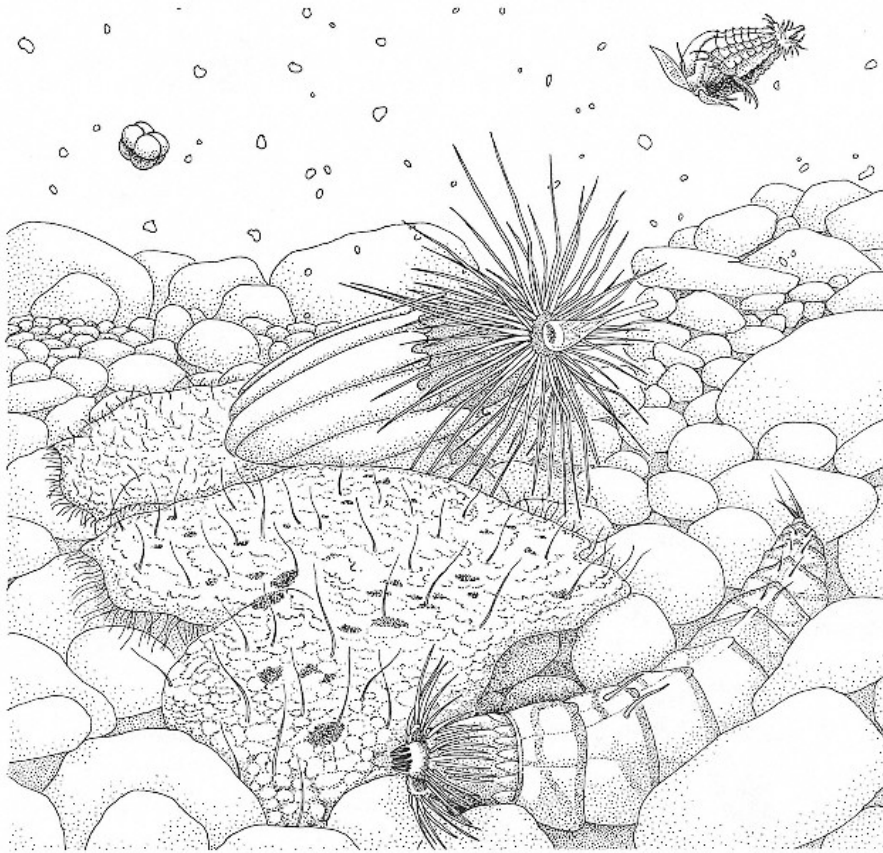


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secrete adhesive, enabling the larvae to stick to sand particles. Adults inch across subtidal sediment particles using their ventral spines.

Loriciferans are complex in form and have thousands of spiny appendages. About eleven species have been described in detail, and preliminary information has been gathered for at least a hundred species. The spiny cuticles and retractable mouth cones of loriciferans and kinorhynchs (see p. 122) probably are homologous, meaning that they may have evolved from a common ancestor.

The natural history of the minuscule loriciferans is sparsely known. They probably pierce prey using sharp stylets around their flexible mouths and suck in food, although we do not know what they eat. We have not yet unraveled their sex lives.



Open Ocean Rock and Sand Bottom

Phylum: Porifera

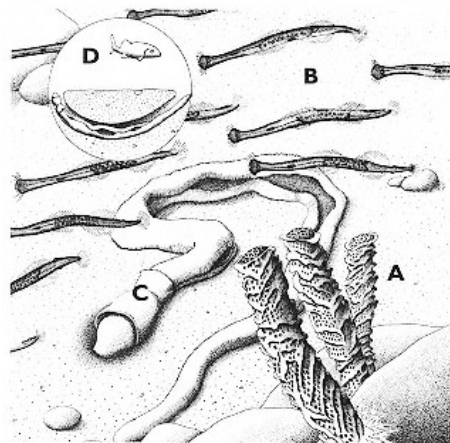
Thousands of pores penetrate the walls of this Venus flower basket sponge, *Euplectella speciosissima* (A). Although sponges lack a digestive tract, nerves, muscles, and respiratory and circulatory organs, they have evolved elegant modes of feeding. Plankton (free-floating aquatic organisms) and detritus raining down through the sea are drawn into the pores of the sponge, then wafted along inhalant canals by microscopic beating organs of motility called undulipodia. Once inside the canals, food particles are engulfed and digested by amebalike cells lining the canals. Part of the feeding current is generated by the physical form of the sponge—smaller incoming openings and larger excurrent opening.

Symbiotic algae provide nutrients and oxygen to many of the 5,000 to 10,000 species of sponges. The symbionts also remove wastes from the sponge host and screen sunlight. The algal symbionts move from mature sponge to offspring by hitching a ride on the gemmules (little balls of sponge cells) by which sponges disperse. Many freshwater and a few ocean sponge species overwinter as gemmules; these resume growth when favorable conditions return. As a second mode of reproduction, fragments generated when a sponge branch is severed then disperse on water currents and establish new individual sponges that are genetically identical to the original. Sponges also reproduce with sperm and eggs. Most sponge species bear both sperm and eggs; these species are hermaphrodites. Sponges are colored by algal symbionts or by their own pigments and may be any color in the rainbow—red, orange, yellow, green, blue, purple, brown, or white. Some sponges bioluminesce, meaning they glow in the dark.

Evidence from molecular makeup of ribosomal RNA suggests that sponges were the earliest animal lineage that branched off from protocists. Those proctocyst ancestors were probably colonial choanomastigotes (p. 72), organisms that strongly resemble collar cells of sponges.

Phylum: Chaetognatha

Flips of the tail send chaetognaths (from the Greek for "hairy jaws"), or arrow worms, darting through the open ocean on migrations to the depths during the day and to the upper ocean at night. Translucent tail and lateral fins stiffened by rays stabilize their arrow-shaped bodies. About seventy species of these plankton abound, especially in warm seas. Deep-water chaetognaths may be tinted pink, red, or orange.



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Fish larvae and other plankton are food for these predators. After piercing their food with teeth and hooks beside their mouths, arrow worms secrete toxins that paralyze prey. Fossils indicate that arrow worms, such as *Sagitta bipunctata* (B), had evolved by the Carboniferous period, about 300 million years ago, when large woody club mosses and treelike horsetail plants dominated great forests.

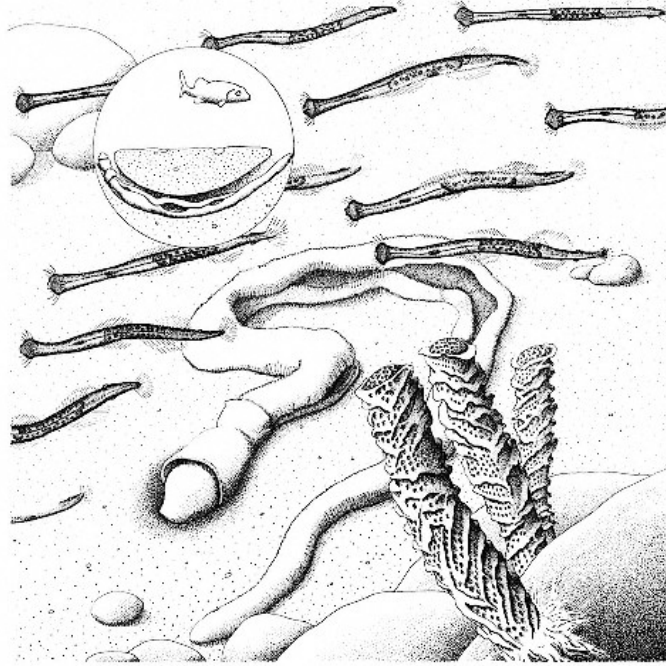
Phylum: Hemichordata

Acorn worms and pterobranchs are both hemichordates; the ninety or so species share a proboscis, collar, and trunk with gill slits but differ in body form. The more common form of hemichordate is

the acorn worm, for example, *Ptychodera flava* (C). The acorn worm burrows into the soft sea bed with its acorn-shaped, muscular proboscis. Some acorn worms line the burrow with mucus, to which food and sediment stick; cilia that cover the acorn worm's soft body transport the food or mucus mass to its mouth, hidden at the base of the proboscis. Other acorn worms ingest sediment, from which they extract nutrients. The tomaria larva, a free-living, ciliated member of the plankton, is characteristic of many hemichordate species (p. 146). Other hemichordates, such as *Saccoglossus kowalevskii*, (p. 146) develop directly from egg to young acorn worm, bypassing the larval stage.

Hemichordate species having a vase-shaped body are called pterobranchs (from the Latin for "feather gills"). These are rare, living in frigid oceans and deep seas; little is known regarding their biology. A pterobranch captures food with tentacles that extend from a pair of arms and secretes a rigid tube within which it creeps, unlike arrow worms, which burrow.

Acorn worms (class Enteropneusta) and pterobranchs belong to an ancient phylum; fossils resembling hemichordates are among the animals of the Burgess shale, a 530-million-year-old fossil deposit in British Columbia, Canada. What evidence links these hemichordates to chordates (p. 148), including humans? Embryos of hemichordates and chordates have a common pattern of development: The blastopore opening of the embryo develops into the adult anus. Most hemichordates and chordates are also characterized by gill slits. In human chordates, the gill openings of the embryo eventually become, among other things, tiny middle-ear bones. Many hemichordates, like fish—which are chordates (D)—have gill slits that extract dissolved oxygen from their watery habitat.



Caribbean Reef Seafloor

Phylum: Cnidaria

Cnidarians (from the Greek word *knide*, meaning "nettle") include the well-known corals, hydras, and jellyfish. The four major classes of cnidarians are the Anthozoa (sea anemones and corals), the Hydrozoa (hydras), the Cubozoa (sea wasps and other cuboidal medusae), and the Scyphozoa (marine jellyfish such as *Obelia*, illustrated here). Almost all of the 9,400 species are marine.

The body forms of cnidarians are polyps (**A**) and medusae (**B**), both radially symmetrical. Some cnidarians are polymorphic (many-formed) and have both polyps and medusae. Other species are polyps only; still others are medusae only. Medusae usually swim free with muscular pulsations of their bells, trailing their snaky tentacles. The lump-shaped gonads of a medusa release gametes—sperm or eggs. The polyps produce reproductive bodies (**C**) in which eggs and/or sperm form at their branches. A fertilized egg develops into a larva (**D**). Polyps can also reproduce by budding. An immature colony (**E**) is shown growing on the sandy ocean floor. Hydrozoans include freshwater hydras as well as the colonial, marine Portuguese man-of-war. The hydrozoan hydra-like polyps outnumber the medusa forms.

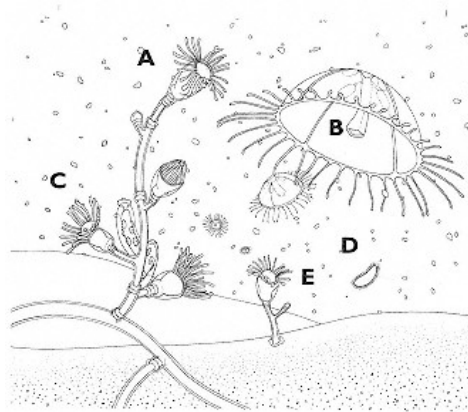
Anthozoans form polyps exclusively and lack medusae. All anthozoans are marine—corals, sea pens, sea fans, and sea anemones, named for the flowerlike polyps. Like hydrozoans, anthozoans form buds or form larvae from fertilized eggs. Anthozoans are able also to just split off a portion of the disc by which they attach to the ocean bottom or to divide in two.

The Cubozoa swim actively in tropical oceans. Their sophisticated eyes enable them to capture fish as their food.

Scyphozoans are exclusively marine. Their medusae are called jellyfish for good reason—a thick jellylike middle layer called mesoglea stiffens the bell.

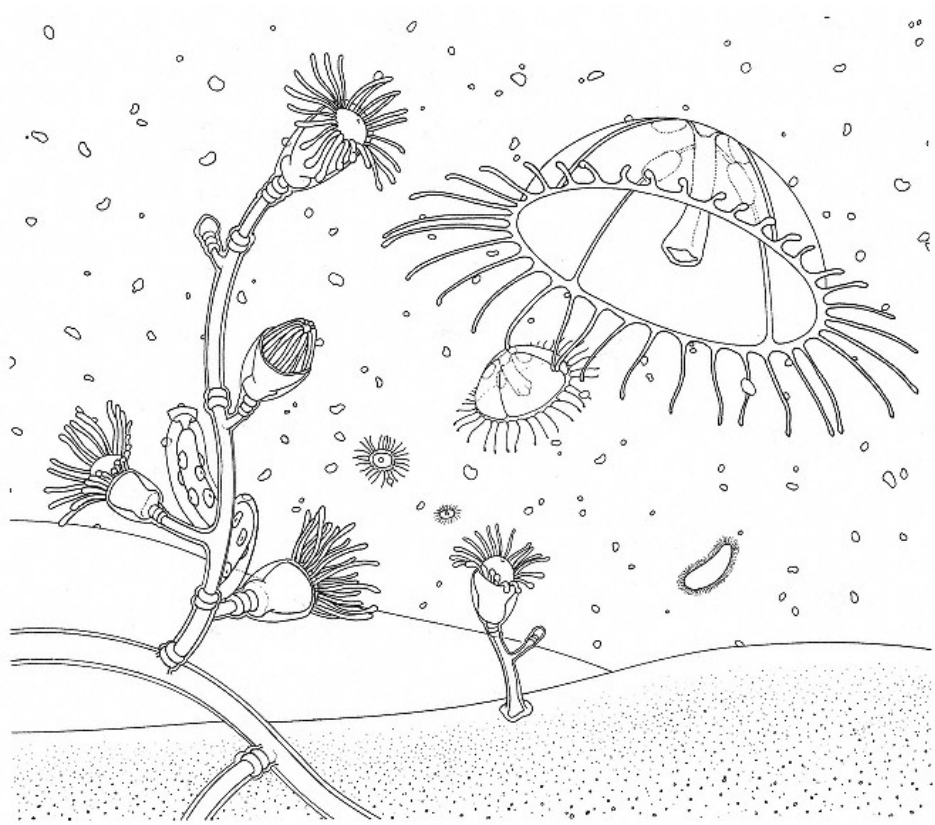
All but a single known herbivorous species of cnidarians are carnivores and have special stinging lasso cells on their tentacles and body walls. Tentacles dangling from the four corners of the cuboidal medusa of the sea wasp can inflict serious damage on humans. After stinging and immobilizing small prey, the tentacles pass the prey to a hollow digestive cavity called the coelenteron, which is the defining feature of all members of this phylum.

Coral reefs are generation upon generation of cnidarian skeletons, cemented by the limestone secretions of cnidarian polyps of coral animals, such as *Eunicella verrucosa* (p. 136). Secretions of other marine organisms, for example chlorophytes (p. 84) and red algae (p. 62), combine with corals in reef formation. Florida, Bermuda, and the Bahama islands originated as coral reefs. Blocks of coral mined from nearby reefs are used as building material in many lands, such as the Philippines. From coral, a newly developed biomaterial is being utilized as a



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three-dimensional scaffold for bone grafts. Bone cells migrate into this "biocoral" as the recipient of the graft reconstitutes bone.



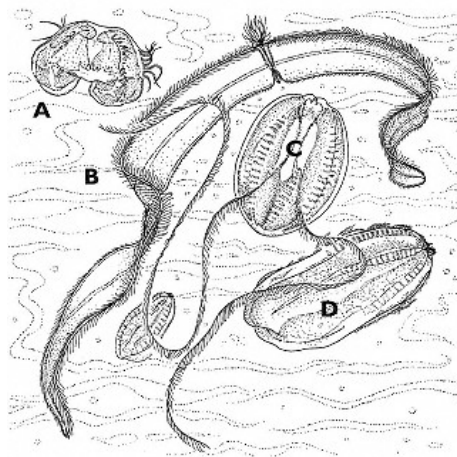
Open Ocean

Phylum: Ctenophora

Multicolored lights flashing in the night sea often are the visible signs of bioluminescence of ctenophores (from the Greek words *kteis*, meaning "comb," and *pherein*, meaning "to bear"), or comb jellies. Comb jellies' nocturnal glow is powered by chemical reactions, like the night lights of fireflies. Symbiotic algae color some comb jellies soft purple, pink, orange, or brown. The beating of their comb plates (bands of thousands of fused cilia that run lengthwise along their bodies) propels the free-swimming comb jellies through the ocean; this is true for most coastal ctenophores. Many open ocean species swim using muscular contractions combined with comb action for food-getting. The tentacles of these gelatinous jellies are solid, whereas the tentacles of cnidarians are hollow. Eight rows of combs distinguish comb bearers from other jellylike, radial animals such as jellyfish and hydras (p. 126). Both ctenophores and cnidarians have a digestive cavity with only one opening (a coelenteron). Adhesive lasso cells cover the tentacles of ctenophores; the touch of prey triggers the sticky cells.

After a storm, glossy cat's eyes, sea gooseberries, sea walnuts, and Venus's girdles—all comb jellies—appear, cast up on the beach by wind and waves. Divers in submersible vehicles, scuba divers, and remotely controlled vehicles collect comb jellies with slurp guns. Marine biologists observe that ctenophores are the most abundant planktonic animals at 400 to 700 meters below the sea surface and have collected comb jellies as deep as 3,030 meters.

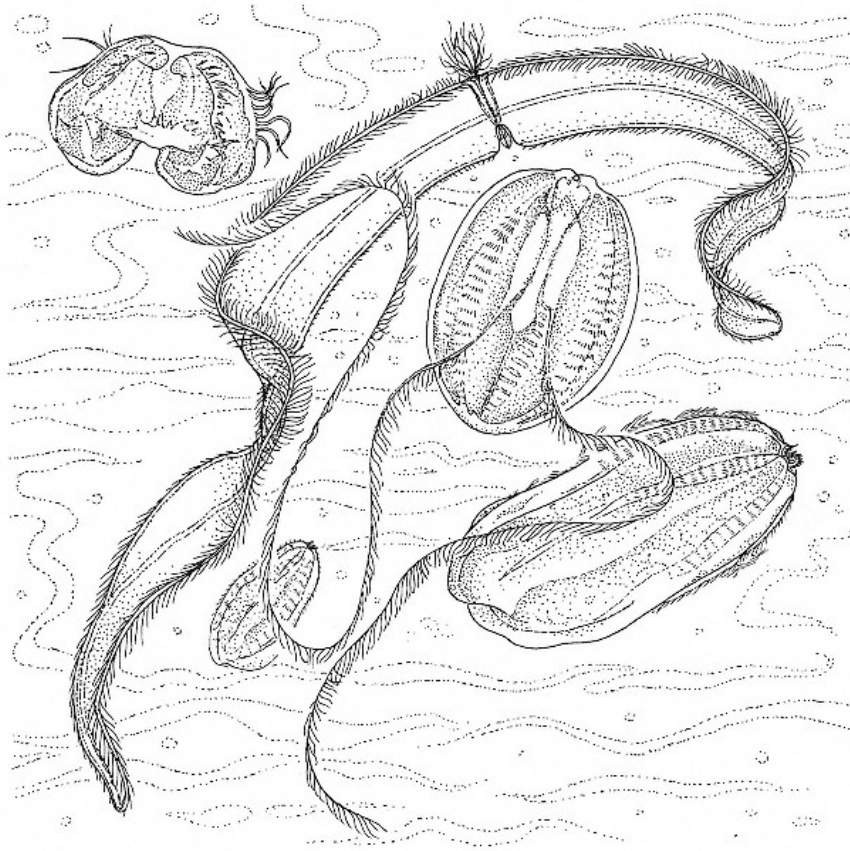
Four genera of ctenophores are shown here: the lobate comb jelly *Bolinopsis infundibulum* (A); Venus's girdle, *Cestum veneris* (B); the sea gooseberry, *Pleurobrachia pileus* (C); and the North Sea thimble jelly, *Beroë cucumis* (D). The one hundred or so comb jelly species' feeding strategies are as diverse as their delicate body forms. *Bolinopsis* (A) forages vertically, collecting prey with ciliated, mucus-coated oral lobes. Cilia transport the prey into the digestive tract. Venus's girdle (B) forages horizontally, often reversing the direction of its undulating, two-meter-long body. In the turbulent wake thus generated, small tentacles that cover the flat, ribbon-shaped sides capture prey such as little crustaceans called copepods (p. 152). The tiny tentacles' adhesive cells stick to the prey. The tentacle then contracts, transferring the food to a ciliated groove that runs the length of the comb jelly. The cilia carry the copepods to the mouth midway along Venus's girdle and into the gut. The sea gooseberry (C), a carnivore like other comb jellies, captures living prey with a pair of sinuous trailing tentacles. After retracting its tentacles, it wipes food off on its lips. *Beroë* (D) forages in a helix and captures prey by peeling apart its large lips on contact with baby herring and other food. The swiftly parted lips generate negative pressure that sucks in prey. Macrocilia shaped like a saw blade line *Beroë*'s lips and trap the food whole or



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tear chunks from it. *Beroë* then zips its muscular lips shut with reversibly adhesive, Velcro-like strips. Unlike the other three species shown, *Beroë* lacks tentacles.

The resemblances between ctenophores and cnidarians probably are superficial. Some differences between the two phyla include the presence in ctenophores of adhesive lasso cells, comb plates, and giant smooth muscle fibers (recently isolated from *Beroë* and another comb jelly)—all characteristics that are absent in cnidarians—and a lack of polyps.



Philippine Coral Sands

Phylum: Rhombozoa

A rhombozoan (from the Greek *rhombos*, meaning "spinning top," and *zoion*, meaning "animal") has only one organ, a gonad. Because rhombozoans absorb nourishment from the urine of the animals they inhabit (such as the rhombozoan *Dicyema truncatum*, **A**), and its host cephalopod mollusc *Nautilus*, **B**), these microscopic animals function without their own circulatory, skeletal, muscular, excretory, digestive, and nervous systems. In a shallow coral sand community, such as this one near the Philippine Islands, rhombozoans are widespread in squid, octopods, and other cephalopod molluscs (see page 148). About sixty-five species of rhombozoans have been described.

Sexual adult rhombozoans develop on the inner surface of the cephalopod's kidney, where they alternate sexual and asexual generations. Within twenty to thirty jacket cells, the hermaphroditic, cylindrical gonad produces both eggs and sperm. Sperm fertilize eggs within the adult, where the tiny zygotes develop into ciliated larvae (**C**), called infusoriform larvae because they resemble ciliates (see page 94). The larvae escape into the ocean in the urine of the mollusc. The free-swimming rhombozoan larvae find young cephalopods on the sea bottom and enter their bodies. In the kidneys of their host, the larvae develop into adult rhombozoans.

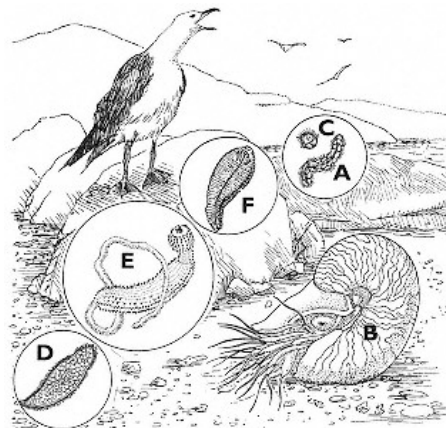
Rhombozoans also reproduce without sexuality. Inside the host cephalopod, rhombozoans release a second type of larva—a wormlike (vermiform) type—which also swims in urine within the kidneys of the mollusc. When the population of rhombozoans becomes high, they again produce sperm and eggs.

Phylum: Orthonectida

Orthonectids comprise twenty marine species of multicellular, ciliated adults producing reproductive cells and embryos that develop within other cells. *Rhopalura* (**D**), like all orthonectids, resides in gonads of clams (p. 26), polychaete annelids (p. 142), flatworms (p. 132), nemertines (p. 136), and brittle stars (echinoderms, p. 132). Nutrients from the host maintain the orthonectid. Orthonectids were once classified as closely related to rhombozoans; the two are now placed in separate phyla. Many open questions remain regarding the life histories of these tiny swimmers.

Phylum: Priapulida

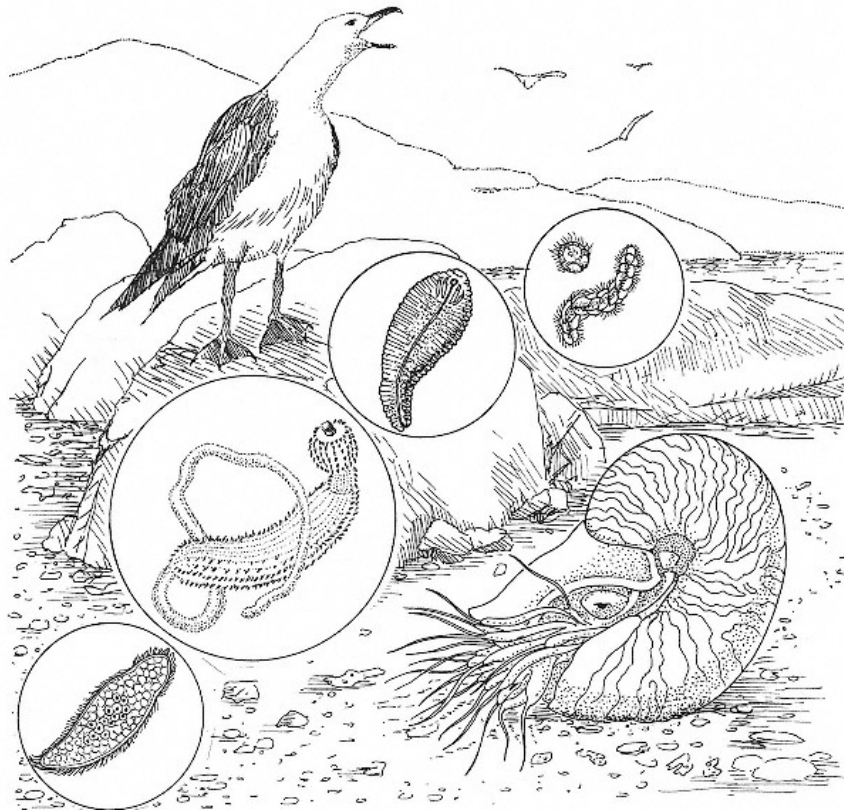
Priapulids are annulated, spiny, warty worms that burrow using circular and longitudinal body muscles in coral sand and marine mud by anchoring their anterior and posterior ends alternately as they go. Both mouth and spine-studded proboscis evert (roll inside out, then inside in), allowing larger priapulids to seize annelid prey (p. 142) and other priapulids whole. One carnivorous species filterfeeds with hollow tentacles and lacks a proboscis. *Tubiluchus* (**E**) scrapes microbes from sand grains. Projections thought to be sensory organs cover the trunk of the priapulid. Adult priapulids molt, shedding the external chitinous cuticle periodically. Most



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priapulid larvae are covered with a thick cuticle with plates that resemble those of kinorhynchs; these and other similarities suggest that these phyla are related.

When polychaete annelids with jaws evolved during the Ordovician period, some 440 to 500 million years ago, polychaetes displaced priapulids from their position as important carnivores of the oceans. Fossils from the Burgess shale in western Canada are evidence that earlier, during the middle Cambrian period (approximately 530 million years ago), the seas were rich in priapulid life. Seventeen species comprise the phylum now.



Sandy Seashore

Phylum: Platyhelminthes

The worm depicted here is an example of the simplest animals that have organs, the platyhelminth worms, or flatworms. (In Greek, *platy* means "flat," and *helmis* means "worm.") This phylum of about 20,000 species includes turbellarians (class Turbellaria), free-living in fresh and salt water (**A**); tapeworms (class Cestoda); and flukes (class Trematoda). The free-living, marine, carnivorous flatworm shown here can evert its pharynx through its mouth; this single opening serves as both mouth and anus for the flatworm's dead-end gut. Some turbellarians are carnivores, feeding on other worms, arthropods, and tunicates. Other turbellarian species scavenge. All flatworms are bilaterally symmetrical; the left half of the body mirrors the right. Their bodies have three layers of tissue, and are solid throughout, lacking body cavity, circulatory system, heart, and lungs. Oxygen and carbon dioxide diffuse through their ribbonlike bodies.

The tapeworms and the flukes are external or internal parasites. Cestodes (tapeworms) lack their own gut, are exclusively internal parasites, and absorb nutrients through tiny projections across their body surface.

Although a trematode (flake) has a gut, it is obligated to live attached by its suckers inside or on the outside of other animals. Trematodes, such as *Cryptochyle*, are common in snails, gulls, such as *larus crassirostris*, p. 130, and fish. These flatworms do not live free but have larvae and other life history stages appropriate to each host animal in which they live. Schistosomes are liver flukes that live in people in wet tropical areas, such as sub-Saharan Africa and the Caribbean. Typical fluke habitats are the liver, muscle, and other tissues of the vertebrate body, in which the flukes mate and carry out their highly specialized lives.

Phylum: Echinodermata

Sea stars are the most familiar echinoderms (from the Greek for "spiny skin"). Sea pansies, sea biscuits, sand dollars, sea cucumbers, sea lilies, and brittle stars are among the 7,000 species of these radially symmetrical invertebrates. Hard spines and tiny protective organs with pincers stud the surfaces of most echinoderms, including the daisy serpent star, *Ophiopholis aculeata* (**B**). A porous sieve plate, called a madreporite, lies at the center of its arms. The star pulls sea water through the sieve into the water vascular system. Sea-water-filled canals of the water vascular system run into each arm where the canals connect to tube feet. Exerting hydraulic pressure by squeezing a flexible bulb shaped like a miniature turkey baster, the star extends the tube feet for food collecting, locomotion, oxygen exchange, and diffusion of nitrogenous waste into the sea.

Reproductive strategies of echinoderms are as diverse as their forms. Male and female are separate in most species. Many lay eggs; a few bear live young. The externally fertilized egg often develops to a pluteus larva (p. 120), eventually metamorphosing into an adult.

Echinoderms range the ocean floors from the Arctic Circle south to Antarctica and are organized into two subphyla, Crinozoa (Pelmatozoa) and Asterozoa (Eleutherozoa). Crinozoa, commonly called crinoids, include sea lilies—attached by a stalk to the seafloor—and feather stars—free-living crinoids; both are suspension feeders on coral reefs. The Asterozoa are more diverse, including

- sea daisies that live on undersea wood
- sea stars, which are carnivores and predators of shellfish such as oysters and scallops
- many-armed basket stars
- garlic-scented leather stars
- flowerlike luminescent sea pansies
- sand dollars and sea urchins, whose calcium carbonate skeletons appear in seashore trinket shops

In some parts of the abyss, sea cucumbers comprise most of the biomass, ingesting nutrients that have drifted to the ocean floor as they burrow through the sediment.

For years, spiny sea urchins snared in fishing nets were the bane of fishermen. Today New Englanders scour coastal waters for urchins to harvest the eggs for human food. From the ability of echinoderms to regenerate missing arms, gonads, stomach, and spines, humans may learn more regarding mechanisms of healing and regeneration.

Ancient echinoderms 600 to 500 million years old are preserved as fossils. The massive extinction at the end of the Permian period 250 million years ago led to a decrease in sea lilies and other sessile forms and expansion of mobile animals, such as active echinoderms.

Phylum: Cephalochordata

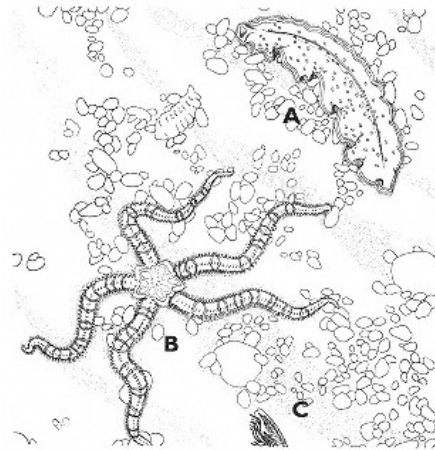
Branchiostoma (amphioxus, **C**) is a cephalochordate, a chordate that lacks a skull. Cephalochordates live in warm, shallow ocean floors with their head sticking out of the sand. The twenty-three species that compose this phylum resemble small fish without scales, bones or cartilage and are about 5 to 15 centimeters in length. Because their flat bodies resemble lances, their common name is lancelet. Like the other acraniate chordates (urochordates, p. 34), lancelets possess the three characteristic features of chordates—pharyngeal gill slits, notochord, and dorsal hollow nerve cord—as adults.

Sandy Seashore*(continued from previous page)*

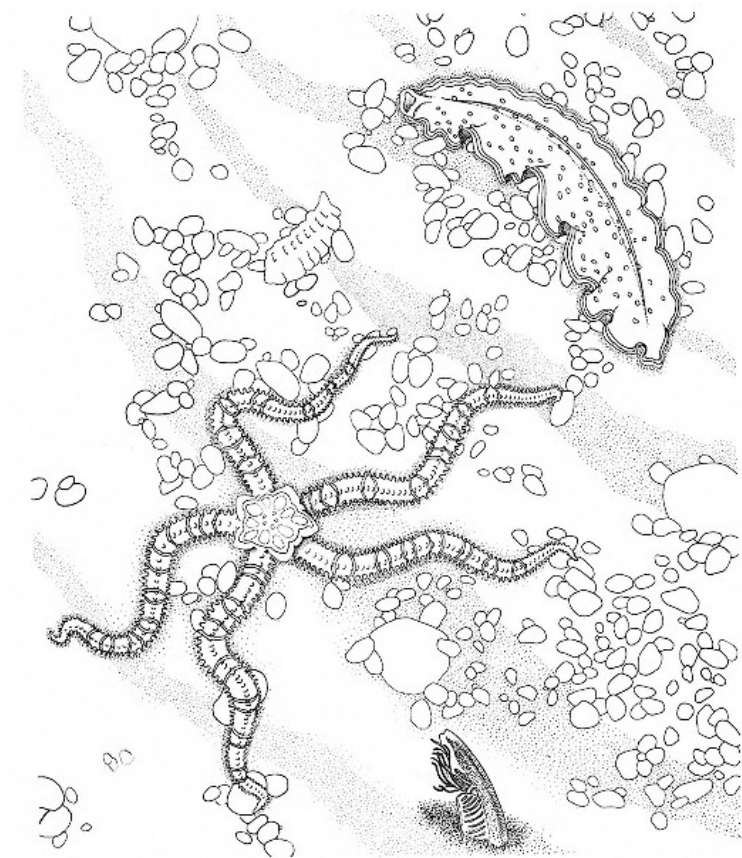
In comparison, in most terrestrial chordates—the human species, for example—both gill slits and notochord are transitory structures present in the embryo but replaced in the adult.

A feeding lancelet pushes into the sand, swivels around with its head projecting out of the sea bottom, and nets plankton from seawater on the little tentacles around its mouth.

Cephalochordates are the closest extant relatives of vertebrates, according to ribosomal RNA evidence.



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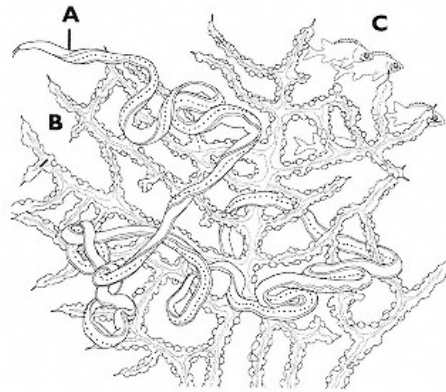
Coral and Squirrel Fish

Phylum: Nemertina

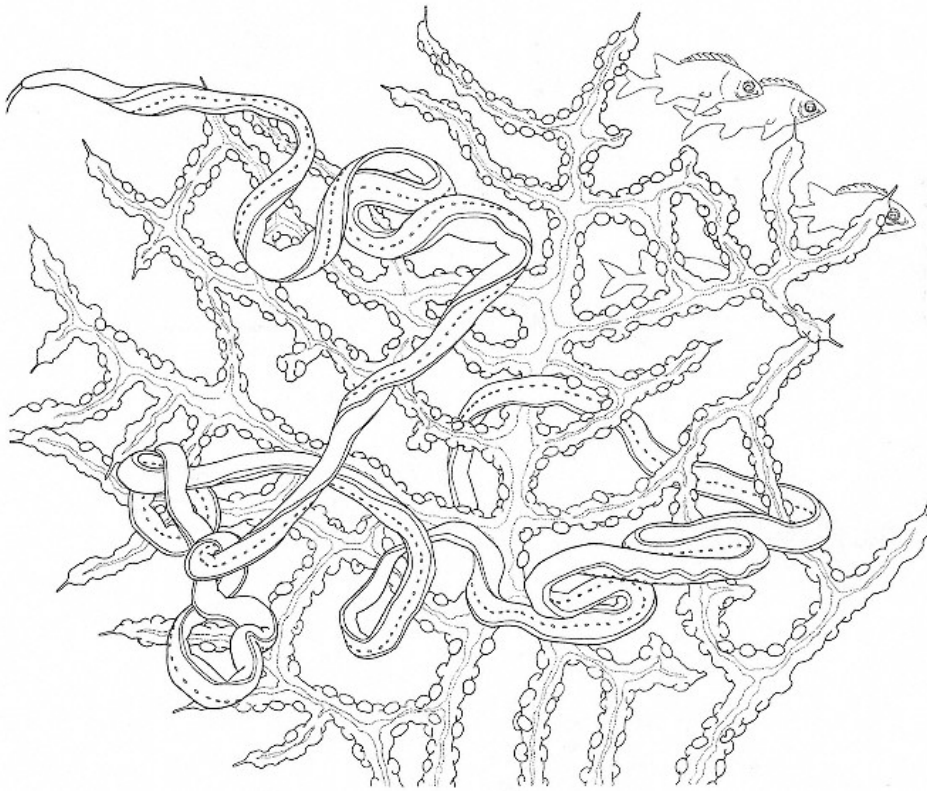
Often very colorful, nemertines such as this ribbon worm (A) clambering over the coral *Eunicella verrucosa* (B) are mostly marine animals. A few of the 900 nemertine species live in damp soil and freshwater. Some ribbon worms shoot out a hook mounted on a proboscis to capture live prey and then retract the harpooned prey into their mouth. Other nemertines suck the juices out of prey such as annelids and roundworms. An elaborate proboscis that is separate from the digestive tract and resides in a fluid-filled cavity when it is retracted is characteristic of the delicate ribbon worms. The one-way digestive tract of ribbon worms, which have a separate mouth and anus, allows gut regions to be specialized for various steps of digestion and therefore is more efficient than the dead-end digestive tube of flatworms (p. 132).

Nonsegmented ribbon worms differ from other sea worms (such as marine annelids, see p. 142), which are segmented and usually bear bristles and paddle feet or parapodia; from tube-dwelling, trophosome-bearing pogonophoran worms (p. 152); and from the much smaller gnathostomulids (p. 138).

The squirrel fish, *Holocentrus xantherythrus* (C), is one of myriad reef fish species (Craniata, p. 148). Coral gardens carpeting shallow seas around the globe nourish fishes and sea turtles in their plankton- and oxygen-rich, sunny, warm waters. Within the elegant branches of corals (p. 126), representative species of nearly every phylum of marine animals take shelter and feed. Coral polyps secrete carbonates—minerals that make up coral skeletons (p. 126). Masses of corals, along with ribbon worms and moray eels (p. 148), barracuda, angelfish (cover illustration), brachiopods (p. 138), bryozoans (p. 144), octopuses (p. 148), feather stars (p. 132), gastrotrichs (p. 138), sharks, sponges (p. 124), monerans, and protocists, make up the reef community.



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Grassy Shoal

Phylum: Gnathostomulida

All of the gnathostomulids (from the Greek words for "jaw" and "mouth"), or jaw worms, have hard, toothed jaws with which they tear apart fungi and graze on bacteria and protoctists that coat black, fine ocean sands worldwide. More than eighty jaw worm species have been described. Some are tinted red, pink, or yellow. These transparent microscopic jaw worms inhabit the sulfuretum, an environment in which sand smells like rotten eggs. The smell comes from hydrogen sulfide produced by marine bacteria under anoxic conditions (i.e., where oxygen gas is absent).

Gnathostomulids such as *Probolognathia minima* (shown here on eelgrass, *Zostera marina*, an angiosperm, **A**) glide over marine algae, eelgrass, and marshgrass (*Spartina*) propelled by their external cilia, as flatworms do (p. 132). Stiff bristles on the head and cilia-lined pits are the sense organs of jaw worms. When samples of black ocean sands are investigated, jaw worms are almost the last animals to emerge from the sand, suggesting that they tolerate anoxic environments having high quantities of sulfide. Details of their anaerobic metabolism are still obscure.

Phylum: Gastrotricha

The cilia that cover the ventral surfaces of gastrotrichs are what give this phylum its name, which comes from the Greek for "hairy stomach." Scales, bristles, and spines adorn the sides and backs of many species. All 400 or so species are free-living. A careful search with a hand lens may disclose these wormlike animals clinging to water lily pads and bog moss by the adhesive tubes on their posterior ends and sides. Gastrotrichs scavenge plankton and bacteria and are among the foods for annelids, crustaceans, insects, free-living flatworms, and hydra.

Marine gastrotrichs, such as *Lepidodermella* (**B**), that glide among coral and in shallow-water sea sands have evolved strategies that maximize reproductive success. Each is a hermaphrodite: An individual gastrotrich produces both sperm and egg, but at different times in most species. Most produce their sperm earlier than they produce eggs. Freshwater gastrotrichs of most species lack males altogether. The unfertilized eggs of females develop, without benefit of male sperm, into the adult organism.

Freshwater gastrotrichs lay two egg types. One type is enclosed by an eggshell and must dry, freeze, or be heated before it cleaves to produce a young gastrotrich. The other is enclosed within a thin wall and divides immediately upon being laid. These reproductive strategies permit gastrotrichs enhanced chance of reproductive success in harsh and changeable environments.



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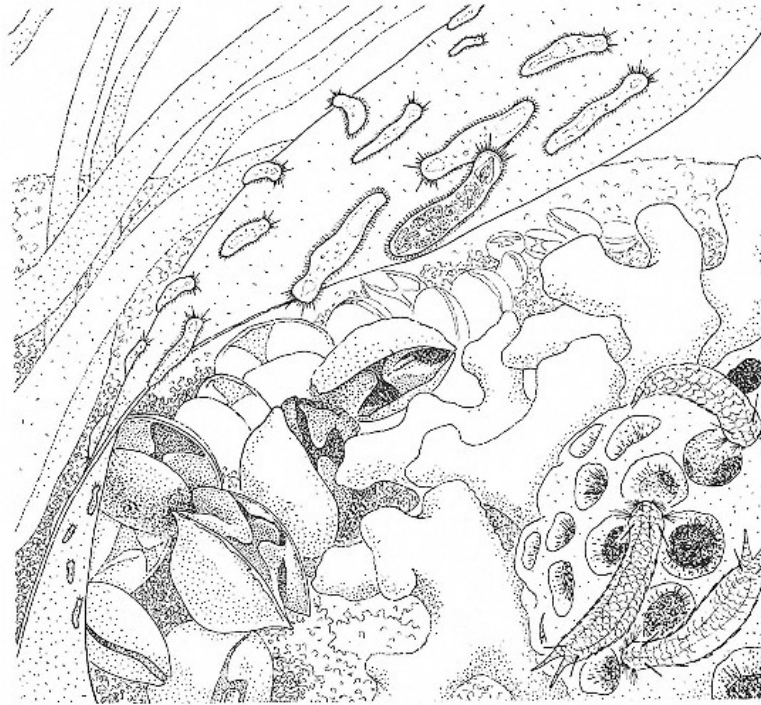
Phylum: Brachiopoda

A pair of calcium carbonate or calcium phosphate shells secreted by mantle tissue within give brachiopods a superficial resemblance to clams. The two shells of a brachiopod are usually dissimilar and are dorsal and ventral to the soft body, unlike the left/right symmetry of a clam shell. Like a clam, a brachiopod is a suspension feeder—its cilia whip plankton-bearing water into its mouth. The resemblance ends there, however. A brachiopod traps plankton on a ridge of hollow, ciliated tentacles near its mouth.

This structure is called a lophophore and graces species of marine animals from three phyla: Phoronida (p. 144), Bryozoa (p. 144), and Brachiopoda. Sea water is circulated within the cavity between shells, facilitating diffusion of oxygen into the brachiopod, and carbon dioxide out, and excretion.

These lamp shells, as *Terebratulina septentrionalis* (C) and other brachiopods are commonly called, once abounded in the seas. More than 30,000 extinct species have been described from their fossils; now fewer than 350 species are living. Since the close of the Paleozoic era, about 250 million years ago, molluscs such as scallops and clams (see p. 148) and diverse, more mobile sea-dwelling organisms from more recently evolved phyla have displaced brachiopods from their ecological niches.

What caused this "mother of mass extinctions," as paleobiologist Douglas Erwin has dubbed the mass decimation at the end of the Permian? Shallow oceanic habitats were destroyed by a gradual drop in sea level that upset the stability of Earth's climate. Increased oxidation of organic material depleted levels of oxygen that dissolved in water and also increased carbon dioxide in Earth's atmosphere. Volcanic eruptions shaded Earth with airborne ash and led to short-term cooling of Earth. After some time—perhaps some hundred thousand years—stagnant oceans rose, wiping out coastal organisms. Shallow-water and reef organisms, especially sessile, filter-feeding echinoderms, corals, and brachiopods, were hard hit. This was the most deadly disaster known in the history of our planet—up to 90 percent of all sea species were extinguished, along with about two-thirds of amphibian and reptile families. Plant extinctions shifted floral diversity as well.



Moss and Lichen Water Film

Phylum: Rotifera

Rotifers comprise about 2,000 species of small, translucent, cosmopolitan, and aquatic invertebrates. Many common rotifers (**A**)—such as *Philodina*—bear a ciliated crown, which wafts food to their mouths by causing a current and propels their swimming. Because the crown looks like a revolving wheel, rotifers used to be called wheel animalcules. Like tardigrades (see this page), rotifers have telescoping cuticle regions and endure adverse environmental conditions. They can reduce their metabolic rate enough to survive subarctic winters and seasonal desiccation. In this condition, rotifers are said to be cryptobiotic. Rotifers and tardigrades share another trait in addition to cryptobiosis: cell constancy (i.e., the number of cells or cell nuclei in an organ is constant).

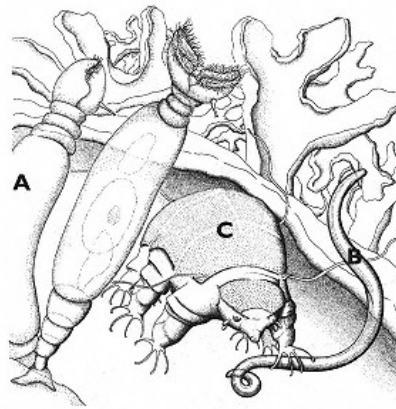
Because of their intriguing resistance to freezing and desiccation, rotifers can inhabit freshwater, brackish, or marine habitats—from hot springs and Antarctic lakes to moss, lichens, tree bark, bird baths, and glacial muds. A few species bear a bristly, lobed funnel at their anterior end that traps prey. Free-living rotifers feed on other rotifers, bacteria, protoctists, and suspended organic material. Not all rotifers live free, however; crustacean gills, snail eggs, and the body cavity of annelids are the habitats of some parasitic rotifers. Rotifers are food for other aquatic animals, such as carnivorous tardigrades and protoctists (e.g., the ciliate *Stentor*, p. 94).

Phylum: Nematoda

Of all the animal phyla, the phylum Nematoda contains the most individuals, called roundworms. Eighty thousand species have been described and up to one million species may be extant. If every nematode were visible but large organisms were invisible, we would still be able to make out the outlines of plants and animals just by the nematodes living within each plant and animal. Free-living nematodes (**B**, feeding on detritus) abound in soil communities, often with rotifers, annelids, and tardigrades, and in salt flats, lakes, and the oceans.

Predatory nematodes with formidable teeth devour tardigrades and rotifers (see this page), as well as small annelids (p. 142). Nematodes of other species live necrotrophically in plants and animals. Canine and feline heartworm, as well as certain diseases of humans—river blindness, filarial elephantiasis, trichinosis, hookworm, and pinworm—are associated with nematode infestations.

Nematodes swim with a unique method of wriggling flip: They generate thrust in S-shaped waves by contracting longitudinal body muscles first on one side and then on the other. Nematodes lack the muscles that characteristically encircle the bodies of most other worms, such as annelids. The eversible proboscis of ribbon worms (p. 136) and some flatworms (p. 132) is also lacking in nematodes.



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Phylum: Tardigrada

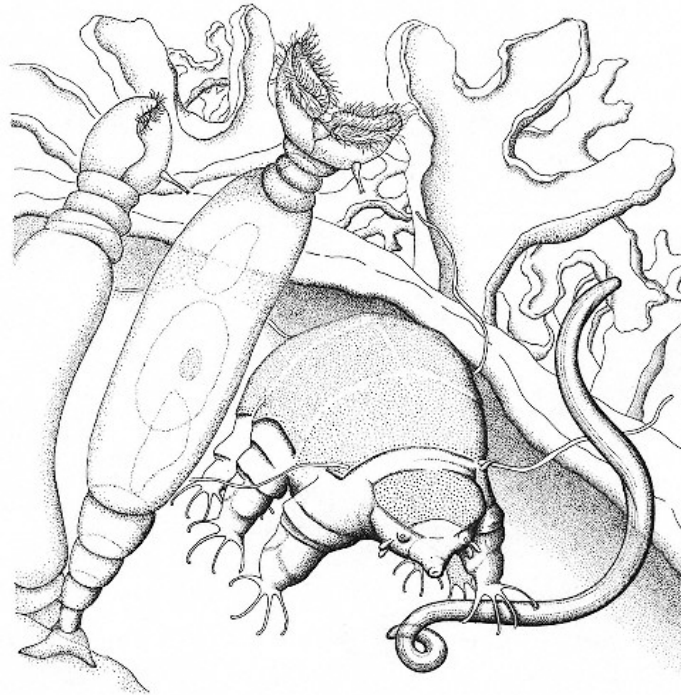
In 1772 the Italian biologist Lazzaro Spallanzani used the name *il tardigrado* (meaning "slow walker") for tardigrades because of their gait. Their common name, water bears, on the other hand, is derived from the habitat in which they live—water that covers lichens, moss, and other terrestrial plants and that permeates beach sand. Chubby little animals, tardigrades such as *Echiniscus arctomys* (**C**) typically are

about as long as the period that ends this sentence, half a millimeter. A chitinous thick cuticle armors some forms, such as *Echiniscus*, others have a very thin cuticle. About 750 species have been described.

Emerging young tardigrades pierce their shell using sharp retractable stylets, then crawl forth as miniature adults. They suck in liquid contents of plant cells, animal cells, nematodes or rotifers (see this page) through holes torn with their stylets. Their food partly determines their color—blue, purple, green, yellow, orange, brown, or even translucent. Claws or suction pads tip each of the tardigrade's four pairs of legs, which lack the joints that characterize legs of arthropods (p. 150). Tardigrades and rotifers both have telescoping cuticles—tardigrade legs and rotifer posterior ends.

A desiccated tardigrade contracts into a tun (a structure shaped like a wine cask that looks nothing like the adult animal and has less than one-tenth the water of the adult; see Figure 13, p. 108). Water molecules in their membranes are replaced by a sugar (trehalose). Tardigrades may remain inert (as tuns) for decades until a water drop revives them from the cryptobiotic ("hidden life") state.

Like mites (chelicerate arthropods, p. 151), tardigrades have segmented bodies, no cilia, four leg pairs, a terminal mouth with stylets, and ventral nerve cords.



Forest Soil Puddle

Phylum: Acanthocephala

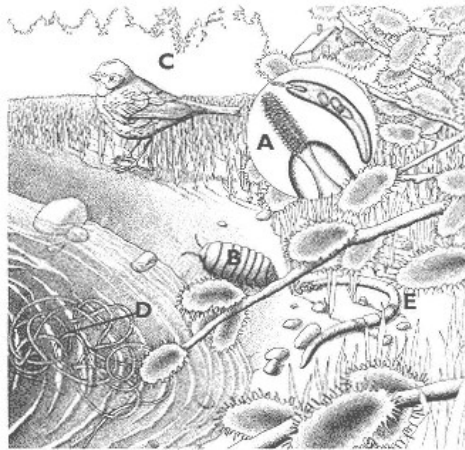
These thorny-headed worms lack any free-living stage; only their cysts exist in the soil. They live at least part of their life cycle in the guts of vertebrate animals—including dolphins, seals, hyenas, moles, shrews, squirrels, pigs, rats, insectivores, turtles, snakes, amphibians, fish, and birds. More than a thousand species of these parasitic worms are known.

This *Plagiorhynchus cylindraceus* larva (A) has burrowed into a pill bug (*Armadillium vulgare*, B), using the spiny head that characterizes acanthocephalan worms. Eventually, a songbird such as the myrtle warbler, *Dendroica coronata* (C), consumes the pill bug along with the worm larva. When eaten by the bird, the acanthocephalan is inside a dark, hard-walled sphere called a cyst. As the bird digests the bug with the *Plagiorhynchus* cysts inside, young acanthocephalans are released into the bird's gut; there a worm absorbs nourishment through its body wall, gripping the intestine of the bird with the hooks on its retractable proboscis.

Mating and embryonic development take place within the female worm while it is still inside the warbler; the female later lays shelled larvae. Worm larvae emerge in the bird's gut and exit the bird's anus with its feces. Eventually the larvae are eaten by an arthropod (p. 150) or mammal (p. 148), thus completing the acanthocephalan life history.

Phylum: Nematomorpha

King Gordius of the kingdom of Phrygia made an elaborate knot for which the wiry worms of this phylum—Gordian worms—are named. According to ancient legend, King Gordius declared that whoever untied the knot would rule Asia. Alexander the Great sliced the Gordian knot with his sword and annexed Asia to his Greek empire. Gordian worms coil like a Gordian knot in the shallow oceans and freshwater lakes in which they live. Nematomorphs are also called horsehair worms because they are only about one millimeter in diameter but can be as long as a meter. About 240 species of nematomorphs are known.



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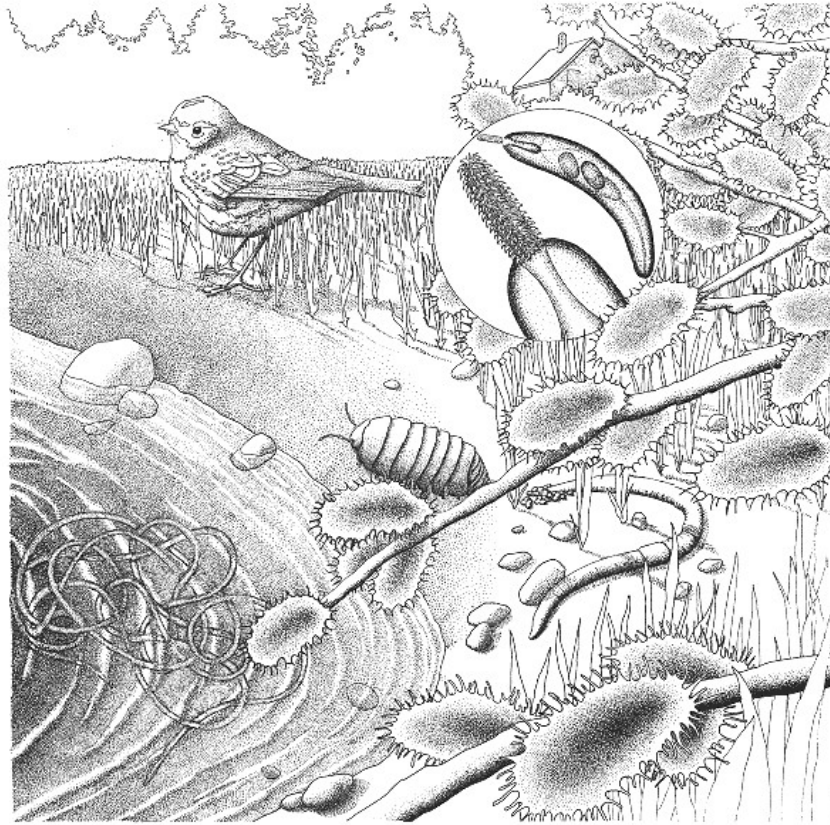
Gordius villoti (D) lays white egg masses. An egg hatches into a larva that resembles some kinorhynch, which absorbs nutrients inside living or dead grasshoppers, beetles, cockroaches, hermit crabs, or spiders after being ingested by the arthropod (p. 150) or after penetrating the host with its spiny front end (proboscis). After metamorphosis, an immature adult bursts forth in or near water, killing the host. Like its larva, the adult, thin, Gordian worm does not ingest food. It completes the free-living portion of its life history aquatically.

Phylum: Annelida

Of all worms, annelids are the most familiar, recognizable by the linear series of rings from which their name is derived (in Latin, *annellus* means "little ring"). The 12,000 to 15,000 annelid species include bristleworms (class Polychaeta), earthworms (class Oligochaeta), and leeches (class Hirudinea). All annelids are soft-bodied worms arranged in muscular segments linked by a ventral nervous system. Polychaetes, or marine bristleworms,

include the feather-duster worm with its elegant crown of tentacles, and the honeycomb worm, *Sabellaria*, which builds its shell and sand tubes in reefs on rocky coasts of Central America. Bundles of chitinous bristles (setae) project from the paddle feet of polychaetes. Leeches are mostly free-living predators that lack bristles and swim like waterborne caterpillars or creep with the aid of suckers over their prey—turtles, frogs, fish, and others.

In his book *Formation of Vegetable Mould through the Action of Worms* (1881), Charles Darwin recognized the contributions of oligochaetes to soil formation. Earth would not support the growth of food plants in the absence of earthworms, which aerate the soil with their burrowing and fertilize it with their body waste. Oligochaetes such as the earthworm *Lumbricus terrestris* (E) and other oligochaete annelids of ponds and mud bear scanty bristles but lack paddle feet, sensory antennae, and the distinctive head (which bears the sensory antennae) of polychaetes.



Shallow Pacific California Coast

Phylum: Entoprocta

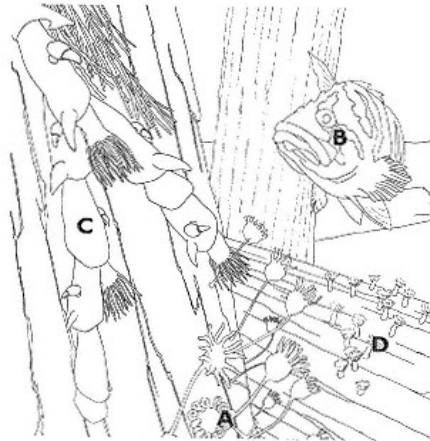
Tiny, transparent entoprocts are invertebrates having stalks that support a cup-shaped body called a calyx. The name entoproct is derived from the Greek words for "inside anus," which is the defining characteristic of this phylum: Both mouth and anus open inside the tentacle crescent. Mucus on their ciliated tentacles traps plankton, then transports food to the mouth. Colonial, sessile entoprocts such as *Barentsia* sp. (A) form animal mats on seaweeds, rock, shell, sponges, and other animals in shallow waters. Most of the 150 species are marine; a few are freshwater. A horizontal stolon links individuals.

Entoprocts reproduce by means of fertilization of eggs by sperm. Like bryozoans (ectoprocts) and phoronids (see this page), entoprocts also reproduce by budding new individuals. In unfavorable environmental conditions some entoprocts shed their calyx, then regenerate it if conditions become favorable. Entoprocts, unlike bryozoans, fold their tentacles when disturbed. Some scientists believe that bryozoans and entoprocts are derived from a common ancestor and therefore should be united into a single phylum.

Phylum: Bryozoa

Bryozoans have a mouth surrounded by tentacles, a U-shaped gut, and ciliated larvae. In these ways the bryozoans, phoronids, and entoprocts depicted here resemble one another. What distinguishes bryozoans (ectoprocts) from phoronids and entoprocts and defines this phylum is that the anus of bryozoans opens outside the crown of tentacles. The term ectoproct comes from the Greek for "outside anus." Of the 4,000 bryozoan species, 3,500 are marine; the remaining are freshwater.

Colonial bryozoans thickly encrust marine shells, ship hulls, sea rocks, kelp, and other algae, such as *Sargassum*. Marine fish, such as the rock fish, *Sebastes serripes* (B), nibble bits of the soft sea bryozoans. Freshwater bryozoans form gel balls on branches that have fallen into lakes. The soft, living bryozoans individual secretes a nonliving shelter either of chitin—a tough, nitrogen-containing polymer—or of a rigid calcium carbonate skeleton overlaid with chitin, within which the body is anchored. The shelter is called a zooecium—literally, "animal house," from the Greek *zoo*, meaning "animal," and *oikos*, meaning "home." The calcified box within which a bryozoan such as *Bugula* sp. shown here (C) takes shelter may each be about one millimeter across; a colony makes up a massive array. Marine bryozoans play a small role as reef formers, along with corals (p. 126), molluscs, brachiopods, and calcareous marine algae.



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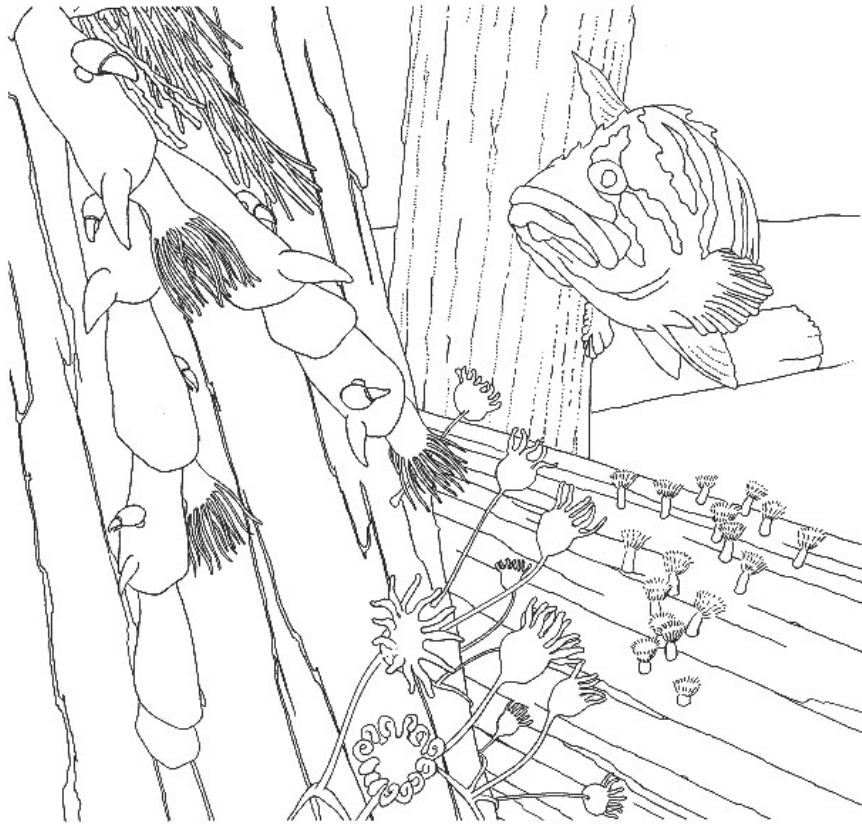
The few species of freshwater bryozoans survive dry and cold conditions by releasing armored balls of cells called statoblasts. Dispersed on bird feet, by wind and water, statoblasts initiate new bryozoan colonies. As the weather warms and the rivers begin to flow again in the spring, the statoblast opens and cells inside resume growth as new individuals.

Phylum: Phoronida

Phoronid worms secrete tubes with only one opening, strengthening the walls with bits of seashell and sand. On the anterior end of *Phoronopsis vancouverensis* (D) is a fully expanded lophophore—a

food-trapping ridge surrounding the mouth and bearing hollow, ciliated tentacles, which phoronids have in common with brachiopods (p. 138) and bryozoans. The lophophore draws detritus and plankton toward the mouth. The mouth opens within the lophophore; the anus opens outside. A phoronid is sedentary and snaps swiftly into its tube, which is about twice the length of the worm, using muscles coordinated by a giant nerve fiber. Both U-shaped gut and sheltering tube are adaptations to sessile life.

Fertilized eggs of some phoronid species are brooded between the adult's tentacles and there develop into ciliated larvae. Larvae swim free, disperse, and encrust pilings, rocks, shells, and ocean bottoms. Leathery or chitinous phoronid tubes can be seen protruding from soft sands or entwined like vermicelli. With only fourteen species in two genera, phoronids make up one of the smallest animal phyla. These yellow, pink, and orange filter-feeders are rare and cosmopolitan in the seas.



Sandy Marine Coast

Phylum: Sipuncula

Sipunculans are marine, sedentary invertebrates. Some species resemble a peanut when their introvert is withdrawn into the trunk; accordingly they are called peanut worms. Bushy, mucus-covered tentacles encircle the mouth at the introvert tip of some sipunculans, collecting suspended food particles, taking dissolved oxygen from sea water, and releasing ammonia (their main nitrogenous waste). In other sipunculans, a crescent of small tentacles gathers food. Like echiurans (see this page) and priapulids (p. 130), sipunculans extend their introvert—an anterior body part that can turn inside out to feed and completely withdraw into the trunk.

Some sipunculans form temporary burrows in soft sea sediments, as does the hemichordate *Saccoglossus kowalevskii* (A). Other sipunculan species occupy marine crevices. The sipunculan *Themiste lageniformis* (B), which nestles among corals (p. 126), extends its contractile introvert over the reef surface and scrapes off films of algae (p. 84) with hooks on its introvert. Sipunculans of shallow seas engulf sand as they burrow along; they rework marine sediments just as earthworms (p. 142) rework soil as they burrow through it eating the detritus. Organic matter dissolved in ocean water may provide up to 10 percent of the diet of sipunculans.

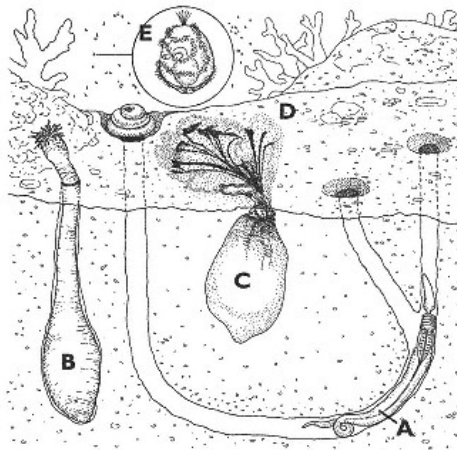
Cilia carry sipunculans' food—detritus, diatoms, larvae, or protoctists—along part of their intestine. The U-shaped digestive system terminates at the base of the introvert, a common internal pattern in burrow-dwelling animals.

Although the 150 sipunculan species are not very abundant locally—except on limestone reefs and rocky shores—sipunculans are widely distributed. They have been observed in the abyss at 7,000 meters deep in the sea, as well as in icy polar oceans, but most peanut worms reside in warm seas between tidemarks, among mangrove stilt roots and eelgrass, in empty mollusc shells, in annelid tubes, or under rocks. One sipunculan species lives inside a large sponge.

Phylum: Echiura

Echiurans are sedentary and marine, living among mangrove roots, rock crevices, or mud. The 140 species are called spoon worms because their proboscis resembles a spoon. An echiuran thrusts forth its grooved, motile, ciliated proboscis to gather detritus as food. An unusual echiuran of the Pacific Coast, *Urechis caupo* (literally, "the innkeeper"), is 50 centimeters long and spins a net within its burrow. This mucus web strains particles as small as 0.04 micrometers wide from sea water. Every several minutes, the innkeeper swallows its food-coated net, then secretes a fresh net.

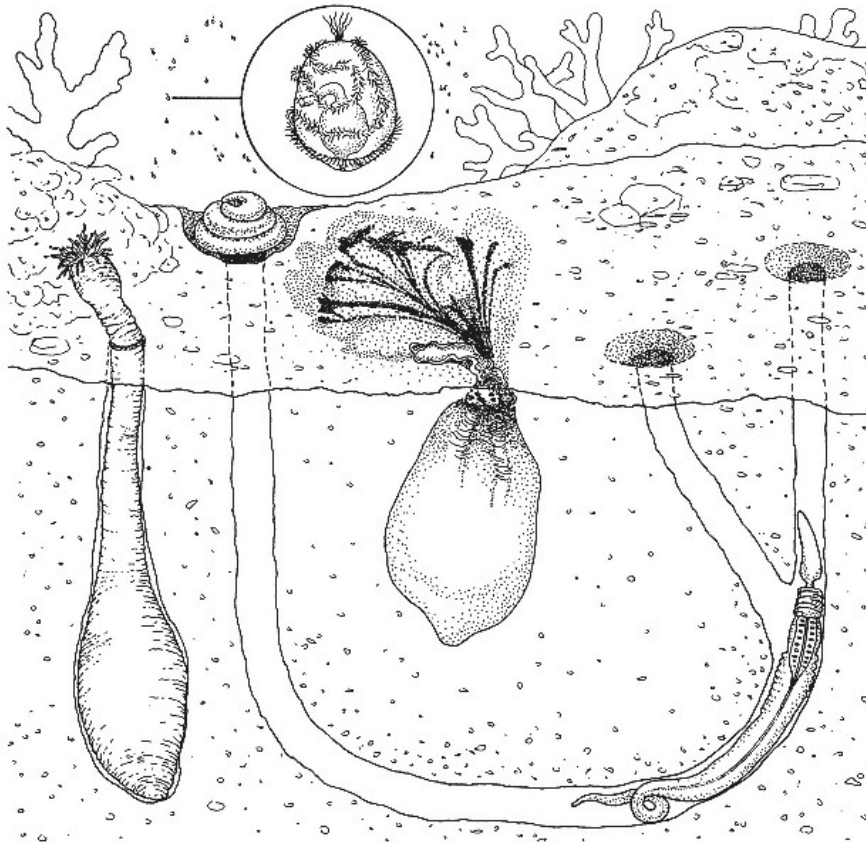
A burrowing echiuran pumps sea water through its burrow by alternately relaxing and constricting its trunk muscles; the currents of water oxygenate its blood, move food through the tunnel, and remove waste. *Urechis* is a suspension feeder; most other echiurans, such as *Listriolobus pellodes* (C), feed by scraping deposits—bacteria, algae, protoctists, and plant



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and animal parts—off the seafloor. The comma-shaped impressions (**D**) are feeding traces made by the echiuran as it sweeps its proboscis over the ocean floor in search of food.

Echiuran and sipunculan larvae greatly resemble the ciliated, free-swimming larvae of the hemichordate (p. 124) *Balanoglossus* (**E**).



California Rocky Intertidal Zone

Phylum: Mollusca

Familiar molluscs include scallops, snails, squid, and octopi. Molluscs comprise 50,000 species, one of the most diverse phyla. The greatest of these is the giant squid, perhaps twenty meters in length counting its sixteen-meter tentacles. The most minute is the size of a grain of sand. "Shellfish" is a culinary, not a biological term; it refers to various shelled molluscs, including clams, oysters, and mussels. (Molluscs are not fish, however; nor do all molluscs have a shell.) Mollusc bodies are soft and unsegmented; most have an internal or external shell. All molluscs also have a mantle, a fold in the body wall that lines the shell and secretes the calcium carbonate of which the shell is made. The radula is a unique molluscan structure; this hard, chitinous strap bores and scrapes like a file and is used to gather food.

Molluscs live in mud and sand flats, forests, soils, rivers, lakes, and the abyss of the sea. Certain species are commensals or parasites of annelids, echinoderms, crustaceans, and sea squirts. Molluscs are divided into groups, including gastropods, cephalopods, chitons (polyplacophorans), bivalves (pelecypods), and the less familiar tooth shells (scaphopods), monoplacophorans and aplacophorans.

The gastropods include the black abalone, *Haliotis cracherodii* (A, shown here being eaten by a sea otter); the naked shell-less slug, the purple nudibranch, *Flabellinopsis iodinea* (B); and terrestrial molluscs. Cephalopods include the common squid, *Loligo pealei* (C); the Pacific giant octopus, *Octopus dofleini* (D); and *Nautilus* (p. 130). Bivalves (having two shells or valves), such as the California mussel, *Mytilus californianus* (E), are members of the class Pelecypoda. Chitons, such as *Stenoplax* sp. (F), belong to the class Polyplacophora; they have eight distinctive external shells—overlapping plates embedded in their mantle.

The octopus and squid, both cephalopods, show the head and mantle of molluscs most clearly. A calcareous shell shelters the more sedentary molluscs, such as the abalone (A) cradled on the chest of the otter (J). Descending into the sea, chitons, mussels, and limpets (G) cling to rocks. Although at first glance the barnacle (*Balanus*, H) appears to be a shelled mollusc, closer inspection reveals that its legs are jointed, a feature characteristic of crustaceans (p. 152). A forest of *Laminaria* (I)—a brown marine alga or phaeophyte (p. 62)—carpets this rocky subtidal zone of the California sea otter's world.



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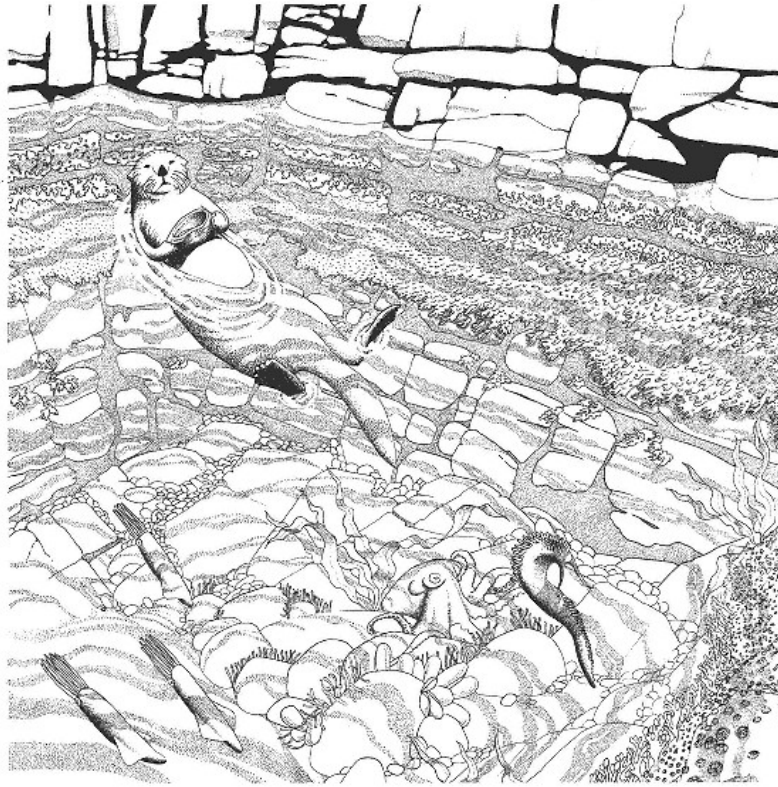
Phylum: Craniata

The craniates include mammals (4,500 species), birds (9,000 species), reptiles (6,300 species), amphibians (4,200 species), and fish (25,000 species)—the most visible animals. All craniates, such as the sea otter (*Enhydra lutris*, J), have a skull called a cranium that encloses the brain. Craniates also have a pharynx with gill slits, a notochord, and a hollow dorsal nerve cord at some time during their life history. The term craniate comes from the Greek word *kranio*, meaning "skull." Craniates were formerly grouped with chordates that lack a skull—Urochordata (tunicate, p. 36), and Cephalochordata (p. 133)—in phylum Chordata.

The gill slits of otters and other mammals close during embryonic development; fish and an amphibian, the axolotl, retain permanent gill slits. The notochord, a flexible dorsal support rod that runs from head to tail, is permanent in adult hagfish and lampreys (class Cyclostomata) and sharks and other cartilaginous fishes (class Chondrichthyes). All craniates belong to the subphylum Vertebrata. In adult vertebrate animals, including otters, the extinct dinosaurs, and humans, a segmented vertebral column—the familiar neck and back bones—replaces the embryonic notochord.

Humans (members of the genus *Homo* and species *sapiens*) have notochords only before birth in the fetal stages of life. Bony fish, amphibians, reptiles, birds, and mammals have bony vertebrae. The dorsal hollow nerve cord that characterizes chordates is the spinal cord of humans. Nonchordate animals with well-developed nervous systems differ distinctly from chordates—nonchordates have solid nerve cords on the ventral (belly) side of their bodies rather than on the dorsal (back) side.

The rainbow bee-eater, lesser flamingos, Ituri chameleon, Atlantic Queen angelfish, and lined sea horse in the cover illustration exemplify the diversity of craniates.



Costa Rican Tropical Forest at Night

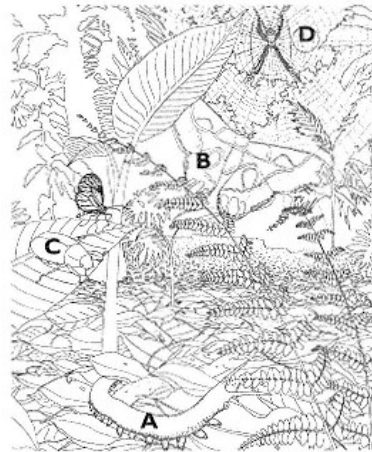
Phylum: Onychophora

Onychophorans are commonly called velvet worms because the textured, thin cuticle feels like velvet. Many onychophorans are brown, although some are iridescent blue, green, orange, red, or white. *Peripatus* sp. (A) ventures forth in the night or rain to feed in wet, warm woods such as this Costa Rican forest, moving on fourteen to forty-three pairs of hollow, unjointed legs. Carnivorous onychophorans hunt wood lice, terrestrial molluscs, and spiders. The eyes of onychophorans have a retina and a lens; they determine the direction of predators and prey. Champion spitters, these velvety animals rear up and spit whitish fluid 80 to 300 millimeters—farther than their body length of 14 to 200 millimeters—at prey. Adhesive glands secrete the fluid, which gels in contact with air, tangling prey in a sticky net. An onychophoran bites trapped prey, then secretes saliva into the prey, which kills and partially liquefies it. All of the 100 species in this phylum for which eating habits have been observed are carnivorous.

Onychophorans may have originated from segmented ancestors of annelids or onychophorans may link annelids with arthropods. Evidence supporting these affiliations is drawn from many facets of onychophoran biology. For example, both velvet worms and centipedes (myriapods) use adhesives to capture prey. Each velvet worm body segment has a pair of nephridia (excretory organs); annelid excretory organs are arranged similarly. Velvet worm fossils have been elusive because velvet worms have no bones; fossil mandibles discovered recently in China may be onychophoran.

Phylum: Mandibulata

Mandibulate arthropods (from the Latin for "joint-footed") include insects, such as this saturniid moth, *Rothschildia lebeau* (B), and myriapods (centipedes and millipedes). The distinguishing feature of mandibulates is a single pair of antennae; mandibles (crushing jaws); and three distinct body parts—head, thorax, and abdomen. Most are terrestrial, such as termites (p. 72) and, besides bats and birds, only insects have evolved flight. The golden beetle (*Plusiotis resplendens*, C), like other mandibulate arthropods, is distinguished by unbranched appendages that consist of a series of jointed segments. Approximately one in every four known species is a beetle; 350,000 beetle species have been described. Tropical biologist Terry Erwin estimated 163 species of beetle in one tree species alone in the rain forest. He estimated that tropical forest is home to 30 million arthropod species, most of which are insects. Worldwide, 751,000 species of insects, 10,000 species of millipedes, and 2,500 species of centipedes have been described, as well as 123,000 species of noninsect arthropods such as crabs and ticks (chelicerates, see p. 151).



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Formerly, mandibulates, crustaceans (p. 152), and chelicerates were united in one great arthropod phylum; we separate them into three separate phyla because each may have arisen independently. Mandibulates, crustaceans, and chelicerates share characteristics common to all arthropods: The cuticle contains chitin, the body cavity (hemocoel) is fluid-filled and is part of the circulatory system, the tubular heart opens via slits called ostia to the hemocoel, and the exoskeleton is segmented.

Collectively the arthropod phyla have the largest number of described species in the animal kingdom.

Phylum: Chelicerata

Chelicerates include spiders, scorpions, mites, ticks, harvestmen, horseshoe crabs, and sea spiders. The silver argiope, *Argiope argentata* (**D**), hangs head downward in the center of its web. Like all chelicerates, it has anterior feeding appendages called chelicerae, and two main body segments—a cephalothorax with four pairs of attached legs, and an abdomen. The pair of chelicerae rip food into small bits. Chelicerates lack antennae, unlike all insects, which have a single pair of antennae, and all crustaceans, which have two pairs of jointed antennae.

The horseshoe crabs are ocean-dwelling chelicerates. Fossil horseshoe crabs abound in Paleozoic ocean deposits. They may be the ancestors of spiders and their arachnid kin—scorpions, ticks, and mites.

Chelicerate habitats are diverse: sea spiders have been seen down to 6,800 meters deep in the ocean, horseshoe crabs paddle in shallow coastal waters, spiders are mostly terrestrial with a few freshwater species, and ticks and mites consume fungi, plants, vertebrate blood, and invertebrates. Scarcely visible to the eye, the follicle mite *Demodex folliculorum* lives in the hair follicles of most healthy humans.

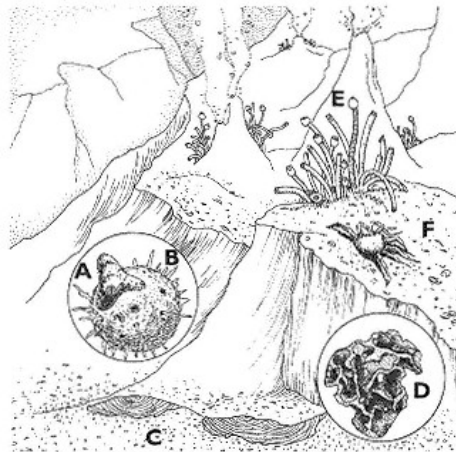


Marine Abyss

Phylum: Pogonophora

This dark community of tube worms, crabs (crustaceans), and clams (molluscs, p. 148) functions far below the sun-driven food webs on the thin skin of Earth. In these submarine gardens, sea vents spew steam and hot water as much as 2.5 kilometers below the ocean surface. Pogonophorans—also called beard worms—and the stouter vestimentiferans gain life-supporting energy by means of symbiotic bacteria that oxidize sulfide and methane. (The oxygen involved originates at Earth's surface.) Tube worms such as *Riftia pachyptila* (E) are supported by bacteria packed in a brown, spongy organ within the tube worm's trunk. These bacteria oxidize methane and sulfide. The worm may either absorb soluble organic molecules synthesized by the bacteria or may digest some of the bacteria. The slender pogonophorans may be nourished by soluble molecules such as amino acids and fatty acids absorbed through the plume of tentacles that projects from their tough tubes, but probably they also depend on symbiosis with the bacteria that pack their midgut.

From the tiniest (0.75 millimeters long) to the giant (1.5 meter long) members, all 120 or so species in this phylum lack gut and mouth as adults. Free-living bacteria may pass through the transient mouth of the young worm, then later reproduce and pack the midgut (trophosome) of the tube worm. Animals of most other phyla derive energy and nutrients such as nitrogen, carbon, and phosphorus from organic compounds; such organisms are heterotrophs. In contrast, pogonophorans harbor chemoautotrophic bacteria (p. 40) within their bodies and are autotrophs (self-feeders)—organisms that grow and synthesize organic compounds by oxidizing inorganic compounds such as sulfur-containing compounds. Hydrogen sulfide is generally poisonous to animals; pogonophorans bind the sulfide reversibly so that they are not poisoned as they transport the sulfide from their tentacles to their bacterial symbionts. As explorations continue, our understanding of the diversity of life in the abyss grows.



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Three billion years in the past, hydrothermal vents belching forth sulfides and methane were probably typical environments for pogonophorans. (See page 66 for a discussion of the xenophyophores A, B, C, and D.)

Phylum: Crustacea

Two pairs of antennae distinguish crustaceans from chelicerates and mandibulates (see previous page). Approximately 45,000 species comprise this phylum. Members include pill bugs (p. 142), barnacles (p. 148 and cover), amphipods (p. 104), pentastomes, and crabs (F). On crabs and lobsters the branched appendages of crustaceans are readily visible; these distinguish crustaceans from mandibulates. In the lobster a careful observer can also see the feathery gills with which crustaceans typically obtain oxygen dissolved in sea water. In comparison, most insects such as the leafhopper (see cover illustration) extract oxygen from air that passes into thin tubes called tracheae that pass

through their cuticle into their tissues. Readers who have attempted to snatch crayfish from under rocks in freshwater will bear witness that crayfish are quick—crustaceans' striated muscle contracts more rapidly than the smooth muscle found in most nonarthropods.

The external covering, sometimes called a shell, in lobsters, for example, is a cuticle strengthened by deposition of calcium carbonate. Insect cuticle lacks this hardening, but a horseshoe crab shares it. Wax and protein on the outer layer of the crustacean cuticle impart impermeability. When it molts, a crustacean sheds its external cuticle, accommodating growth.



Chapter 5— Plantae

All species in Kingdom Plantae are eukaryotic, multicellular organisms that develop from diploid embryos enclosed in maternal tissue. Plant embryos result from sexual reproduction—the fertilization of a female gamete (egg or embryo sac nucleus) by a male gamete (sperm or pollen nucleus) (figure 15). In addition, some plants reproduce without fusion of gametes by forming new individuals called plantlets or gemmae. A strawberry plant reproduces by forming horizontal stems on which new individual plantlets grow. Mosses and liverworts can also reproduce without fusion of gametes—the parent moss plant produces gemmae, which are tiny balls of cells that form new individual mosses. Adult diploid plants are called the sporophyte and produce haploid spores by meiosis. From these spores, haploid organisms grow. These haploid plants are gametophytes—they form gametes. The gamete-forming haploid phase of the plant life cycle generally alternates with the spore-forming diploid phase. The gametophyte is said to be dominant—that is, of longer duration and generally more noticeable—in mosses, but the sporophyte dominates in flowering plants and conifers. Embryos of all land plants are protected from desiccation by maternal tissues that range from a jacket of cells in mosses to an exposed seed in conifers to a fruit-enclosed seed in flowering plants. Plants never develop from blastula embryos; blastulas are characteristic only of animals.

Plant cells usually have green plastids (chloroplasts); these are cytoplasmic, photosynthetic, pigmented organelles. Photosynthesizing bacteria, in comparison, lack plastids. In the process of photosynthesis, plants use enzymes within their plastids to synthesize organic compounds from inorganic compounds and carbon dioxide, producing as a by-product the oxygen that sustains the biosphere. One such organic compound is the cellulose present in plant cell walls. Most plants obtain energy for photosynthetic processes from sunlight; and most plants are autotrophs. Autotrophs are organisms that synthesize the nutritive substances that they require from inorganic substances. Carnivorous plants photosynthesize and supplement their low nitrogen source by trapping and digesting insects or small mammals. The sundew *Drosera* is a

carnivorous plant that traps and digests bog insects as its nitrogen source. A few plant species are saprophytic and parasitic. These procure nourishment from other plants. Two examples are *Cuscuta* (dodder) and pinesap, *Monotropa hypopithys* (see cover). A familiar parasitic plant of temperate northern forests is *Epifagus* (beechdrops); it takes up nutrients from the roots of its host, the beech tree.

Plant cells lack the complex cell junctions that commonly link animal cells to one another. Plasmodesmata—cell-to-cell interconnections—link the walls of adjacent plant cells and are sufficiently large that macromolecules such as sugar pass through the plasmodesmata by way of strands of cytoplasm. Even though plants lack nervous systems, some plants respond to light, touch, or pheromones—molecules that transmit chemical messages between individual plants. *Helianthus* (sunflower) gets its scientific and common names from its ability to turn to face the sun as it traverses the sky. *Mimosa pudica* (sensitive plant) closes its leaves and leaflets in response to touch. The basis of its response to mechanical stimulation is a change in turgidity of special cells at the leaflet base in response to touch and to movement of sucrose, water, and potassium ions. The resulting change in turgidity causes the leaf base to act like a hinge, closing leaves and leaflets.

An aggregation of cells that have similar functions and are organized into a structural and functional unit constitute a tissue. For example, vascular tissue is a complex tissue comprising four cell types that have a common function—transport of nutrients and water upward from the roots and sugars downward from the leaves. Flowering plants have vascular tissues running through their leaves, stems, and roots; specialized reproductive tissues such as those that produce gametes; and storage tissues in various structures—seeds, tubers as in potatoes, roots as in beets, and enlarged leaf bases as in garlics. Tissues of most land plants avoid dryness by a noncellular wrapping called a cuticle. Terrestrial plants require supporting tissues to withstand wind and to counter gravity. In familiar woody shrub, vine, and tree species, this support tissue contains lignin, a polymer that strengthens the wood and holds the plant upright. (In contrast, water supports aquatic organisms.) Humans utilize the strength of plants for their own purposes when they choose wood as a building material and linen for clothing.

Plants are subdivided in our classification into two groups: nonvascular plants, which lack lignified xylem and phloem; and vascular plants (tracheophytes), which have vascular tissue. Tracheophytes include nine phyla: club mosses (Lycophyta), whisk ferns (Psilophyta), horsetails (Sphenophyta), ferns (Filicinophyta), cycads (Cycadophyta), ginkgo (Ginkgophyta), conifers (Coniferophyta), gnetophytes (Gnetophyta), and flowering plants (Anthophyta). Nonvascular plants include three phyla: mosses (Bryophyta), liverworts (Hepatophyta), and hornworts (Anthoceroophyta). Mosses, hornworts, and perhaps liverworts have lignin-like molecules in their transport cells but lack lignified cells. Water moves into a moss by diffusion from the moist environs and is conducted within the moss by transport cells that are not stiffened by lignin.

Plants are also further subdivided into those that bear seeds: cycads, ginkgo, conifers, gnetophytes, and flowering plants; and the nonseed plants: ferns, horsetails, whisk ferns (Psilotum), club mosses, hornworts, liverworts, and mosses. By the Devonian period, about 360 million years ago (Figure 8), seed plants had evolved. By the time of the dinosaurs—the Triassic, Jurassic, and Cretaceous periods of the Mesozoic era—forests of plants that bear seeds but not flowers—cycads, ginkgos, conifers, and other

gymnosperms—dominated the forests. Flowering plants evolved during the Cretaceous period. The ways that seeds form are immensely diverse. Seed formation in cycads is among the most spectacular in the plant kingdom: cycad cones of both sexes produce heat as well as odor, and male cycad cones produce pollen that releases giant swimming sperm. Beetles transport the pollen grains from the male to the female cycad cones (p. 164). All seeds contain the new sporophyte generation as well as stored food that will contribute to development of the embryo within the seed. Seeds such as cycads and mango contain sugars and oils as food rewards to animals that eat them; when an animal defecates the seed remnants in feces, the animal disperses the embryo plant. If the embryo lands in a suitable habitat, it will grow into a new plant.

Classification schemes of plants are derived from various sources of evidence: form (morphology), pattern of embryonic development, chromosome makeup, molecular biology, and biochemistry of both living (extant) plants and plant fossils. The most ancient plantlike fossils appear in rocks dated as 430 to 408 million years old (Silurian period). Some plant fossils are imprints of leaves and stems, other fossils are pollen or 120-million-year-old flowers. In 400 million-year-old black silica rock called the Rhynie chert, botanists observe microscopic details such as vascular tissue in plant stems, spore-bearing structures at plant stem tips, and fungi within plant roots. Evidence from both the fossil record and from living plants leads to the conclusion that plants and green chlorophyte algae share common ancestors. The cells of green land plants often are interconnected by plasmodesmata, like cells of their green algal ancestors (Chlorophyta in Kingdom Protocista, p. 84).

This book classifies plants into twelve phyla. Among these phyla, plants are distributed unevenly in total number of individual plants and in number of plant species. As with all sexually reproducing organisms, a species is defined as a population of organisms that interbreed readily with one another under natural conditions. The diverse members in the plant kingdom are listed here in order of increasing number of species currently known in each phylum.

1	ginkgo (Ginkgophyta)
3	whisk ferns (Psilophyta)
15	horsetails (Sphenophyta)
70	gnetophytes (Gnetophyta)
100	hornworts (Anthocerophyta)
185	cycads (Cycadophyta)
550	conifers (Coniferophyta)
1,000	lycophytes (Lycophyta)
6,000	liverworts (Hepatophyta)
10,000	mosses (Bryophyta)
12,000	ferns (Filicinophyta)
230,000	flowering plants (Anthophyta)

The total of all living species of plants currently named and described—about 270,000 species—is considerably lower than the 1,032,000 animal species. Indeed, the plant species number is less than the approximately 290,000 living species of beetles

(Coleoptera). Bear in mind that the number of described species is often a function of the perceived economic value of a particular group of plants and of the number of specialists trained in their classification.

Are the habitats of plants as diverse as the habitats occupied by animals? Because of the requirement of solar energy for photosynthesis, a green plant never lives with its entire body in soil or in water below the depths to which sunlight penetrates. As a consequence, plants are absent from deep freshwater as well as from the deep salt-water habitat of most animal phyla. Green plants are primarily terrestrial. The embryo and symbiotic partnerships are two factors that promoted the spread of plants from the seas to freshwater and, subsequently, to land. Evolution of the plant embryo enclosed in tissue of the maternal plant provided protection from desiccation and from other terrestrial hazards. The symbiotic partnership between fungi and the green algal ancestors of plants facilitated water and mineral uptake. Plants live in freshwater lakes and streams, deserts, and other land surfaces. Pelted by waterfalls or caked in winter ice, many liverworts and mosses pass their lives in water. The wettest plant habitat is the muddy Alakai Swamp in the mountains of the Hawaiian island of Kauai. The Alakai is drenched with 1500 centimeters of rain each year and has the heaviest mean annual precipitation based on long-term records. At the other extreme, the habitat of *Welwitschia* (p. 170) is one of the most harsh deserts on the face of this planet, the Namib desert in Africa, with only 3 to 100 millimeters of water annually. Plants live neither in air alone nor in hot springs, but a number of plant species disperse spores (ferns), pollen (corn), and winged seeds (maples) through the air. An estimated 28,000 known plant species—many tropical—are epiphytes, which grow on the surface of other plants. The resurrection fern (*Polypodium polypodioides*) is an epiphyte that perches on limbs of the live oak tree. No plant lives completely within the internal tissues of other plants, fungi, or animals. A few parasitic plant species such as dodder (*Cuscuta*) have lost chlorophyll. Plants such as the nipa palm, mangrove, and the coconut palm thrive at the ocean's salty rim. The coconut palm and red mangrove disperse seeds with flotation layers that survive floating in sea water. Emergent plants such as fragrant waterlily (*Nuphar advena*) grow rooted in shallow freshwater with some leaves submerged and other leaves and flowers floating on the water surface. Churning of the shallow water habitat of waterlilies by watercraft motors is extinguishing this lovely plant from many lakes.

Some locally rare orchids have been discovered in the most recently explored tropical ecosystems. Orchid species (about 24,000) make up nearly 10 percent of all flowering plants and contribute greatly to plant diversity. Some orchids inhabit temperate bogs and forests. Tropical orchids are particularly abundant in moist cloud forests of South and Central America.

The smallest flowering plants are duckweeds (*Wolffia*—less than one millimeter across. These minute stemless fronds float like green grains on the surface of quiet temperate and tropical waters. The giants of living plants are conifers: coastal redwoods (*Sequoia*) and giant sequoia (*Sequoiadendron giganteum*). The coastal redwood of the Oregon and California coast is the tallest organism on Earth; the tallest specimen measures 113 meters in height. The plant with the greatest bulk is the giant sequoia, which attains eight meters in width, 100 meters in height, and an estimated weight of 1.2 million kilograms (1,350 tons) in the Sierra Nevada mountain forests of northern California.

Of the quarter million known plant species, only 150 provide most of the food, fiber (cotton, linen, ramie), plant oils, and wood used by humans. Supplying most of the calories of the human population are banana, coconut, the legumes soybean and bean, sugar cane and sugar beet, white potato, sweet potato, and manioc (cassava, tapioca), as well as the major cereal crops of corn, rice, and wheat. Exploration by economic botanists such as the late Julia Morton has catapulted to our attention wild plants with medicinal importance. Alkaloid compounds (vinblastine and vincristine), which are effective against lymphocytic leukemia and Hodgkin's disease, come from the rosy periwinkle (*Catharanthus roseus*), native to Madagascar. The medicine taxol from the Pacific yew (*Taxus brevifolia*), a potent anti-ovarian cancer drug, comes from a conifer once regarded as a junk tree in forests of the Pacific northwest. From the Andes comes the coca plant (*Erythroxylon coca*), the source of cocaine, a local anesthetic. A wild yam contains a natural compound that can be converted to progesterone, a substance that suppresses ovulation and is the basis for the birth-control pill. Like progesterone, at least 25 percent of our prescription medicines are natural substances synthesized by seed plants, compared to 13 percent synthesized by microbes. Indigenous people have utilized the medicinal qualities of thousands of plant species for generations. The medicinal properties of ginkgo (see the cover illustration) have been fine-tuned in 5,000 years of Chinese healing practice; Western medicine has only recently been willing to investigate ginkgo's medically active compounds. Fewer than three percent of the flowering plants have been screened for alkaloids—organic, nitrogen-containing compounds produced by plants. Many alkaloids are physiologically active in animals and, therefore, have potential medicinal value. Of the 121 biologically active plant-derived medicinal compounds in current use, 74 percent were uncovered by research to verify ethnomedicinal use (Soejarto and Farnsworth, 1989). As pharmaceutically active compounds are identified in wild plants, plant diversity of tropical rain forests and the botanical knowledge of indigenous people are viewed as a priceless resource of new pharmaceuticals.

Where on Earth is plant diversity highest? Fauna and flora together of rain forests (moist tropical forests) comprise half of the number of species on this planet; this species-rich ecosystem occupies about 6 percent of the surface of our globe. Three to thirty million plant and animal species live in tropical forests, 120,000 of the 155,000 tropical seed plants are species of moist tropical forest (rainforest)— $\frac{3}{5}$ in tropical America, $\frac{1}{5}$ in tropical Asia, and $\frac{1}{5}$ in Africa (Soejarto and Farnsworth, 1989). Tropical richness is exemplified by botanist Alwyn Gentry's census of around 300 species of trees growing in each of two one-hectare sample plots in Iquitos, Peru; in comparison, about eight tree species grow in one hectare of New Hampshire woodland.

Hybridization and polyploidy generate plant diversity. Polyploidy is the duplication of chromosome sets in either of two ways—in a single individual organism or following the hybridization of two species that were previously distinct. Polyploid individuals arise spontaneously, but can also be generated by chemicals such as colchicine. Polyploid species constitute more than half of the total plant species, including many that impact human well-being profoundly, such as cotton cultivated for fiber, bread wheat, bananas, potatoes, sugar cane, and chrysanthemums. Hybridization between species, like polyploidy, sometimes generates plant species with advantageous characteristics compared to those of the parents; for example, hybrid oaks that grow more vigorously than either parent.

What is the current status of plant biodiversity? Botanists at the Smithsonian Institution announced results of the first global census of plant diversity in 1998. The survey found that habitat fragmentation, cutting and burning, and pollution endanger one in eight plant species worldwide, including more than 4,640 seed-bearing plants and ferns in the United States.

Incentives to maintenance of biodiversity include economic incentives such as sustainable harvest of wild plants: medicines such as tubocurarine (the drug used to temporarily paralyze patients during surgery) from *Chondodendron*; fiber such as the coir in doormats from coconut palms; oil from the babassú palm (*Orbignya phalerata*), which grows in the Amazon forest; and Brazil nuts from *Bertholletia excelsa*, a tree of the Amazonian rain forest. Plant biodiversity has nonconsumptive value as well—ecotourism is growing rapidly. Undisturbed natural ecosystems preserved for large (redwoods) or highly visible (wild orchids) species tend to preserve less spectacular vegetation along with the watersheds and other native organisms of the natural community. The species diversity of wild plants is an irreplaceable resource as the genetic storehouse of life.

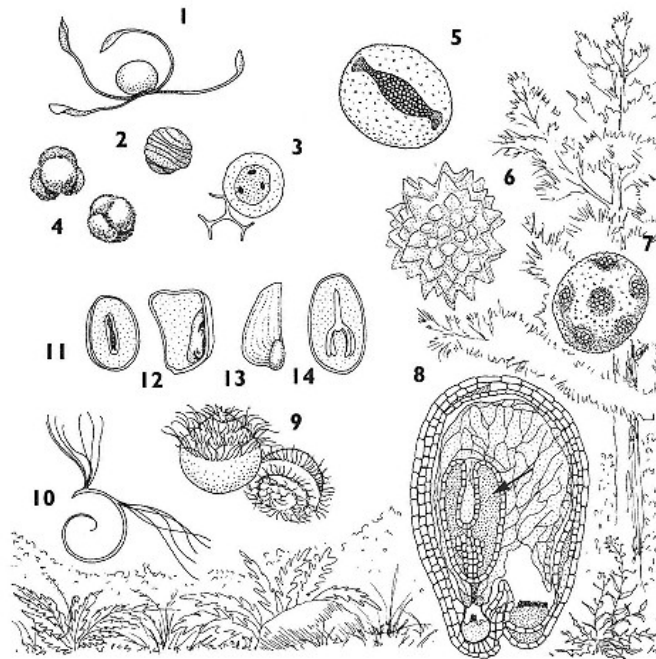


Figure 15

Plant reproductive structures. **Spores:** *Equisetum* sp., horsetail, with elaters open (1) and coiled (2); microspore of *Ginkgo biloba*, and empty tetrad walls (3); *Sphaerocarpos* sp., liverwort (4). **Pollen grains:** *Cometes surattensis* (5); *Pelucha trifida* (6); *Cerastium alpinum* (7). Horseshoe-shaped **embryo** (arrow) within seed of flowering plant *Capsella bursa-pastoris*, shepherd's purse (8). **Sperm:** *Zamia* sp., coontie, a cycad (9); *Polytrichum juniperinum*, haircap moss (10). **Seeds:** generalized dicot (11) and monocot (12) seeds; winged seed (13) and longitudinal section of *Pinus* sp., pine, conifer seed with embryo (14).

Woods

Phylum: Bryophyta

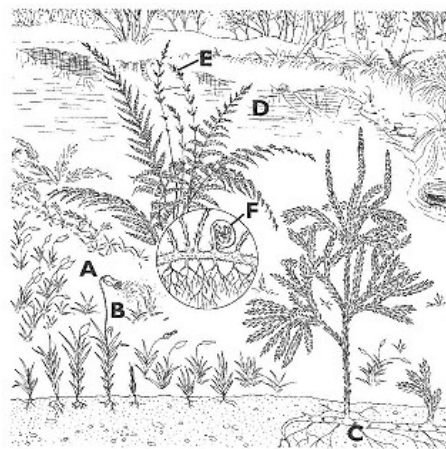
The most common bryophytes (low-lying, leafy, nonvascular plants) are the mosses (class Musci), such as *Polytrichum juniperinum* (**A**), haircap moss. Mosses closely resemble their protist chlorophyte ancestors (p. 84)—both have sperm that are dependent on water and pigments that are similar in molecular structure. Although the familiar form of flowering plants (p. 172) and other vascular plants is the spore-bearing (sporophyte, diploid) generation, the most familiar form of mosses is the gamete-bearing (gametophyte, haploid) generation.

Sexual reproduction in bryophytes requires moisture in which the male gametes—the sperm (each with two forward-directed undulipodia, *Polytrichum* sperm, p. 161)—travel from the male sex organs (antheridia) to the female sex organs (archegonia) that produce female gametes. The archegonia usually harbor unfertilized egg cells at the tip of the female gametophyte. After the sperm fertilizes the egg, the zygote forms in the archegonium. From the zygote the sporophyte develops (**B**), with its slim stalk topped with a spore capsule. Spore capsule and stalk are the sporophyte generation. Spores, produced in the capsule by meiosis, are released and develop into a leafy green gametophyte. Alternation of gametophyte and sporophyte is universal in plants.

Sphagnum moss of peat bogs and about 10,000 other moss species grow throughout the world in bogs, forests, and the Arctic tundra; no moss is completely marine. Mosses together with other nonvascular plants, such as liverworts (phylum Hepatophyta) and hornworts (phylum Anthocerophyta), total about 16,100 species.

Phylum: Lycophyta.

The lycophytes known as lycopods, club mosses, or ground pines are represented by the genus *Lycopodium* and live throughout temperate forests worldwide. Others, such as the quillworts (*Isoetes*), are less common. These nonflowering vascular plants have distinctive sterile evergreen leaves called microphylls ("little leaves") that probably evolved as outgrowths of the main photosynthetic axis.



Kathryn Delisle

Lycopods alternate sporophyte and gametophyte generations. The underground rhizome of *Lycopodium obscurum* (**C**) connects the above-ground, green branches of the herbaceous sporophytes. Some species of club mosses have their sporophylls interspersed among the evergreen leaves. Atop the sporophytes of other lycophytes such as the species illustrated here are cones called strobili, which bear spore-forming organs called sporangia, on fertile leaves. Meiosis within the sporangia produces haploid spores. Spores drop to the soil, where they germinate to form the gametophyte. The haploid gametophytes grow from the spores and are often subterranean, living in symbiosis with mycorrhizal fungi. Club moss gametophytes produce eggs and swimming sperm. The embryo results from fertilization and develops into the photosynthesizing sporophyte.

Although strobili are club-shaped, club moss is a misnomer because lycopods are not mosses. Huge woody ancestral lycopods were the size of trees; many of these species dominated the wet coal-forming forests of the Car-

boniferous period. Contemporary lycopods comprising perhaps 1,000 species are denizens of temperate coniferous and deciduous forests, the dry southwest of the United States, and also live as epiphytes in the tropics.

Phylum: Filicinophyta

Ferns are the most widespread and well known of the seedless, vascular plants. Ferns have distinctive megaphylls ("big leaves") (**D**)—large, photosynthetic structures that develop and disperse spores. Megaphylls, with their web of veins, differ from the tiny, single-veined microphylls of mosses. In the life cycle of a fern, a small, heartshaped gametophyte produces eggs and/or motile sperm. If fertilization takes place, the embryo begins the familiar sporophyte (**D**) generation.

Some fern species, such as the cinnamon fern, *Osmunda cinnamomea* (**E**), produce sporangia on a separate stalk; other species form clusters of sporangia on the undersides of their leaves. An underground stem called a rhizome develops a bud called a fiddlehead (**F**) in the spring. Many of the 12,000 species of ferns are tropical and epiphytes. Some ferns, such as the tiny *Azolla*, grow on the surface of water. In wet rice fields, photosynthesizing bacteria that live in *Azolla* supply nitrogen to the rice. In the plant kingdom, the number of species per phylum of ferns, as a measure of diversity, is second only to that of flowering plants.



Florida Bush

Phylum: *Hepatophyta*

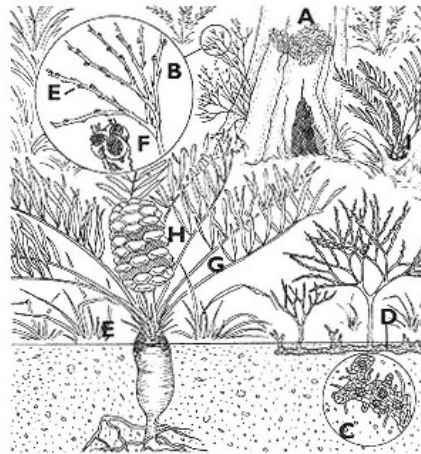
Many liverworts, as members of this phylum are called, are distinguished by their lobe-shape, similar to the shape of the liver. These nonvascular, nonflowering seedless plants—about 6,000 species—live in tropical and temperate habitats in fresh running streams and waterfalls, as epiphytes on tree trunks and branches, in moist soil, and on rocks and logs.

The lobed liverwort gametophyte is called a thallus; the thallus is thick in certain species known as the "leafy liverworts" or thin as in "thallose" liverwort species, such as *Marchantia* (A). From the lower thallus surface, single-celled rhizoids anchor the thallus, absorbing minerals and water. Liverworts usually are less than 5 centimeters in height, a size limit imposed by their lack of vascular tissues, stem, roots, and water-resistant cuticle.

Liverwort reproduction resembles moss reproduction—gametophyte alternating with sporophyte. Stalked reproductive structures develop on the thallus and bear archegonia, female organs, or antheridia, male organs. The liverwort sperm produced in the umbrella-like antheridium is carried by rain to an egg produced in the archegonium on a separate thallus.

After fertilization, and still connected to the female gametophyte, the liverwort embryo develops a sporophyte. The liverwort sporophyte consists of a tiny capsule under the umbrella of the female. Inside the capsule meiosis produces haploid spores. When environmental conditions are favorable, the capsule opens, discharging spores. Animals, wind, and water help to disperse the tiny spores. The liverwort spore germinates into a thallus, the young gametophyte.

Liverworts also reproduce by fragmentation: bits break free and give rise to new individual liverworts. Mosses and liverworts share this mode of reproduction and also give rise to new plants by production of little green spheres called gemmae. Gemmae grow in little cuplike organs on the liverwort thallus; later, raindrops disperse the gemmae.



Kathryn Delise

Phylum: *Psilophyta*

This phylum consists of just two living genera, one of which is the whisk fern, *Psilotum* (B). Plants of this genus of seedless vascular plants are unique; they lack both leaves and roots, giving them a resemblance to the earliest vascular plants, the rhyniophytes, although whisk ferns are linked by DNA similarities to a fernlike ancestor. Psilophyte branches and stem grow in a simple forking pattern. Like the other plants, psilophytes alternate sporophyte and gametophyte. The sporophyte is diploid and is the prominent form, developing small sporangia that shed spores. These spores are haploid and develop into gametophytes (C) that are inconspicuous, bisexual, subterranean plants bearing both female and male reproductive organs. Endomycorrhizae, which are fungal connections that have subterranean, rootlike projections, live within both gametophyte and sporophyte. As with *Lycopodium* (p. 162), whisk ferns grow from a rhizome (D), an underground stem. Sporangia, borne along the stem in groups of three called synangia (E), produce spores (F). The two genera of the leafless, herbaceous psilophytes live in the tropics and subtropics.

Phylum: Cycadophyta

Cycads are classified into about 185 living species. Cycad seeds are exposed (naked, not inside a fruit); therefore, cycads are grouped as gymnosperms along with conifers, ginkgo, and gnetophytes. Cycads are vascular plants that have fern- or palmlike leaves and produce seeds but neither fruit nor flowers. Most cycads are shrubs and small trees of the tropics and subtropics. *Zamia* (coontie, **G**), grows in Florida and Georgia where native vegetation has not been destroyed and is the only cycad native to the continental United States.

Nitrogen-fixing symbiotic bacteria live in cycad roots. The nitrogen that these microbes "fix," that is, make available to their plant host, may enable cycads to inhabit nitrogen-poor habitats.

Most cycads are dioecious, meaning male and female are different individual plants. The cycad female gametophyte is a few cells that produce egg cells in the female cone (**H**). The male cone (**I**) produces pollen grains; these are immature male gametophytes. Pollen is carried by beetles to the female cone. Wind also carries pollen from male to female. Sperm are liberated from the germinating cycad pollen grains (see Figure 15, p. 161). These giant, motile plant sperm are almost 0.5 millimeter in diameter. Cycad sperm are drawn by a pollination droplet to a fertilization chamber containing the egg. If fertilization results, the embryo is nourished by the female tissues surrounding it. The colorful cycad seeds are sought for their starchy seedcoats by mammals such as elephants in Africa, birds such as cassowaries and squirrels in Florida.

Cycads were very abundant and diverse in the Mesozoic era, the time of dinosaurs. Rain forests, semitropical deciduous forests such as the Florida habitat of *Zamia*, deserts, grasslands, and mangrove forests are cycad habitats. Seminole Indians leached starch from cycad roots and underground stems; the cooked starch was a staple food. Cycad species are all endangered due to overcollecting for lawn and home decorating and by habitat destruction.



Pitch Pine Barrens

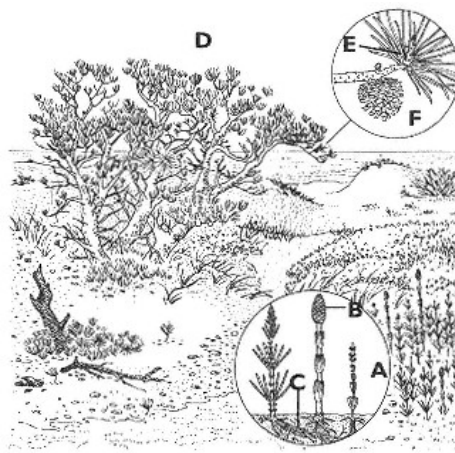
Phylum: Sphenophyta

Sphenophytes include the common horsetail, *Equisetum arvense* (A), and are easily recognized by their jointed hollow stems and rough, ribbed texture. Silicon dioxide (SiO₂) embedded in the tissue of horsetails makes the plant good for cleaning pans and gives the plant its nickname, scouring rush. The presence of silica in the tissue indicates that sphenophytes are capable of biomineralization, the incorporation of minerals by living cells.

Ancestors of the sphenophytes flourished in the Carboniferous period, 300 million years ago. At that time, many treelike horsetail relatives of these seedless vascular plants were as tall as fifteen meters and had a woody stem. Today only forty species of the sphenophytes remain, smaller than their ancient ancestors, and all are members of one genus, *Equisetum*.

The most familiar form of the horsetail plant is the green horsetail shoot. Most shoots are sterile—without reproductive structures—and bear whorls of leaves that roughly resemble the brush of a horse's tail, hence the common name horsetail. Sporangia develop in the strobilus, or cone, at the top (B) of fertile shoots. The cones are the sites of meiosis, during which diploid cells develop haploid spores. Tiny winglike elaters may aid in dispersing spores (Figure 15, p. 161). Spores drop to the ground and develop into free-living, green gametophytes. The tiny gametophytes give rise to swimming sperm and/or eggs. The zygotes that result from fertilization grow to be independent, diploid sporophyte plants.

Horsetail sporophytes also propagate by underground stems (C). Colonies of horsetails propagated by underground stems are composed of genetically identical individuals, or clones. As with some fern species (see p. 163), horsetail sporangia often are borne on shoots separate from those bearing the photosynthetic leaves. *Equisetum arvense* is common in wasteland areas such as urban alleys, saltflats, stream banks, and on silica-rich soils.



Kathryn Delise

Phylum: Coniferophyta

Conifers such as pitch pine, *Pinus rigida* (D), are the most familiar of the gymnosperms (plants that produce naked seeds). Conifers are grouped into approximately 550 species in fifty genera, including *Pinus* (pine), *Cedrus* (cedar), *Taxus* (yew), *Abies* (fir), *Picea* (spruce), and *Larix* (larch). This phylum of cone-bearing seed plants also includes *Sequoiadendron gigantea*, the giant sequoia of California, the largest plant living today, up to 100 meters tall and 8 meters in diameter. Most of these cone-bearing (coniferous) plants are softwood trees with slender leaves called needles. Some are shrubs or low, prostrate plants.

The seeds of conifers are exposed, not enclosed in a fruit (*Pinus* seed, p. 161). At maturity, the winged seeds usually are dispersed by wind. If a conifer seed germinates, it gives rise to a seedling, the young sporophyte. Most conifers are monoecious, that is, an indi-

vidual sporophyte plant bears both male and female reproductive structures. The conifers are heterosporous: Male microsporangia are borne on pollen-producing cones (E), whereas female megasporangia are borne on the larger, more familiar female pine cones (F). In the microsporangium, microspores become dusty, yellow pollen grains; these are immature male gametophytes. In the megasporangium, a cell divides to produce a female gametophyte that forms egg cells. Wind carries conifer pollen from the male to the female cone. Pollination, sometimes after a gap of many months, may be followed by fertilization. Pollen germinates, producing sperm and a pollen tube that conveys sperm (male gametes) to eggs (female gametes). In contrast to fern sperm, which may bear more than 100 undulipodia, the sperm of conifers are not motile and therefore function in a nonmoist environment.

The conifer embryo that results from fertilization is nourished by the female haploid gametophyte tissue in which it is embedded. If you examine a female conifer cone you may see papery brown wings, each bearing two small seeds. Each seed, enclosed in its seed coat, contains a dormant, young sporophyte conifer (p. 161). Nutrients stored in the conifer seed support the embryo until photosynthesis is able to provide adequate nourishment, as is also true in cycads and other seed plants.



Hillside in China

Phylum: *Ginkgophyta*

Only one species of the living fossil ginkgo exists today—a hardy, exotic ornamental often planted along streets for its golden autumn leaves and striking form. Like all other gymnosperms—conifers, cycads, and gnetophytes—ginkgo is a plant with exposed seeds. Ginkgo seeds are borne in pairs at the end of a flexible stalk. Although the fleshy seedcoat that surrounds the ginkgo seed is stinky, the interior seed is considered delicious when roasted. A ginkgo tree that is injured at its base forms what the Chinese call *chi-chis*. These outgrowths are capable of healing and restore the tissue so well that from the swollen *chi-chi* (A), healthy young tissue sprouts.

Ginkgo biloba is the only contemporary descendant of a group of trees that, during the Mesozoic era, was far more extensive. In the state of Washington, remains of a petrified ginkgo forest can be seen in a state park. Although ginkgo is very popular in gardens, on city streets, and on temple grounds in Asia, where people tend it and eat its roasted "nuts," in the wild the ginkgo tree is restricted to extremely steep mountain slopes in southern China. Its fan-shaped and notched leaves are borne close to the highly branching stems, imparting the characteristic ginkgo silhouette that makes them easy to recognize. Because ginkgo leaves are shed in the autumn, ginkgos are deciduous trees, like many flowering trees (maple, dogwood) but few coniferous trees (tamarack).

The ginkgo tree is the sporophyte generation. Ginkgos are dioecious: Male (B) and female (C) reproductive structures are borne on different plants. On male trees, microspores form in male cones. On female trees, megaspores form in female cones. A microspore develops a pollen grain. Each megaspore forms a female gametophyte that produces a female gamete—the egg. Pollen is carried by wind to female trees, where each pollen grain that happens to land on an ovule is drawn by a liquid drop into a pollen chamber. There the pollen releases motile sperm that ultimately fertilize the egg. The outside skin of the ovule forms a fleshy seed coat after fertilization (D); the orange ginkgo seed coat is not a fruit because it is not enclosed by a mature ovary, unlike the seed of a flowering plant. After the ginkgo seed falls from the tree, the embryo sporophyte commences growth. Unless the seed is consumed, for instance, by a North American squirrel or an Asian wild cat, the seed eventually may germinate and grow into a tree.



Kathryn Delise

Ginkgos are sometimes referred to as maidenhair trees because ginkgo leaves resemble the fronds of the maidenhair fern. Ginkgo extract, long in the medical armamentarium in Asia, is now one of the most widely used prescription drugs in western Europe for infirmities from asthma to Alzheimer's disease. The therapeutic properties of ginkgolides, the active biochemicals in ginkgo leaves, are currently being evaluated in the United States.

Phylum: *Anthocerophyta*

Hornworts, also called horned liverworts, are horn-shaped plants that live on damp river banks, tree trunks, and cliffs in the tropics

and in temperate habitats. Like the other nonvascular plants—mosses and liverworts, the hornworts lack true roots, leaves, and vascular systems. Moisture and nutrients diffuse from the soil into their flattened green thallus (**E**) that often grows on moist soil or a rock surface. Inside the thallus live cyanobacteria; these microbes "fix" gaseous nitrogen present in air, converting the nitrogen to a form that the hornwort can use to synthesize the nitrogen-containing compounds it requires for life.

Like mosses and liverworts, hornworts can reproduce by forming little balls of cells called gemmae. Hornworts also reproduce sexually with sperm that swim like those of mosses. The male and female reproductive structures develop on the hornwort thallus, which is a haploid gametophyte.

The hornlike sporophyte grows from the thallus, remaining embedded in it. The slender sporangia (**F**), which constitute most of the sporophyte, photosynthesize and bear stomata, minute openings through which oxygen and carbon dioxide gases exchange between the hornwort and air. When a sporangium matures, it splits open lengthwise, discharging haploid spores. Hornworts resemble horsetails and liverworts—spores and sterile elaters develop in their sporangia (p. 161). The helical elaters absorb moisture, dry when exposed to the air, and then unwind, helping to disperse the spores from the sporangium. Hornwort spores germinate, forming young gametophytes.



African Desert

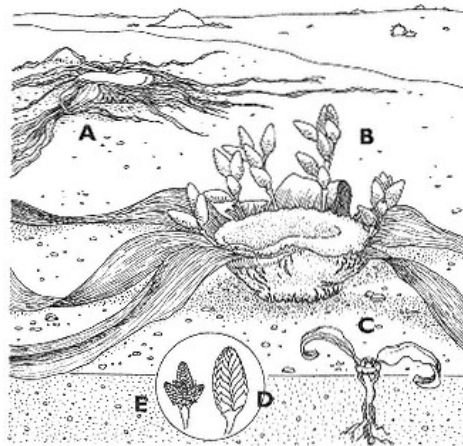
Phylum: Gnetophyta

Gnetophytes include three genera of cone-bearing, seed-producing, vascular plants: *Gnetum*, *Ephedra*, and *Welwitschia*. Like other gymnosperms—conifers, cycads, and ginkgo—gnetophytes bear cones and exposed seeds and lack flowers and fruits. Gnetophytes differ from other gymnosperms in their formation of extensive, water-carrying vessels; this structure is part of the vascular tissue and also is present in flowering plants.

Welwitschia mirabilis (A, mature plant with tattered leaves; B, younger plant; C, young plant) is a unique plant that lives only in the deserts of Namibia, in southwestern Africa. To see this remarkable plant alive, one must visit Namibia or one of the great botanical gardens of the world (e.g., Montreal Botanic Gardens or the Botanical Gardens in San Marino, California).

With only two distinctive, strap-shaped leaves growing from the rim of a woody, cup-shaped stem, *Welwitschia* lies on the desert sand. The leaves grow continuously for the life span of the plant, perhaps a thousand years. The stem is mostly underground and, along with the root that reaches down to the water table, serves as the water-storage facility of the plant. Like conifers (p. 166), *Welwitschia* is dioecious and heterosporous, with female (D) and male (E) cones, each having distinctive spores, borne on separate individual plants. The cones of *Welwitschia*, with opposite or whorled bracts (D), lack resin ducts and so differ from those of conifers.

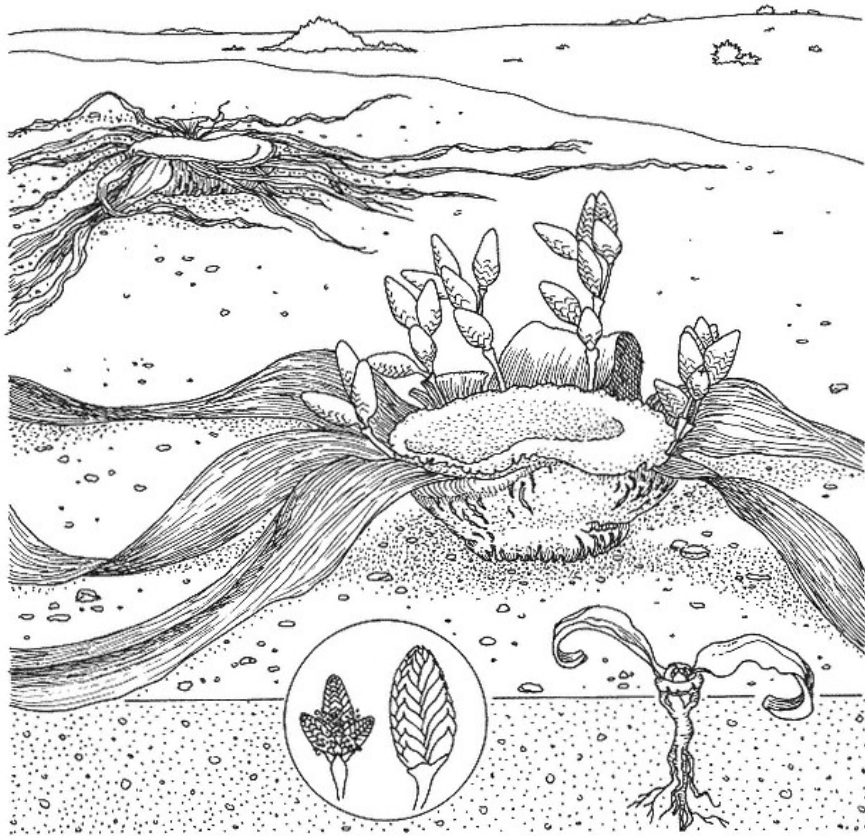
The other two genera of this phylum, *Gnetum* and *Ephedra*, do not live in the African desert and are not illustrated here. *Gnetum* grows in the tropical rain forest, deserts, and mountainsides and comprises several dozen species of woody vines, shrubs, and woody trees of Asia, South and Central America, and Africa. Unlike most gymnosperms, *Gnetum* seed is surrounded by a juicy layer called a pseudofruit. Fruit-eating birds eat the pseudofruit and subsequently disperse the *Gnetum* seed along with bird feces that provide fertilizer. Insects are attracted by nectar and pollinate at least some species of *Gnetum* and the other gnetophytes. Insect pollination is more efficient than wind pollination because insect pollination places pollen closer to the female gamete than does wind pollination.



Kathryn Delise

Species of *Ephedra* produce the vasoconstrictor drug ephedrine, which is used for treating asthma, emphysema, and hay fever as well as to stop nosebleeds. Growing wild in the deserts of the southwestern United States and Mexico as a perennial shrub, *Ephedra* is called Indian tea because the medicinal value of its infusions is recognized by native Americans. *Ephedra* is also called joint fir because its evergreen stems are jointed.

The three genera of gnetophytes may prove to be unrelated. Similarities between flowering plants and gnetophytes include seeds having two cotyledons, leaves with netlike veins (dicots and *Gnetum*), and also the sequence of their genes.



Rain Forest Canopy

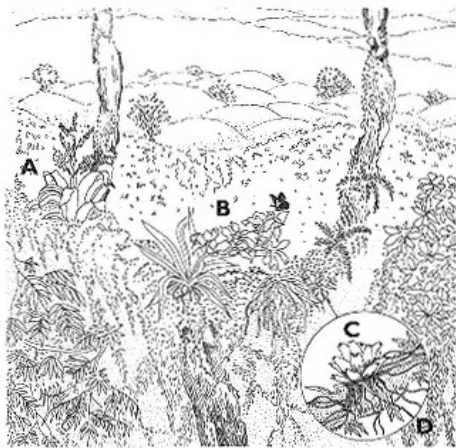
Phylum: Anthophyta

With more than 270,000 species, the flowering plants, or angiosperms, are today the most widespread, diverse, and successful plants. During the past 100 million years, Anthophyta has replaced cycads (p. 164), ginkgos (p. 168), and conifers (p. 166) as the dominant phylum of plants on Earth. Divided into some 350 families, such as the Bromeliaceae (**A**; e.g., *Vriesea ringens* or *Tillandsia asplundia*) and the Orchidaceae (**B**; e.g., *Epidendrum* or *Encyclia*), angiosperms have evolved diverse life forms including trees, herbs, lianas (vines), and epiphytes (**C**) that grow in the tropical rain forest canopy and other terrestrial habitats worldwide.

Bromeliads (**C**) grow perched on canopy plants. Bromeliad's aerial roots ("air roots," **D**) transport water and dissolved minerals into the bromeliad, which uses these for photosynthesis.

The flower and its ovaries, which develop into fruit that enclose seeds, are the distinctive characteristics of flowering plants (see flowers and fruit of a prickly-pear cactus, *Opuntia*, on the cover, and *Capsella* seed, p. 161). In the flowering plants, the gametophyte—so distinctive in plants of other phyla—is reduced to microscopic size. The male gamete-bearing generation—called the microgametophyte or pollen grain—consists of just three cells. The female gamete-bearing generation—called the megagametophyte or embryo sac—consists of just seven cells. A flowering-plant pollen grain grows a tube that conveys sperm nuclei to eggs inside the ovary, which is located deep within the flower.

Insects (p. 150), such as the butterfly shown here, are crucial to the survival of flowering plants; many of these plants depend on insects, birds, bats, or other small mammals for pollination. Wind transports pollen of other angiosperms. The pollination interrelationships suggest that insects have co-evolved with angiosperms, enabling both groups to spread around the planet, and enjoy immense diversity.



Kathryn Delise

Flowering plant species, our principal source of plant food, are grouped as monocots and dicots. The 50,000 monocot species include corn (maize), rice, wheat, oats, millet, barley, and rye—our cereal crops—as well as coconuts, other palms, and bananas. These and other monocots are distinct from dicots: Monocots have a single cotyledon, or seed leaf. The leaf veins of monocots run parallel to each other, the petals often develop in threes, and the vascular tissues in their stems form a complex pattern. Monocots grow in length by means of shoots and root tip growth but lack the tissue that increases trunk girth in a tree; this tissue is called secondary cambium tissue.

The 170,000 dicot species are distinguished by two cotyledons, forking leaf veins, vascular tissue that forms a ring in the stem, petals and other flower parts that grow in fours or fives, and woody tissue, which strengthens woody shrubs and trees. Dicots include many medicinal and food plants—foxglove (source of

digitalis), belladonna (source of atropine), the cinchona tree (source of quinine), coffee, tomatoes, beans, potatoes, sunflowers, oaks, cotton, cacao, and soybeans.



Appendix: Classification

Listed here are the phyla illustrated in our five-kingdom classification, the representative genera included in the drawings, and the habitats in which they are found. Common names are given where applicable. Organisms discussed but not illustrated also may be located with the Index.

Chapter 1— Bacteria

BACTERIA

Actinobacteria	<i>Cellulomonas</i>	Woodland Stream (44)
	<i>Frankia</i>	Woodland Stream (44)
	<i>Streptomyces</i>	
Aphragmabacteria	<i>Mycoplasma</i>	Barnyard (24)
	<i>Spiroplasma</i>	
Chlorobia	<i>Chlorochromatium aggregatum</i>	Saline Habitats (46)
Chloroflexa	<i>Chloroflexus</i>	Saline Habitats (46)
Crenarchaeota (thermoacidophilic bacteria)	<i>Thermoplasma acidophilum</i>	Mud Flats and Hot Springs (22)
Cyanobacteria	<i>Gloeotheca</i>	Salt Marsh (32)
	<i>Johannesbaptista</i>	Salt Marsh (32)
	<i>Microcoleus</i>	Salt Marsh (32)
	<i>Oscillatoria limnetica</i>	Salt Marsh (32)
	<i>Prochlorococcus</i>	
	<i>Prochloron</i>	South Pacific Coral Reef (34)

	<i>Prochlorothrix</i>	
	<i>Spirulina</i>	Salt Marsh (32)
Endospora (endospores)	<i>Arthromitus</i>	
	<i>Bacillus</i>	Rocky Brook (28)
Endospora (fermenting bacteria)	<i>Clostridium</i>	
	<i>Lactobacillus</i>	Foods (42)
	<i>Leuconostoc</i>	
	<i>Streptococcus</i>	
Euryarchaeota (halophils)	<i>Halobacterium</i>	Mud Flats and Hot Springs (22)
	<i>Halococcus</i>	Mud Flats and Hot Springs (22)
Euryarchaeota (methanogens)	<i>Methanobacterium ruminantium</i>	Pasture (20)
	<i>Methanogenium cariaci</i>	Pasture (20)
	<i>Methanogenium marirgen</i>	Pasture (20)
	<i>Methanosarcina</i>	Pasture (20)
Pirellulac	<i>Gemmata obscuriglobus</i>	Pond Scum (31)
	<i>Isosphaera</i>	
	<i>Pirellula</i>	
Proteobacteria (anaerobic phototrophic bacteria)	<i>Rhodomicrobium vannielii</i>	Pond Scum (30)
Proteobacteria (chemoautotrophic bacteria)	<i>Nitrobacter winogradskyi</i>	Ocean Edge (40)
	<i>Nitrococcus</i>	
	<i>Nitrocystis</i>	
	<i>Nitrosococcus</i>	Ocean Edge (40)
	<i>Nitrosolobus</i>	Ocean Edge (40)
	<i>Nitrosomonas</i>	
	<i>Nitrosovibrio</i>	Ocean Edge (40)
	<i>Nitrospina</i>	
	<i>Nitrospira</i>	Ocean Edge (40)
	<i>Thiobacillus</i>	
Proteobacteria (myxobacteria)	<i>Stigmatella aurantiaca</i>	Garden Soil (36)
Proteobacteria (nitrogen-fixing aerobic bacteria)	<i>Azomonas</i>	

	<i>Azotobacter</i>	Garden Soil (36)
	<i>Rhizobium</i>	
Proteobacteria (omnibacteria)	<i>Aeromonas punctata</i>	Lake Shore (38)
	<i>Caulobacter</i>	Lake Shore (38)
	<i>Neisseria</i>	
	<i>Vibrio</i>	
	<i>Escherichia coli</i>	Lake Shore (38)
Proteobacteria (pseudomonads)	<i>Bdellovibrio</i>	
	<i>Pseudomonas multivorans</i>	Pond Scum (30)
	<i>Xanthomonas</i>	Pond Scum (30)
	<i>Zoogloea</i>	
Proteobacteria (thiopneutes)	<i>Desulfovibrio</i>	Rocky Brook (28)
Saprospirae	<i>Saprospira</i>	Saline Habitats (46)
Spirochaetae (spirochetes)	<i>Clevelandina</i>	
	<i>Borrelia</i>	
	<i>Cristispira</i>	Clam Camp (26)
	<i>Diplocalyx</i>	
	<i>Hollandina</i>	
	<i>Leptonema</i>	Clam Camp (26)
	<i>Leptospira</i>	Clam Camp (26)
	<i>Mobilifilum</i>	
	<i>Pillotina</i>	
	<i>Spirochaeta</i>	Clam Camp (26)
	<i>Spirosymplokos</i>	
	<i>Treponema pallidum</i>	
Thermotogae	<i>Aquifex</i>	
	<i>Fervidobacterium</i>	
	<i>Thermosipho</i>	
	<i>Thermotoga thermarum</i>	Saline Habitats (46)

Chapter 2—
Protoctista

KINGDOM PROTOCTISTA

Actinopoda (actinopods)	<i>Challengeron wyvillei (phaeodarian)</i>	Ocean Water Column (80)
	<i>Clathrulina fragilis</i>	Ocean Water Column (80)
	<i>Phyllostaurus siculus</i>	Ocean Water Column (80)
	<i>Spongosphaera polyacantha</i>	Ocean Water Column (80)
Apicomplexa (apicomplexans)	<i>Plasmodium</i>	Mosquito and Blood (98)
	<i>Toxoplasma</i>	
Archaeoprotista	<i>Lophomonas</i>	Fallen Log (72)
	<i>Pelomyxa palustris</i>	Swamp (52)
	<i>Trichomonas</i>	Fallen Log (72)
	<i>Trichonympha</i>	Fallen Log (72)
Chlorophyta (chlorophytes)	<i>Chaetosiphon moniliformis</i>	Atlantic Sheltered Bay (84)
	<i>Chlamydomonas</i>	
	<i>Klebsormidium</i>	
	<i>Ulva lactuca</i>	Atlantic Sheltered Bay (84)
Chrysomonada (chrysophytes; golden-yellow algae)	<i>Dinobryon</i>	Farm Pond (90)
	<i>Mallomonas</i>	
	<i>Ochromonas</i>	Farm Pond (90)
	<i>Synura</i>	Farm Pond (90)
Chrysomonada (raphidophytes)	<i>Chattonella</i>	River Delta (70)
	<i>Olisthodiscus luteus</i>	
	<i>Vacuolaria</i>	River Delta (70)
Ciliophora (ciliate)	<i>Acineta</i>	
	<i>Bursaria</i>	Pond Rocks (94)
	<i>Ophrydium</i>	
	<i>Paramecium</i>	
	<i>Sorogena</i>	
	<i>Stentor</i>	Pond Rocks (94)
	<i>Tetrahymena</i>	Pond Rocks (94)
	<i>Vorticella</i>	Pond Rocks (94)

Cryptomonada (cryptophyta)	<i>Copromonas</i>	
	<i>Cyathomonas truncata</i>	Ice-Covered Lake (68)
Cryptomonada (glaucocystophytes)	<i>Cyanophora paradoxa</i>	
	<i>Glaucocystis nostochinearum</i>	
	<i>Gloeochaete</i>	River Delta (70)
Diatoms	<i>Amphora</i>	Oceanside (100)
	<i>Cocconeis</i>	Oceanside (100)
	<i>Fragilaria</i>	Oceanside (100)
	<i>Gomphonema</i>	Oceanside (100)
	<i>Melosira</i>	Oceanside (100)
	<i>Opephora</i>	Oceanside (100)
	<i>Rhoicosphenia</i>	Oceanside (100)
Dinomastigota (dinomastigotes)	<i>Gonyaulax tamarensis</i>	Coastal Red Tide (88)
	<i>Polykrikos</i>	
	<i>Pyrocystis</i>	Coastal Red Tide (88)
Discomitochondria	<i>Euglena gracilis</i>	
	<i>Euglena spirogyra</i>	Outfall Pipe (74)
	<i>Phacus</i>	Outfall Pipe (74)
	<i>Trypanosoma</i>	
Ebridians	<i>Ebria tripartita</i>	Pacific Nearshore Waters (104)
Ellobiopsida (ellobiopsids)	<i>Thalassomyces marsupii</i>	Pacific Nearshore Waters (104)
Eustigmatophyta (eustigmatophytes)	<i>Vischeria</i>	Lake Surface (78)
Gamophyta (gamophytes)	<i>Cosmarium</i>	Shallow Pond (64)
	<i>Micrasterias denticulata</i>	Shallow Pond (64)
Granuloreticulosa	<i>Globigerinoides</i>	Tropical Coast (96)
	<i>Heterotheca lobata</i>	Tropical Coast (96)
	<i>Textularia</i>	Tropical Coast (96)
Haplosporia (haplosporans)	<i>Haplosporidium nelsoni</i>	Estuary with Oyster Bar (54)
Haptomonada (prymnesiophytes)	<i>Emiliana huxleyi</i>	Marine Chalk Cliffs (76)
	<i>Phaeocystis poucheti</i>	
	<i>Prymnesium parvum</i>	Marine Chalk Cliffs (76)

Labyrinthulata (labyrinthulids)	<i>Labyrinthula</i>	Atlantic Sheltered Bay (84)
Microspora (microsporans)	<i>Glugea stephani</i>	Continental Shelf with Flounder (58)
Myxomycota (plasmodial slime molds)	<i>Fuligo septica</i>	Birch Forest Floor (60)
Myxosporea (myxozoans)	<i>Myxobolus cerebralis</i>	Salmon (56)
Oomycota (oomycetes)	<i>Phytophthora infestans</i>	
	<i>Plasmopara viticola</i>	
	<i>Saprolegnia parasitica</i>	Pond Bottom (102)
Paramyxa (paramyxans)	<i>Paramyxa paradoxa</i>	
	<i>Marteilia refringens</i>	Estuary with Oyster Bar (54)
Pelobiontae	<i>Pelomyxa palustris</i>	Swamp (52)
Phaeophyta (phaeophytes)	<i>Fucus vesiculosus</i>	North Atlantic Coast (62)
	<i>Laminaria</i>	
	<i>Sargassum</i>	
Plasmodiophora (plasmodiophorids)	<i>Plasmodiophora brassicae</i>	Cabbage Field (86)
Rhizopoda (acrasids)	<i>Acrasis rosea</i>	Birch Forest Floor (60)
	<i>Copromyxa spicata</i>	Birch Forest Floor (60)
Rhizopoda (chlorarachnids)	<i>Chlorarachnion reptans</i>	River Delta (70)
Rhizopoda (dictyostelids)	<i>Dictyostelium discoideum</i>	
	<i>Polysphondylium violaceum</i>	Birch Forest Floor (60)
Rhizopoda (rhizopods)	<i>Amoeba proteus</i>	Swamp (52)
	<i>Arcella polyopora</i>	Swamp (52)
	<i>Entamoeba histolytica</i>	
	<i>Mayorella penardi</i>	Swamp (52)
Rhodophyta (rhodophytes)	<i>Gracilaria</i>	
	<i>Polysiphonia harveyi</i>	North Atlantic Coast (62)
	<i>Porphyra</i>	
Xanthophyta (xanthophytes)	<i>Botrydiopsis</i>	Lake Surface (78)
	<i>Ophiocytium</i>	Lake Surface (78)

Xenophyophora (xenophyophores)	<i>Galatheammima tetradea</i>	Marine Abyss (66)
	<i>Psammetta globosa</i>	Marine Abyss (66)
	<i>Reticulammina lamellata</i>	Marine Abyss (66)
	<i>Stannophyllum zonarium</i>	Marine Abyss (66)
Zoomatigota	<i>Opalina</i>	(72)

Chapter 3—
Fungi

KINGDOM FUNGI

Ascomycota (ascomycotes)	<i>Ceratocystis ulmi</i>	
	<i>Endothia parasitica</i>	
	<i>Morchella esculenta</i>	Orchard (110)
Ascomycota (deuteromycotes)	<i>Titaeosporina</i>	Forest Clearing (112)
Ascomycota (lichens)	<i>Parmelia conspersa</i>	Orchard (111)
Basidiomycota (basidiomycotes)	<i>Amanita</i>	Forest Clearing (112)
	<i>Armillaria (honey mushroom)</i>	Forest Clearing (112)
	<i>Boletus</i>	Forest Clearing (112)
	<i>Fomes</i>	Forest Clearing (112)
Deuteromycota	<i>Aspergillus</i>	
	<i>Candida albicans</i>	
	<i>Penicillium</i>	
	<i>Rhizoctonia</i>	
	<i>Titaeosporina</i>	Forest Clearing (112)
	<i>Trichophyton</i>	
Lichens	<i>Parmelia conspersa</i>	Orchard (111)
Zygomycota (zygomycotes)	<i>Dactylaria</i>	Orchard (111)
	<i>Dactylella tylopaga</i>	Orchard (111)
	<i>Endosporella</i>	
	<i>Glomus</i>	
	<i>Mucor</i>	
	<i>Rhizopus (black bread mold)</i>	

Chapter 4—
Animalia

KINGDOM ANIMALIA

Acanthocephala (acanthocephalans; thorny-headed worms)	<i>Plagiorhynchus cylindraceus</i>	Forest Soil Puddle (142)
Annelida (annelids)	<i>Lumbricus terrestris</i> (earthworm)	Forest Soil Puddle (142)
Branchiopoda (brachiopods)	<i>Terebratulina septentrionalis</i> (marine lamp shell)	Grassy Shoal (138)
Bryozoa (bryozoans; ectoprocts)	<i>Bugula</i>	Shallow Pacific California coast (144)
Cephalochordata (lancelets)	<i>Branchiostoma</i> (amphioxus)	Sand Seashore (133)
Chaetognatha (chaetognaths; arrow worms)	<i>Sagitta bipunctata</i>	Open Ocean Rock and Sand Bottom (124)
Chelicerata (chelicerates)	<i>Argiope argentata</i> (silver argiope spider)	Costa Rican Tropical Forest (151)
Cnidaria (cnidarians)	<i>Eunicella verrucosa</i> (coral)	Coral and Squirrel Fish (136)
	<i>Hydra viridis</i> (hydra)	Lake Shore (38)
	<i>Obelia</i> (moon jelly)	Caribbean Reef Seafloor (126)
Craniata (craniate chordates)	<i>Bos taurus</i> (cattle)	Pasture (20)
	<i>Chamaeleo ituriensis</i> (Ituri chameleon)	Cover
	<i>Dendroica coronata</i> (myrtle warbler)	Forest Soil Puddle (142)
	<i>Enhydra lutris</i> (sea otter)	California Rocky Intertidal Zone (148)
	<i>Holacanthus ciliarsis</i> (Atlantic Queen angelfish)	Cover
	<i>Holocentrus xantherythrus</i> (squirrel fish)	Coral and Squirrel Fish (136)
	<i>Larus crassirostris</i> (black-tailed gull)	Philippine Coral Sands (130)
	<i>Merops ornatus</i> (rainbow bee eater)	Cover
	<i>Onchorhynchus nerka</i> (sockeye salmon)	Salmon (56)
	<i>Perca flavescens</i> (yellow perch)	Pond Bottom (102)
	<i>Platiclothus stellatus</i> (starry flounder)	Continental Shelf with Flounder (58)
	<i>Procyon lotor</i> (raccoon)	Clam Camp (26)
	<i>Sebastes serripes</i> (rock fish)	Shallow Pacific California Coast (144)

Crustacea (crustaceans)	<i>Armadillium vulgare</i> (pill bug)	Forest Soil Puddle (142)
	<i>Balanus</i> (barnacle)	California Rocky Intertidal Zone (148) and Cover
	crab	Marine Abyss (152)
	<i>Parathemisto</i> (amphipod)	Pacific Nearshore Waters (104)
Ctenophora (ctenophores; comb jellies)	<i>Beroë cucumis</i> (North Sea thimble jelly)	Open Ocean (128)
	<i>Bolinopsis infundibulum</i> (comb jelly)	Open Ocean (128)
	<i>Cestum veneris</i> (Venus's girdle)	Open Ocean (128)
	<i>Pleurobrachia pileus</i> (sea gooseberry)	Open Ocean (128)
Echinodermata (echinoderms)	<i>Ophiopholis aculeata</i> (daisy serpent star)	Sandy Seashore (132)
Echiura (echiurans; spoon worms)	<i>Listriolobus pelloides</i>	Sandy Marine Coast (146)
	<i>Urechis caupo</i>	Sandy Marine Coast (146)
Entoprocta (entoprocts)	<i>Barentsia</i>	Shallow Pacific California Coast (144)
Gastrotricha (gastrotrichs)	<i>Lepidodermella</i>	Grassy Shoal (138)
Gnathostomulida (gnathostomulids; jaw worms)	<i>Probognathia minima</i>	Grassy Shoal (138)
Hemichordata (hemichordates)	<i>Balanoglossus</i> (acorn worm)	Sandy Marine Coast (147)
	<i>Ptychodera flava</i>	Open Ocean Rock and Sand Bottom (124)
	<i>Saccoglossus kowalevskii</i>	Sandy Marine Coast (146)
Kinorhyncha (kinorhynchs)	<i>Echinoderes kozloffii</i>	Pebbled Sea Bottom (122)
Loricifera (loriciferans)	<i>Nanaloricus mysticus</i>	Pebbled Sea Bottom (122)
	<i>Pliciloricus enigmaticus</i>	Pebbled Sea Bottom (122)
Mandibulata (mandibulates)	<i>Anopheles</i> (mosquito)	Mosquito and Blood (98)
	<i>Graphocephala coccinea</i> (leafhopper)	Cover
	<i>Plusiotis resplendens</i> (golden beetle)	Costa Rican Tropical Forest at Night (150)
	<i>Pterotermes occidentis</i> (termite)	Fallen Log (72)
	<i>Rothschildia lebeau</i> (saturniid moth)	Costa Rican Tropical Forest at Night (148)
Mollusca (molluscs)	<i>Crassostrea virginica</i> (American oyster)	Estuary with Oyster Bar (54)

	<i>Flabellinopsis iodinea</i> (purple nudibranch)	California Rocky Intertidal Zone (148)
	<i>Haliotis cracherodii</i> (black abalone)	California Rocky Intertidal Zone (148)
	<i>Loligo pealei</i> (common squid)	California Rocky Intertidal Zone (148)
	<i>Mytilus californianus</i> (California mussel)	California Rocky Intertidal Zone (148)
	<i>Nautilus</i> (chambered nautilus)	Philippine Coral Sands (130)
	<i>Octopus dofleini</i> (Pacific giant octopus)	California Rocky Intertidal Zone (148)
	<i>Stenoplax</i> (chiton)	California Rocky Intertidal Zone (148)
Nematoda (nematodes)	free-living nematode	Moss and Lichen Water Film (140)
Nematomorpha (nematomorphs; Gordian worms; horsehair worms)	<i>Gordius villoti</i>	Forest Soil Puddle (142)
Nemertina (nemertines; ribbon worms)	ribbon worm	Coral and Squirrel Fish (136)
Onychophora (onychophorans; velvet worms)	<i>Peripatus</i>	Costa Rican Tropical Forest at Night (150)
Orthonectida (orthonectids)	<i>Rhopalura</i>	Philippine Coral Sands (130)
Phoronida (phoronids)	<i>Phoronopsis vancouverensis</i>	Shallow Pacific California Coast (144)
Placozoa (placozoans)	<i>Trichoplax</i>	Pebbled Sea Bottom (122)
Platyhelminthes (platyhelminths; flatworms)	flatworm	Sandy Seashore (132)
Pogonophora (vestimentiferans; tube worms; pogonophorans)	<i>Riftia pachyptila</i>	Marine Abyss (152)
Porifera (poriferans; sponges)	<i>Euplectella speciosissima</i> (Venus flower basket)	Open Ocean Rock and Sand Bottom (124)
Priapulida (priapulids)	<i>Tubiluchus</i>	Philippine Coral Sands (130)
Rhombozoa (rhombozoans)	<i>Dicyema truncatum</i> (dicyemid)	Philippine Coral Sands (130)
Rotifera (rotifers)	<i>Philodina</i>	Moss and Lichen Water Film (140)
Sipuncula (sipunculans; peanut worms)	<i>Themiste lageniformis</i>	Sandy Marine Coast (146)
Tardigrada (tardigrades; water bears)	<i>Echiniscus arctomys</i>	Moss and Lichen Water Film (140)
Urochordata (tunicate)	<i>Lissoclinum</i> (sea squirt)	South Pacific Coral Reef (34)

Chapter 5—
Plantae

KINGDOM PLANTAE

Anthophyta (angiosperms)	<i>Alnus</i> (alder)	Woodland Stream (44)
	<i>Brassica oleracea</i> (cabbage)	Cabbage Field (86)
	<i>Cercidium</i> (paloverde)	Fallen Log (72)
	<i>Epidendrum</i> (orchid)	Rain Forest Canopy (172)
	<i>Opuntia</i> (prickly pear cactus)	Cover
	<i>Tillandsia</i> (bromeliad)	Rain Forest Canopy (172)
	<i>Utricularia</i> (bladderwort)	Pond Rocks (94)
	<i>Viburnum nudum</i> (possum-haw)	Cover
	<i>Zostera marina</i> (eelgrass)	Atlantic Sheltered Bay (84)
	<i>Zostera marina</i> (eelgrass)	Grassy Shoal (138)
Anthocerphyta (hornworts)	<i>Anthoceros</i>	Hillside in China (168)
Bryophyta (bryophytes; mosses)	<i>Polytrichum juniperinum</i> (haircap moss)	Woods (162)
Coniferophyta (conifers)	<i>Pinus rigida</i> (pitch pine)	Pitch Pine Barrens (166)
Cycadophyta (cycads)	<i>Zamia</i> (coontie)	Florida Bush (165)
Filicinophyta (ferns; Pterophyta; Pterodactylina)	<i>Osmunda cinnamomea</i> (cinnamon fern)	Woods (163)
Ginkgophyta (ginkgo)	<i>Ginkgo biloba</i> (maidenhair tree)	Hillside in China (168)
Gnetophyta (gnetophytes)	<i>Welwitschia mirabilis</i>	African Desert (170)
Hepatophyta (liverworts)	<i>Marchantia</i>	Florida Bush (164)
Lycophyta (lycophytes; club mosses; ground pines; lycophytes)	<i>Lycopodium obscurum</i> (tree club moss)	Woods (162)
Psilophyta (psilophytes)	<i>Psilotum</i> (whisk fern)	Florida Bush (164)
Sphenophyta (sphenophytes)	<i>Equisetum arvense</i> (common horsetail)	Pitch Pine Barrens (166)

Glossary

Abbreviations used in the Glossary:

abbr.	abbreviation	s.	singular
adj.	adjective	usu.	usually
esp.	especially	v.siatfr	verb
pl.	plural	var.	variation

A

aboral (adj.)

Away from the mouth.

abyss

Deep ocean; the organisms and material usu. found beyond the continental shelf.

acervulus (pl. acervuli)

Mat of hyphae that gives rise to conidiophores packed together closely to form a bedlike mass.

acraniate (adj.)

Chordate that lacks a cranium or skull.

adult

Fully developed and mature individual capable of producing sex cells (eggs, sperm, or pollen) that can fuse to form an embryo.

aerobe

Organism that lives in the presence of and uses oxygen. Obligate aerobes are unable to live without oxygen; facultative aerobes can live in oxic or anoxic environments.

agamont

Adult life-cycle stage that is capable of reproduction but does not produce gametes.

agar

Hardening substance for cultivating bacterial, protocist, and fungal microorganisms; constituent of some gels used for electrophoresis that is prepared from a gelatinous substance (agar-agar) extracted from red algae.

agglutination

Formation of clumps of cells, esp. pollen, bacteria, red blood cells, spermatozoans, and some protocists, either spontaneously or after treatment with a specific antibody or other agent.

aggregate (v.)

To form a cluster (e.g., of organisms or cells).

algae (s. alga)

Heterogeneous group of eukaryotic, unicellular, colonial, or multicellular aquatic organisms that are photosynthetic at some stage in their life history. (Photosynthesis occurs in plastids.) Although traditionally classified as plants, the major groups of algae are now phyla in Kingdom Protocista.

alternation of generations

Reproductive cycle in which haploid phases alternate with diploid phases.

amastigote

Microorganism or life-history stage of an organism that lacks undulipodia.

ameba (pl. amebas, var. amoeba)

(1) Unicellular, protocist life-cycle stage that moves by means of pseudopods and whose shape is therefore subject to constant change. (2) Informal name for a member of the protocist phylum Rhizopoda.

ameboid (adj.; var. amoeboid)

Resembling an ameba in shape, properties, or mode of movement.

amebomastigote

(1) Ameba that undergoes a transformation to a mastigote stage. (2) Informal name of a member of the zoomastiginid class Amebomastigota.

amino acid

An organic acid containing the amino group (NH_2) and a carboxyl group ($-\text{COOH}$); subunit of proteins.

anaerobe

Organism living in the absence of oxygen. Obligate anaerobes are unable to live in even low concentrations of oxygen; facultative anaerobes live in oxic or anoxic environments; aerotolerant organisms can live in the presence of oxygen but do not use it. Compare *aerobe*.

analogous (adj.)

Convergent; relating to structures or behaviors with the same function that have not evolved from common ancestors (e.g., the wings of insects and bats). Compare *homologous*.

anastomosis

Formation of a network by the fusion of branches, filaments, or tubes.

angiosperm

Plant that produces its seeds inside flowers; commonly called a flowering plant; member of the plant phylum Anthophyta.

anoxic (adj.)

Devoid of molecular oxygen.

antenna (pl. antennae or antennas)

Sensory appendage on the head for detecting movement, sound, touch, etc.; segmented sensory organ on the head of an organism.

antennule

Small antenna or similar appendage.

antheridium (pl. antheridia)

Multicellular male sex organ; sperm-producing gametangium of plants, such as mosses, other than seed plants. Compare *archegonium*.

anthrax

Disease affecting the lungs of warm-blooded animals that is caused by the bacterium *Bacillus anthracis*.

antibiotic

Substance produced by organisms (typically fungi or bacteria) that injures, kills, or prevents the growth of other organisms (typically bacteria).

antibody

Protein produced by vertebrate blood cells that is capable of defending the animal against a specific virus, bacterium, biochemical, or other imposition.

anus

Posterior opening of the animal digestive tract, through which fecal waste is excreted.

apical complex

Specialized structure at the apex of an apicomplexan that facilitates attachment and penetration of the organism into the tissue cell of the animal in which the apicomplexan resides.

archaeobacteria (s. archaeobacterium)

Subkingdom of prokaryotes that includes thermoacidophiles, halophiles, and methanogens, typically found in extreme environments (e.g., hot springs or salt lakes). Some scientists think that archaeobacteria are the most ancient group of organisms still living.

archegonium (pl. archegonia)

Multicellular female sex organ; egg-producing gametangium of a plant, for example, a moss, other than a seed plant. Compare *antheridium*.

ascospore

Spore contained in an ascus formed by karyogamy followed by meiosis.

ascus (pl. asci)

A saclike cell of a hypha that contains a definite number of ascospores (usu. eight).

astropyle

Main opening of the central capsule of phaeodarian actinopods.

ATP

Adenosine triphosphate; molecule that is the primary energy carrier for cell metabolism and motility.

autogamy

Self-fertilization; the union of two nuclei, both of which are derived from the nucleus of a single parent.

autopoiesis

Organismal self-maintenance.

autotroph

An organism that grows and synthesizes organic compounds from inorganic compounds by using energy from sunlight or from oxidation of inorganic compounds.

autotrophy

Mode of nutrition in which organic compounds are synthesized from inorganic compounds by organisms that use energy from sunlight or from the oxidation of inorganic compounds.

axoneme

Microtubule or shaft of microtubules extending the length of an undulipodium, pseudopod, or axopod.

axopod

Permanent pseudopod stiffened by a microtubular axoneme.

B**bacillus**

Bacterium that is rod-shaped.

basal cell

Cell in the lowest layer of stratified tissue (such as epidermis and other epithelia) from which the tissue is renewed.

basal disc

Platelike structure at the base of a cell process; part of the sporophore of a dictyostelid slime mold.

basidiocarp

Mushroom or other reproductive structure of a fungus that bears basidia.

basidiospore

Spore borne on a basidium that results from karyogamy and meiosis.

basidium (pl. basidia)

Club-shaped structure bearing basidiospores on its surface.

benthic (adj.)

Of, relating to, or occurring at the bottom of a body of water.

binary fission

Reproduction in which one parent cell divides into two offspring cells of roughly equal size.

binomial nomenclature

System of naming and identifying organisms that assigns each organism two names, a genus name and a species name.

binucleate (adj.)

Having two nuclei.

bioassay

Determination of the relative strength of a substance by comparing its effect on a test organism with the effect of a standard preparation.

biochemical

Substance produced by chemical reaction in a living organism.

biodiversity

The variety of organisms considered at all levels, from genetic variants belonging to one species through arrays of species, genera, families, and phyla; abbrev. of biological diversity.

biogenic (adj.)

Produced by living organisms or their remains.

bioluminescence

Light generated biochemically and emitted by an organism.

biomass

Total mass of living organisms in a given area.

biomaterial

Material that originates from an organism, such as biocoral.

biome

Huge, contiguous territory that is geographically definable (e.g., the world ocean, the northern tundra).

biomineralization

Formation of minerals by living organisms.

biosphere

The part of the Earth's volume that harbors life.

biota

All living matter on Earth at a given time; the flora, fauna, and microbiota taken together.

blastopore

Opening that connects the internal cavity of the gastrula stage of an embryo with the outside; the future mouth of some animals and the anus of others.

blastula (pl. blastulae)

Animal embryo after cleavage and before gastrulation; usu. hollow, liquid-filled ball of cells.

bothrosome

Organelle on the membrane of labyrinthulomycetes that produces new membrane, sequesters calcium, and filters cytoplasm for the production of the proteinaceous, extracellular slime-net matrix. Also known as a sagenogen.

brackish (adj.)

Of or relating to water with a salinity between that of sea water and that of freshwater.

bract

Modified, often colored leaf beneath a flower or flower cluster.

broadleaf (adj.)

Having broad leaves (as opposed to needles).

Brownian motion

Random movement of tiny particles in solution, such as the components of cells.

bryophyte

Member of a group of nonvascular plants that consists of the mosses, hornworts, and liverworts.

bud

Projection that develops into a flower.

bud

(v.) To reproduce by the outgrowth of a protrusion (bud) from a parent cell or body of an animal, plant, or fungus.

Burgess shale

Mid-Cambrian sedimentary rocks in British Columbia, Canada, that contain extraordinarily well-preserved fossils of soft-bodied animals from approximately 530 million years ago.

C**calcareous (adj.)**

Containing calcium, usu. in the form of calcium carbonate (CaCO_3).

calyx (pl. calyxes or calyces)

(1) In animals, cup-shaped structure of crinoids and entoprocts. (2) In plants, the sepals; the cup-shaped outer series of two series of floral leaves.

Cambrian period

Earliest geological period of the Paleozoic era, from about 590 million to 505 million years ago, during which many phyla of multicellular animals first arose.

capsular wall

Wall of a spherical or nearly spherical structure.

carbohydrate

Compound composed of carbon, oxygen, and hydrogen of the general formula $\text{C}_x(\text{H}_2\text{O})_y$. Carbohydrates include sugars (monosaccharides and disaccharides) and their derivatives and polysaccharides, such as starch and cellulose.

Carboniferous period

Geological period of the late Paleozoic era, from about 360 million to 286 million years ago, during which coal beds were formed.

carboxysome

Organelle inside plastids that is thought to contain the CO_2 -fixing enzyme ribulose biphosphate carboxylase.

carnivory

Mode of nutrition by which an organism obtains nutrition and energy by eating live animals.

carotenoid

Red, orange, or yellow isoprenoid pigment (e.g., carotene, xanthophyll) found in plastids.

cartilage

Translucent, elastic, skeletal connective tissue.

cell

Basic structural building block of living organisms, consisting of protoplasm bounded by a membrane and—in plants, bacteria, and fungi—also surrounded by a nonliving rigid wall.

cell process

See *process*.

cellulose

Polysaccharide composed of glucose units; chief constituent of the cell wall in plants and chlorophytes.

centimeter (abbr. cm)

0.01, or 10^{-2} , meter. (2.56 cm = 1 inch.)

centric (adj.)

Of or relating to radial symmetry of the valves in diatoms.

centriole

Eukaryotic cell organelle; barrel-shaped organelle 0.25 micrometer in diameter that is composed of a $[9(3)+0]$ array of microtubules. Centrioles appear during animal and some protocist cell divisions at each pole of the mitotic spindle. Centrioles are absent at the poles of mitotically dividing cells of fungi, plants, and many protocists.

centriole-kinetosome

$[9(3)+0]$ microtubular structure that is naked (centriole) or is at the base of an undulipodium (kinetosome).

centromere

Kinetochore; structure on each chromosome that attaches it to microtubules of the mitotic spindle.

cephalothorax

Fused head and thorax of some arthropods.

chaeta

(pl. chaetae) Bristle; seta.

chasolithic (adj.)

Living inside fissures and cracks in rocks; referring to the colonization of surfaces of rock by microorganisms incapable of dissolving the rock.

chemotrophy

Mode of nutrition in which energy is obtained—either from inorganic sources (chemoautotrophy) or from organic sources (chemoheterotrophy)—by chemical reactions independent of light.

chitin

Tough, resistant, nitrogen-containing polysaccharide that is a component of arthropod exoskeletons and cell walls of some protocists and fungi.

chlorophyll

Green pigment that absorbs visible light energy and helps convert it to usable chemical energy in photosynthesis.

chloroplast

Green plastid; plastid that contains chlorophylls *a* and *b*; organelle that is the site of photosynthesis.

chlorosome

Membranous spherical or vesicular structures made of light-harvesting pigments (chlorophylls, carotenoids) in the green sulfur bacteria.

cholesterol

Steroid alcohol with the chemical formula $C_{27}H_{45}OH$ that is a major component of membranes of eukaryotic organisms.

chordate

Animal having a notochord, a dorsal, hollow nerve cord, and pharyngeal gill slits.

chromatin

Complex of nucleic acid (DNA) and basic proteins (histones) of which chromosomes are made during mitotic cell division.

chromosome

Organelle inside the nucleus of eukaryotic cells that is made of chromatin and contains most of the cell's genetic material (DNA).

chrysoplast

Yellow plastid; membrane-bounded photosynthetic organelle of chrysophytes, diatoms, and prymnesiophytes that contains chlorophylls *a* and *c*.

chytrid body

Structure of chytridiomycetes in which zoospores form.

cilium (pl. cilia)

Short undulipodium; intracellular but protruding organelle of motility composed of microtubules in the $[9(2)+2]$ configuration and underlain by the $[9(3)+0]$ kinetosome from which it develops.

class

Taxonomic level below phylum and above order.

clast

Rock particle or fragment.

cloaca

Exit chamber common to the digestive system (the gastrointestinal tract), the reproductive system, and the urinary system from which feces, gametes, and liquid waste are excreted.

clone

Genetically identical individuals derived by asexual division of an individual or cell.

coccoid

Spherical, nearly spherical, or berry-shaped structure.

coccolith

External, platelike structure on some prymnesiophytes that is made of calcium carbonate.

coccolithophorid

Prymnesiophyte that bears coccoliths.

coelenteron (pl. coelentera)

Hollow digestive cavity that is characteristic of cnidarians.

coelom

Body cavity that encloses the vascular system and digestive tract; characteristic of nearly all animal phyla (except acoelomates and pseudocoelomates).

coenocytic (adj.)

Having more than one nucleus in common cytoplasm (referring to cells or organisms). Multinucleate; syncytial; plasmodial.

collar cell

Cell with a single undulipodium that generates currents by which sponges draw water through their ostia and catch food particles.

colonial (adj.)

Refers to genetically identical cells or organisms that live in a permanent association. Although each is capable of growth by division, colony members live in stable but loose association.

comb plate (var. ctene)

Ciliated plate used by comb jellies for swimming; var. ctene.

commensalism

Physical, nonnecrotrophic association between members of two or more species in which neither species necessarily takes nutrients from the other.

community

Set of populations of organisms of different species in the same place at the same time.

cone

Modified ovule-bearing leaves or scales grouped on an axis. See *strobilus*.

conidiophore

Specialized hypha that bears conidia.

conidium (pl. conidia)

Propagule of fungi; mitotically produced spore borne on a conidiophore or on a nonspecialized hypha that is capable of further growth in the absence of sex and fusion.

conifer

Cone-bearing plant of the phylum Coniferophyta.

conjugation

In prokaryotes, cell-to-cell contact between a donor and a recipient bacterium at which the transmission of genetic material occurs. In eukaryotes, fusion of nonundulipodiated gametes or gamete nuclei.

cortex

Outer layer of an organism or organ.

cotyledon

Leaflike structure of plant seeds; stores nutrients for dicot plant embryo and absorbs nutrients for monocot embryo.

cranium

Bony or cartilaginous skull that encloses the brain of craniate chordates.

crinoid

Member of a class of the phylum Echinodermata that includes sea lilies and feather stars.

cristae (s. crista)

Tubular or pouchlike and inwardly directed folds of the inner membrane of a mitochondrion that are the site of ATP production during aerobic metabolism.

crypt

Pit or depression (gullet) characteristic of cryptomonads.

cryptobiosis (cryptobiotic, adj.)

Temporary dormancy of a propagule; suspension of metabolic activity induced by starvation, desiccation, or extreme temperatures.

crystalline style

Enzyme-releasing organ of the digestive system of bivalve molluscs.

cuticle

Outer layer or covering composed of metabolic products (wax) rather than of cells, usu. of an animal or a plant.

cyanelle

Intracellular structure, considered to be a cyanobacterial symbiont or an organelle derived from symbiotic cyanobacteria, that, containing thylakoids, is active in oxygenic photosynthesis.

cyclosis

See *cytoplasmic streaming*.

cyst

Propagule; encapsulated form, often a dormant stage, of one of several types of organisms that forms in response to extreme environmental conditions.

cytology

Study of cells.

cytoplasm

In a cell, the fluid-filled part exterior to the nucleus or nucleoid and containing enzymes and metabolites in solution.

cytoplasmic streaming

Circulation of cytoplasm in the cell; characteristic intracellular motility of eukaryotic cells. Cyclosis; protoplasmic streaming.

cytostome

Cell mouth; ingestive opening of protists (e.g., euglenids).

deciduous (adj.)

Shed or sloughed off seasonally or at a certain stage in the life cycle; having deciduous parts (e.g., the antlers of deer or the leaves of some temperate-zone trees).

dehiscence

Opening of a structure by drying or by programmed death of certain structures or cells (e.g., to allow propagule escape).

deposit feeding

Act or process of eating material that has settled or has been deposited on the bottom of a body of water.

desmosome

Intercellular membranous junction fastening cells together in animal tissues.

detritus

Loose natural material, such as rock or organic particles, that results from disintegration of rocks or organisms; organic-rich clastic sediment.

dicotyledon (var. dicot)

Plant that has two cotyledons in the seed; member of a subphylum of angiosperms (flowering plants). Compare *monocotyledon*.

differentiation

Process characteristic of animal and plant development in which unspecialized cells become tissue components specialized for different functions.

dikaryon

Cell or hypha, typically of fungi, that contains any number of nuclei of two genetically distinct forms (the sources of which may not be known), usu. one from each parent after sexual fusion. Compare *heterokaryon*.

dikaryotic (adj.)

Containing two nuclei, each usu. from a different parent.

dioecious (adj.)

Having male and female organs on different individuals of the same species.

diploid (adj.)

Having two complete sets of chromosomes (the chromosome complement of sexually produced eukaryotic cells), one each from the maternal and paternal parents; 2N. Compare *haploid*.

DNA

Deoxyribonucleic acid; a long molecule composed of nucleotides in a linear order that constitutes the genetic information of cells and that is capable of replicating itself and of synthesizing RNA.

dormant (adj.)

Nongrowing; resistant; in a state of suspended activity (referring to propagules, tissues, or organisms).

dorsal (adj.)

Toward or on the back or upper side; compare *ventral*.

E**ecology**

Study of relationships between organisms and their environment.

ecosystem

Community of organisms that inhabit a specific environment and the physical forces that impact those organisms.

ectomycorrhiza (pl. ectomycorrhizae)

Symbiosis between plant roots and soil fungi, typical of basidiomycotes and trees, in which the fungi cover the plant root with a mantle but do not penetrate the root cell.

ectoplasm

Outermost, relatively rigid, transparent layer of cytoplasm.

Ediacaran biota

Protocist and animal fossils from Ediacara, South Australia, and some two dozen other fossil localities worldwide that are about 700 million years old.

egg

Female gamete or oocyte, which is nonmotile and usu. larger than the male gamete.

elater

Hygroscopic cell or band, usu. attached to the spore (e.g., of a horsetail or moss), that aids in dispersing spores

electrophoresis

Gel electrophoresis; laboratory technique used to separate macromolecules on the basis of electrical charge or size.

embryo

Early developmental stage of a multicellular organism (animal or plant) that develops from a zygote (fertilized egg).

encyst (v.)

To form or become enclosed in a cyst.

endobiotic (adj.)

Endosymbiotic; of or relating to an association in which one partner lives within the other partner.

endolithic (adj.)

Living inside of rocks, in limestone, by active penetration of the rock by microorganisms capable of dissolving the rock.

endomycorrhiza (pl. endomycorrhizae)

Symbiosis between plant roots and soil fungi, typical of zygomycetes and herbaceous plants, in which the fungi do not cover the plant roots with a mantle but do penetrate the root cells.

endoplasm

Inner, relatively fluid central portion of cytoplasm of eukaryotic cells.

endoplasmic reticulum (abbr. ER)

Extensive endomembrane system found in most protocist, animal, and plant cells.

endosperm

Tissue surrounding a plant embryo in a seed that contains stored food.

endospore

Desiccation- and heat-resistant spore produced inside bacteria.

endosymbiosis

Association of partners, members of different species, in which one organism lives inside the body or cell of another.

enzyme

Biological catalyst for a specific substrate and product; molecule that accelerates but does not enter metabolic reaction.

epibiosis (epibiotic, adj.)

Association of organisms in which one lives on the surface of another.

epidermis

Outer layer of skin or of leaves.

epiphyte

Plant or fungus that lives supported, but not nourished, by a plant of another species; epibiotic plant such as bromeliad and certain lichens.

epithelium (pl. epithelia)

Tissue that covers the inner or outer surface of a body or structure.

esophagus (pl. esophagi)

Muscular tube through which food is passed from the pharynx to the stomach; gullet.

etioplast

Undeveloped plastid that lacks chlorophyll, typical of plants grown in the dark.

eubacteria (s. eubacterium)

All bacteria other than the archaeobacteria. Eubacteria have distinctive lipids, RNAs, and RNA polymerases, and most have cell walls that contain muramic acid.

eukaryote

Organism composed of cells with membrane-bounded nuclei, chromatin organized into more than one chromosome, and usu. organelles (such as mitochondria and plastids).

eukaryotic (adj.)

Having characteristics of a eukaryote, composed of cells with nuclei.

excyst (v.)

To exit the cyst stage, convert from dormant propagule to active organisms.

exoskeleton

External supportive covering.

eyespot

Small, pigmented, and probably light-sensitive structure in certain undulipodiated protists.

facultative (adj.)

Optional; exhibiting a certain lifestyle under some environmental conditions but not others.

family

Taxonomic level below order and above genus.

fat

Compound composed of carbon, hydrogen, and oxygen with a lower proportion of oxygen to carbon than that of carbohydrates; the major form of lipids in some animals and in some plants.

fauna

Animal life (inappropriate term for protocists and bacteria); compare *flora*.

feces

Solid waste from the gastrointestinal tract of animals.

fermentation

Anaerobic respiration; mode of nutrition in which organic compounds are degraded in the absence of oxygen, with organic compounds serving as terminal electron acceptors, yielding energy and organic end products.

fertilization

Fusion of two haploid cells, gametes, or gamete nuclei to form a diploid nucleus, diploid cell, or zygote.

fetal (adj.)

Relating to a fetus, the unborn or unhatched vertebrate after it has attained its basic structural plan.

fibril

Thread-shaped solid structure; filament.

flagellin

Polymeric protein that is the main constituent of flagella.

flagellum (pl. flagella)

(1) In prokaryotes, the long, thin, solid, extracellular structure of motility composed of one of a number of flagellin proteins. (2) In eukaryotes, a confusing term for an undulipodium; the long, fine, intrinsically motile intracellular structure used for sensing, for locomotion, for feeding, and so on, that is underlain by microtubules composed of tubulin and other nonflagellin proteins. (Figure 2, p. 4)

flora

Plant life (inappropriate term for protocists or fungi).

food web

Feeding relations in a biological community such that each organism in the web obtains nutrients from another organism(s) and in turn provides nutrients to yet another organism(s), ranging from the simplest autotroph at the bottom to the carnivore at the top of the web.

fossil

Physical evidence of an organism from past geological ages that has been preserved in Earth's crust, for example, dinosaur footprint, leaf imprint, plant pollen, or fungus spore.

free-living (adj.)

Living unattached, or attached but not symbiotrophically, to other organisms.

frond

(1) Large leaflike structure, usu. with many divisions (as in ferns or palms). (2) Divided thallus that resembles a leaf (as in seaweed).

fruit

Mature, ripened ovary (or ovaries), the seed-bearing structure, and associated structures of a flowering plant.

fruiting body

Structure that contains or bears seeds, spores, cysts, or other propagules (ill-advised botanical term).

fucoxanthin

Brown carotenoid found in chrysophytes, phaeophytes, and other algae.

Gaia

The whole Earth living system; the biota—the sum of the microbiota, plants, and animals—embedded in the biosphere. The Vernadskian space where life exists.

gametangium (pl. gametangia)

Organ of plants or prototists in which mitosis occurs and gametes or gamete nuclei are generated, and from which they are released.

gamete

Mature haploid reproductive cell (egg or sperm) capable of fusion with another gamete, of a different mating type, to form a diploid zygote.

gametophyte

Haploid gamete-producing generation in plants and some prototists. Compare *sporophyte*.

gamont

Body of an organism; adult life-cycle stage that produces gametes.

gap junction

Intercellular, membranous, discontinuous junction that fastens cells together in animal tissues and that is thought to regulate the flow of ions between cells.

gastrodermal (adj.)

Relating to the thin layer of tissue that lines the digestive tract of marine animals.

gastrula (pl. gastrulae or gastrulas)

Animal embryo in which the blastula with its single layer of cells becomes a three-layered embryo and the inner digestive tissue begins to form (a process called gastrulation).

gemma (pl. gemmae; var. gemmule)

Propagule; asexual reproductive structure; a small mass of cells from body tissue that can be released and develop into a new individual.

gemmule

See *gemma*.

gender

The sum of the behavioral and physiological traits that identify potential mating types (e.g., sexual partners or conjugants) prior to a sexual union.

gene

Smallest physical unit of heredity; sequence of nucleotides in DNA that is sufficient to specify a protein product.

generative (adj.)

Capable of further growth and/or reproduction.

genome

Complete set of genetic material required for life of a cell or organism.

genus (pl. genera)

Taxonomic level below family and above species; the first part of the two-part name in binomial nomenclature.

germ tube

Tube-shaped structure capable of continued growth.

germinate (v.)

To begin to grow (for seed); to begin to form gametophyte (for spore).

giant cell

Unusually large cell among cells of normal size.

gill

(1) One of the plates on the underside of the cap of a basidiomycote. (2) Respiratory organ used for uptake of oxygen and release of CO₂ by aquatic animals.

glucose

Carbohydrate with the chemical formula C₆H₁₂O₆.

Golgi apparatus (var. Golgi body)

Layered, cup-shaped organelle composed of modified endoplasmic reticulum that plays a role in storing and secreting metabolic products. Golgi body; dictyosome (referring to plants).

Golgi body

See *Golgi apparatus*.

gonad

Animal organ composed of tissues that produce gametes; e.g., the ovary (which produces eggs) and the testis (which produces sperm).

gonomere

Reproductive structure of ellobiopsids, borne on a trophomere, that contains spores.

Gram-negative (adj.)

Failing to retain the purple stain when subjected to the Gram staining method, indicating the presence of certain component layers in the cell wall (e.g., Gram-negative bacteria). The result of Gram staining is a characteristic used to classify bacteria.

granellare

The plasma body (protoplasm) of a xenophyophoran together with its surrounding branched, yellowish tubes.

grex

Multicellular, migratory slug phase of dictyostelid slime molds.

gullet

Oral cavity.

gymnosperm

Seed plant in which the seeds are not enclosed in an ovary (e.g., a conifer).

habitat

Natural environment in which an organism lives.

haploid (adj.)

Cell or organism with cells containing one set of chromosomes, the chromosome complement of sexually produced eukaryotic cells after meiosis; 1 N. Compare *diploid*.

haplosporangium

Spherical, membrane-bounded organelle, of haplosporans and possibly myxosporans and paramyxans, with unknown function.

haptosome

Intracellular, protruding, microtubular organelle of prymnesiophytes, usu. coiled, often used as a holdfast.

hemocoel (var. hemocoelom)

Fluid-filled body cavity that functions as part of the circulatory system.

herbaceous (adj.)

Nonwoody (referring to plants).

herbivory

Mode of nutrition by which an organism obtains nutrition and energy by eating plants or algae.

hermaphrodite

Organism that simultaneously possesses male and female organs on the same body.

heterokaryon

Cell or hypha, typically of fungi, that contains any number of nuclei of two genetically distinct forms (the sources of which are known), usu. one from each parent after sexual fusion. Compare *dikaryon*.

heterokont (adj.)

Having two undulipodia of unequal length, usu. one forward-directed and the other trailing (referring to mastigote or algal cells).

heterosporous (adj.)

Bearing spores of two different kinds (typically, microspores and megaspores) simultaneously. Compare *homosporous*.

heterotroph

Organism that obtains carbon and energy ultimately produced by autotrophs; osmotrophs, parasites, carnivores, and others are heterotrophs.

Higgins larva

Juvenile stage of loriciferans.

histone

Member of a class of proteins rich in nitrogenous bases that complexes with nuclear DNA in eukaryotes.

homologous (adj.)

Relating to structures or behaviors that have evolved from common ancestors, even if the structures or behaviors have diverged in form and function.

homosporous (adj.)

Relating to a plant body that is capable of forming haploid spores as products of meiosis, of only one kind.

hormone

Substance that is secreted directly into body fluid or blood by ductless glands and is carried to a specific target cell or organ, where, in minute amounts, the hormone brings about a specific physiological response.

host

Nonspecific term for an organism that provides nutrition or lodging for symbiotrophs, or the larger member of a symbiotrophic association. (Should be replaced by a more precise term.)

hybridization

Formation of offspring between two genetically unlike parents.

hydrostatic (adj.)

Relating to fluids at rest or to the pressures they exert or transmit.

hydrothermal (adj.)

Relating to hot water.

hydrothermal vent

Vent in Earth's crust that emits hot water.

hygroscopic (adj.)

Readily taking up and retaining moisture.

hypertrophy

Overgrowth; unusual increase in size or number of cells or organisms.

hypha (pl. hyphae)

Threadlike tubular filament, a component of a mycelium, usu. of a fungus or a funguslike protocist.

hypnocyst

Resting cyst of a dinomastigote. A hystrichosphere is a fossil hypnocyst.

infection

Initiation of a symbiotrophic (usu. necrotrophic) relationship between organisms of different species.

infusion

Liquid extract obtained by steeping or soaking a substance, usu. leaves or other dry organic material, in usu. hot or boiling water.

infusoriform larva

Ciliated, immature mesozoan; a swarm larva.

inoculation

Introduction of bacteria, protists, or fungi into a medium suitable for their growth or introduction of cell or chemical material into a competent animal that stimulates the production of antibodies in the latter.

inorganic (adj.)

Lacking carbon-hydrogen bonds.

integument

skin or enveloping layer of an organism.

intertidal (adj.)

Relating to or occurring in the zone between the tides, which is covered with sea water at high tide and exposed at low tide.

introvert

Slender anterior body part that can be turned inside out and completely withdrawn into the trunk of an animal body.

invertebrate

Animals that lack vertebrae or spinal column; compare *vertebrate*.

ion

Atom or group of atoms that carries a positive or negative electric charge.

isoprenoid

One of a class of organic compounds that are synthesized from multiples of a ubiquitous five-carbon compound precursor (isopentenyl pyrophosphate).

jacket cells

Ciliated cells that comprise the outer layer of cells in mesozoans.

karyogamy

Fusion of nuclei, usu. in fertilization that precedes meiosis.

kinetid

Kinetosome and associated microtubules and fibers in all undulipodiated cells (e.g., the unit of structure of the ciliate cortex).

kinetosomal fiber

Fiber found proximally to cilia and undulipodia; part of the kinetid and therefore diagnostic for ciliate taxonomy.

kinetosome

Organelle at the base of an undulipodium that is responsible for its formation and that is composed of microtubules in the [9(3)+0] configuration; centriole without an axoneme.

kinety

Row of kinetids; structure of the ciliate cortex.

kingdom

The most inclusive taxonomic level, immediately above phylum.

lamella (pl. lamellae)

Flat, thin scale or flattened saclike structure.

larva (pl. larvae)

Immature form of an animal, morphologically distinguishable from the adult form.

lasso cell

Sticky, threadlike cell, found on the tentacles of cnidarians and ctenophores, that stings and captures prey.

legume

Plant that is a member of the pea and bean family (Leguminosae).

leucoplast

Cell organelle of algae; colorless or white plastid that often stores starch.

life cycle

Sum of the events throughout the development of an individual organism that correlate environment and morphology with genetic and cytological observations (e.g., ploidy of the nuclei, fertilization, meiosis, karyokinesis, or cytokinesis).

life history

Sum of the events throughout the development of an individual organism that correlate environment with changes in external morphology, formation of propagules, and other observable aspects (e.g., spore, ameba, pseudoplasmodium, slug, or sporophore).

lignin

Polymer related to cellulose that is a major constituent of the secondary cell walls of many vascular plants that contributes strength and stiffness to woody plants.

lipid

Member of a class of chemicals made by living beings, organic compounds soluble in organic but not aqueous solvents. Lipids include fats, waxes, steroids, phospholipids, carotenoids, and xanthophylls.

littoral zone

Marginal zone of the sea or lake shore in which light reaches the bottom.

lobate (adj.)

Having lobes.

lophophore

Ridge surrounding the mouth that bears hollow, ciliated tentacles and traps food, found in several phyla of animals: phoronids, bryozoans, brachiopods.

lorica

Secreted protective covering, test, shell, valve, or sheath.

M**macrocyt**

Propagule; large cyst (e.g., of dictyostelids or myxomycetes).

macronucleus (pl. macronuclei)

The larger of the two kinds of nuclei in ciliate cells; site of messenger RNA synthesis; "physiological" nucleus that contains many copies of each gene and, unlike the micronucleus, is required for growth and division.

madreporite

External aboral terminus of the water vascular system of an echinoderm. Sieve plate.

mantle

Covering or coat of brachiopods and molluscs; body wall that secretes a shell.

marine

Oceanic.

mastigoneme

Hairlike, lateral projection on undulipodia.

mastigote

Eukaryotic microorganism motile via undulipodia; eukaryotic "flagellated" cell.

mating

Contact or fusion of cells, nuclei, or gamonts of complementary gender.

medulla (pl. medullae)

Inner portion of a gland or other structure surrounded by cortex.

medusa (pl. medusae)

Free-swimming, bell-shaped or umbrella-shaped stage in the life cycle of many cnidarians.

megagametophyte

Female gametophyte—i.e., the haploid generation of the plant (e.g., in angiosperms)—located within the ovule of the seed.

megaphyll

Large leaf having a web of veins or parallel veins. Compare *microphyll*.

megasporangium (pl. megasporangia)

Organ of plants in which female meiotic products form that usu. produce one to four megaspores. Compare *microsporangium*.

megaspore

Cell in the life cycle of plants; haploid spore that develops into a female gametophyte.

meiosis

One or two successive divisions of a diploid nucleus (with two sets of chromosomes) that result in the production of haploid nuclei (with one set of chromosomes each).

merozoite

Life-cycle stage (e.g., in apicomplexan protists) that is the mitotic product of a trophozoite.

mesoglea

Noncellular gel formed between ectoderm and endoderm of cnidarians and comb jellies.

mesokaryotic (adj.)

Relating to dinomastigote nuclei that lack conventional histones and have permanently condensed chromosomes; literally, "between prokaryotic and eukaryotic."

Mesozoic era

Geological time from 248 million to 66 million years ago that is composed of three periods: Triassic, Jurassic, and Cretaceous.

metabolism

Sum of the enzyme-mediated biochemical reactions that occur continually in cells and organisms and provide the material basis for autopoiesis.

metabolite

Small carbon compound that is the substrate, intermediate, or product of a metabolic reaction.

metamorphosis

Abrupt developmental transition from an immature to an intermediate or adult form (e.g., tadpole to frog).

metazoan

Animal; organism classified in the kingdom Animalia.

meter (abbr. m)

Basic metric unit of length; equal to 39.37 inches.

methanogenesis

Production of methane gas (CH_4) by live organisms (bacteria).

methylo trophy

Nutritional mode in some archaeobacteria that involves the consumption of methane or other single-carbon compounds using oxygen as a source of carbon and energy.

microaerobic (adj.)

Relating to environmental conditions in which oxygen is present in less than normal atmospheric concentrations (i.e., less than 20% by volume). Microoxic; dysaerobic.

microbe

Organism that requires a microscope to visualize it; microscopic living thing: bacterium, protist, or small fungus.

microbial mat

Carpetlike community of microorganisms, usually cyanobacteria; living precursor of a stromatolite.

microbiota

Microbial life; sum of the microorganisms in a given habitat.

microcosm

The world of the subvisible; communities of organisms that can be seen only by microscopy.

microgametophyte

Male gametophyte; the smaller haploid plant that produces male gametes by mitosis. Compare *megagametophyte*.

micrometer (abbr. μm)

10^{-6} meter.

micronucleus (pl. micronuclei)

The smaller of the two kinds of nuclei in ciliate cells, it does not synthesize messenger RNA. Most micronuclei are diploid and are required for meiosis and autogamy but not for asexual growth and division.

microorganism

See *microbe*.

microphyll

Small leaf with one vein, characteristic of club mosses.

microsporangium (pl. microsporangia)

Structure in which male meiotic products (microspores) form.

microspore

Haploid spore that develops into a male gametophyte. Compare *megaspore*.

microtubular ribbon

Row of microtubules; component of kinetids, associated with the movement of ciliates.

microtubule

Slender, hollow, proteinaceous, intracellular structure, usu. about 24 nanometers in diameter, found in axopods, axonemes, mitotic spindles, undulipodia, haptonemes, nerve cell processes, and other intracellular structures.

millimeter (abbr. mm)

0.001, or 10^{-3} , meter.

mitochondrion (pl. mitochondria)

Organelle in which the chemical energy in reduced organic compounds (food molecules) is transferred to ATP molecules by oxygen-requiring respiration.

mitosis

Nuclear division in which attached pairs of duplicate chromosomes move to the equatorial plane of the nucleus, separate at their centromeres, and move along the mitotic spindle to form two separate chromosome groups. Subsequent division of the cell after mitosis produces two genetically identical offspring cells.

mitotic spindle

Transient microtubular structure that forms between the poles of nucleated cells, forming the structures along which chromosomes move in mitosis.

molt

To shed an outer covering, such as feathers, skin, or cuticle.

monad

Single unit; single-celled organism.

monocotyledon (var. monocot)

Plant that has only one cotyledon in the seed; member of a subphylum of flowering plants (angiosperms). Compare *dicot*.

monoecious (adj.)

Botanical term describing plant having male and female parts on different structures of the same organism; hermaphroditic. Compare *dioecious*.

monomer

Unit of a polymer; chemical component (e.g., amino acid of protein).

monosaccharide

A simple sugar.

morphology

Form and structure of an organism or any of its parts; study of structure or form.

mucilaginous (adj.)

Of, relating to, full of, or secreting mucilage, a gelatinous substance that contains protein and polysaccharides.

multicellular (adj.)

Organisms composed of more than one cell.

multinucleate (adj.)

Membrane-bounded structure, cell, or organism, that contains more than one nucleus.

mycelium (pl. mycelia)

Mass of hyphae that constitutes the body of a fungus or a funguslike protocist.

mycology

Study of fungi.

mycorrhiza (pl. mycorrhizae)

Symbiotic physical connection between the hyphae of a fungus and the roots of a plant.

myxospore

Spore or other desiccation-resistant stage of a myxobacterium.

N**nanometer (abbr. nm)**

10^{-9} meter.

necrotrophy

Nutritional mode in which a symbiotic partner damages or kills the organism in or on which it resides.

- nectar**
Sugar-rich fluid secreted by gland of angiosperms and some gnetophytes.
- needle**
Slender, modified leaf shape of conifer.
- nematocyst**
Cell of animals (e.g., ctenophores, cnidarians) containing a threadlike stinger—and in some cases, poisonous or paralyzing substances—used for anchoring, defense, or capturing prey.
- nephridium (pl. nephridia)**
Excretory organ of many aquatic animals.
- niche**
Role performed by members of a species in a biological community.
- nomenclature**
System of identification and naming.
- notochord**
Long elastic rod that is the internal skeleton in chordate embryos and that is replaced by the vertebral column in most adult chordates.
- nucleic acid**
Long-chain molecule composed of nucleotides. Found esp. in cell nuclei, these molecules (e.g., DNA and RNA) are the basis of heredity and protein synthesis.
- nucleoid**
DNA-containing structure of prokaryotic cells, not bounded by a membrane.
- nucleoplasm**
Fluid contents of the nucleus of a cell.
- nucleotide**
Compound composed of a sugar, a base, and a phosphate group; building block of nucleic acids.
- nucleus (pl. nuclei)**
Large membrane-bounded organelle that contains most of the genetic information of a cell in the form of DNA.
- nutrition** Sum of the processes by which an organism takes in and utilizes food and energy sources—particularly carbon, nitrogen, phosphorus, and sulfur.
- O**
- obligate (adj.)**
Compulsory; mandatory.
- octopod**
A cephalopod mollusc that has eight arms with sessile suckers.
- omnivory**
Mode of heterotrophic nutrition by which an organism obtains its food from a wide variety of microbes, plants, and animals.
- oocyst**
Desiccation-resistant, thick-walled structure in which apicomplexans are transferred from the tissue of one animal to that of another.
- oogonium (pl. oögonia)**
Unicellular female sex organ that contains one or several eggs; female gametangium.
- order**
Taxonomic level below class and above family.
- organ**
Differentiated structure consisting of cells and tissues that are coordinated to form a specific function in an organism.
- organelle**
Literally, "little organ"; visually distinct intracellular structure composed of a complex of macromolecules and small molecules (e.g. sulfur globule, nucleus, mitochondrion, or undulipodium).
- organic (adj.)**
Of, relating to, or containing reduced (hydrogen-rich) carbon compounds.

osmolyte

Substance that maintains the salt balance in a cell.

osmosis

Movement of a solvent through a semipermeable membrane into a solution of higher solute concentration that tends to equalize the concentrations of solute on the two sides of the membrane.

osmotrophy

Mode of nutrition in which nutrients are obtained by absorption, the direct uptake of food molecules across membranes.

ostium (pl. ostia)

Mouthlike opening into a bodily organ.

ovary

Multicellular female reproductive organ that surrounds the egg(s).

ovule

Structure in seed plants that contains the egg cell and, after fertilization, develops into a seed.

oxic (adj.)

Containing molecular oxygen (referring to habitats).

oxidation

Combination of a molecule with gaseous or atomic oxygen or the removal of hydrogen from a molecule.

oxygenic (adj.)

Producing oxygen.

P**Paleozoic era**

Geological period from about 590 million to 248 million years ago.

papilla (pl. papillae)

Small bump or projection.

parapodium (pl. parapodia)

Fleshy, segmented appendage of polychaete annelids.

parasexuality

Process that forms an offspring cell from more than a single parent without standard meiosis or fertilization.

parasite

Organism that lives on or in an organism of a different species and obtains nutrients from it, usu. referring to a symbiotroph with necrotrophic tendencies.

pathogen

Organism that causes disease, usu. a microorganism that lives necrotrophically on or in an organism of a different species.

pellicle

Thin, typically proteinaceous outer layer of a cell or organism, outside the plasma membrane.

pennate (adj.)

Resembling a feather, esp. in having similar parts arranged on opposite sides of an axis like the barbs on the rachis of a feather.

peptidoglycan

Rigid layer of bacterial cell walls.

perfect (adj.)

Having both male and female reproductive organs on the same flower (referring to plants).

periplasm

Peripheral cytoplasm; in prokaryotes, the space between the inner plasma membrane and the peptidoglycan layer of the cell wall.

periplastidial compartment

Space between the plastid membrane and the plastid endoplasmic reticulum.

pH

Scale for measuring the acidity of aqueous solutions. Pure water has a pH of 7 (neutral), solutions with a pH greater than 7 are alkaline, less than 7 are acidic.

phaeodium (pl. phaeodia)

Pigmented mass consisting primarily of waste products around the astropyle of the central capsule of phaeodarian actinopods.

phagocytosis

Ingestion, by a cell, of solid particles by flowing over and engulfing them whole.

phagotrophy

Mode of nutrition involving cell motility; active ingestion of particles via formation of food vacuoles.

pharynx (pl. pharynges or pharynxes)

Throat; part of the digestive tract between the mouth cavity and the esophagus.

pheromone

Hormone transported through air to its target organism. If the pheromone is produced by one sex and responded to by the other sex, that hormone is a sex hormone.

phloem

Vascular tissue of plants that transports photosynthate, such as sugar, and other products of photosynthesis throughout the plant.

phospholipid

Lipid that contains phosphate esters. Cell membranes are made of layers of phospholipids in which proteins are embedded.

photic zone

Region of surface waters in which enough sunlight penetrates to support photosynthesis. The photic zone may extend 200 meters (approximately 600 feet) deep in clear lakes or open ocean or may be less than a centimeter in turbid water.

photoautotrophy

Mode of nutrition in which all nutrient and energy requirements are met by using inorganic compounds and visible light; characteristic of cyanobacteria, algae, and plants.

photoheterotrophy

Mode of bacterial nutrition in which all nutrient and energy requirements are met by using organic compounds and visible light.

photoplankton

Free-floating microscopic or small aquatic organisms that are capable of photosynthesis; motile algae. (Same as phytoplankton, but better term because phototrophic bacteria and algae are not plants.)

photosynthate

Chemical product of photosynthesis (e.g., glucose, starch).

photosynthesis

Production of organic compounds from carbon dioxide and a hydrogen donor (e.g., water, hydrogen sulfide [H₂S], or hydrogen) using light energy captured by chlorophyll and releasing oxygen gas (O₂), sulfur globules, etc., as waste.

phototrophy

Mode of nutrition in which light is the energy source.

phycobilin

Water-soluble, protein-bound pigment, generally bluish or red, that is found in red algal plastids and cyanobacteria.

phycobiliprotein

Complex of phycobilin pigments with protein.

phycobilisome

Intracellular structure that contains phycobilin pigments and is arranged as a protrusion on the surface of or within the thylakoid membrane of a plastid.

phylogeny

Evolution of a genetically related group of organisms; schematic diagram ("family tree") representing that evolution.

phylum (pl. phyla)

Taxonomic level below kingdom and above class.

phytoplankton

See *photoplankton*.

pigment

Chemical substance made by the cell(s) or tissue of an organism body that imparts color.

pit connections

Protoplasmic connections that join cells into tissues.

plankton

Free-floating, microscopic or small, aquatic organisms; ecological, not taxonomic, term for some bacteria, protocists, and animals.

planozygote

Motile zygote of dinomastigotes; enlarged, undulipodiated, and sometimes thick-walled mastigote formed just after fusion.

plantlet

Small plant that is produced asexually and shed, forming new individual club moss, fern, or flowering plant.

plasma membrane

Outer or cell membrane, composed of lipids and proteins, that surrounds a cell and regulates the exchange of material between the cell and its environment.

plasmodesma (pl. plasmodesmata or plasmodesmas)

Minute cytoplasmic threads that interconnect plant cells through pores in adjacent cell walls.

plasmodial reticulum (pl. plasmodial reticula)

Cytoplasmic network through which ameboid cells move, characteristic of chlorarachnids.

plasmodium (pl. plasmodia)

Multinucleate mass of cytoplasm lacking internal cell membranes or walls.

plastid

Cytoplasmic, photosynthetic pigmented organelle (such as a chloroplast) or its nonphotosynthetic derivative (such as a leucoplast or etioplast).

polar capsule

(1) In myxosporans, apical, thick-walled vesicle of a spore containing a spirally coiled, extrusible polar filament. (2) In heliozoan actinopods, region of dense cytoplasm that appears at opposite sides of the nucleus during mitosis.

polar filament

Closed, tubelike structure coiled within the polar capsule of a myxosporan, which, when everted, has a sticky surface and may anchor the hatching spore to the surface of the intestine of the animal in which it resides.

polar membrane

See *polar organelle*.

polar organelle

Proteinaceous structure inside a bacterial cell (e.g., of *Cristispira* or *Desulfovibrio*) near the flagellum, which is believed to be associated with motility.

polar tube

Tubular, extruding organelle of microsporans spores that forcibly injects sporoplasm into single cells of animal tissue.

pollen

Propagule; microspore of seed plants that contains a mature or immature male gametophyte, also called pollen grain

pollination

Transfer of pollen from the stamen (the male reproductive organ) to the stigma (the female reproductive organ) in angiosperms (flowering plants).

polymer

Chemical compound that consists of repeating structural units called monomers.

polymerase

Enzyme that catalyzes the formation of polymers (e.g., DNA or RNA) by linking monomers.

polymorphism

Morphological (form) or genetic differences between individuals that are members of the same species.

polyploid

An organism, tissue, or cell that has more than two complete sets of chromosomes.

polyp

Life-cycle stage of cnidarians that is a cylindrical tube closed and attached at one end and open at the other end by a central mouth usu. surrounded by tentacles.

polypodial (adj.)

Having more than one pseudopod.

polysaccharide

Carbohydrate composed of many monosaccharide units joined to form long chains (e.g., starch and cellulose).

population

A group of organisms of the same species in the same place at the same time.

predation

Mode of heterotrophic nutrition that is necrotrophic but not symbiotrophic involving preying on moving bacteria, protocists, or animals.

primary producer

Ecological term for photo- or chemoautotrophic organisms; autotroph.

proboscis

Tubular protrusion or elongation of the head or snout.

process

Extension of a cell—e.g., a spicule, a heliozoan spine (axopod), or a foraminiferan reticulopod.

prokaryote

Organism composed of cells that lack a membrane-bounded nucleus, membrane-bounded organelles, and DNA coated with histone proteins; member of Kingdom Bacteria.

propagule

Unicellular or multicellular structure produced by an organism and capable of survival, dissemination, and further growth (e.g., cyst, spore, seed, and some types of egg).

protein

Macromolecule composed of linked amino acids that is an essential constituent of all living cells.

Proterozoic eon

Geological period from 2,600 million to 520 million years ago, preceded by the Archean eon and followed by the Phanerozoic eon.

protist

Single-celled (or very few celled), and therefore microscopic, protocist.

protocist

Nucleated organism that contains more than a single bacterially derived genome per cell but is not animal, plant, or fungus. Protocists include the group of organisms traditionally called "protozoans" and all fungi with mastigote stages, as well as all algae (including kelps), slime molds, slime nets, and many other obscure eukaryotes. All protocists are products of coevolved bacterial symbioses, and some, such as kelp, are too large to be called protists.

protoplasm

Fluid contents of a cell (i.e., cytoplasm and nucleoplasm).

protoplast

Nucleus and cytoplasm of a cell from which the cell wall has been removed.

protozoan

Informal name of a member of the animal phylum Protozoa in the traditional two-kingdom (plant/animal) classification system consisting primarily of heterotrophic, microscopic eukaryotes (i.e., the smaller heterotrophic prototists and their immediate photosynthetic relatives). (Obsolete term.)

pseudocilium (pl. pseudocilia)

Protoplasmic protrusion of a cell that contains microtubules and is derived from the typical axoneme but is immotile; mastigoneme found on glaucocystophytes.

pseudoplasmodium (pl. pseudoplasmodia)

(1) Structure resembling a multinucleate plasmodium that has retained its cell membrane boundaries. (2) Aggregate of amebas. (3) Uninucleate trophozoite cell containing one to several generative cells.

pseudopod (var. pseudopodium)

Temporary cytoplasmic protrusion of an ameboid cell used for locomotion or phagocytotic feeding.

pseudopodium (pl. pseudopodia)

See *pseudopod*.

pycnidium (pl. pycnidia)

Asexual, hollow, dark-staining, multicellular structure lined on the inside with spore-bearing conidiophores, characteristic of fungi.

pyrenoid

Proteinaceous organelle inside some plastids that is a center of starch formation.

R**radula (pl. radulae or radulas)**

Horny, toothed organ of molluscs; used to rasp food and carry it into the mouth.

recombinant

Organism or molecule derived from sexual processes such as fertilization or recombination of DNA.

red tide

Sea water discolored by the presence of large growing populations of dinomastigotes. Blooms of some chrysophytes, euglenids, and the ciliate *Mesodinium rubrum* have also been correlated with red tides.

replication

Process that increases the number of DNA or RNA molecules.

reproduction

Process that increases the number of individuals. Asexual reproduction requires only one parent; sexual reproduction requires at least two parents.

respiration

Oxidative breakdown of food molecules and release of energy from them in which the terminal electron acceptor is an inorganic compound such as oxygen or nitrate.

resting cyst

Dormant life-cycle stage.

reticulopodium (pl. reticulopodia)

Very slender, anastomosing pseudopod that is part of a network of cross-connected pseudopods, characteristic of foraminiferans.

rhizoid

Rootlike structure in chytridiomycotes, algae, and many other prototists, which anchors and absorbs.

rhizome

Subterranean or creeping plant stem that sends out shoots from near its tip or at nodes along its length.

rhodoplast

Red plastid; the membrane-bounded photosynthetic structure of red algal cells.

rhyniophytes

Group of fossil plants from the Devonian period that contains genera of the earliest vascular plants.

ribosome

Spherical organelle composed of protein and ribonucleic acid; site of protein synthesis.

RNA

Ribonucleic acid; a molecule composed of a linear sequence of nucleotides that can store genetic information, RNA is a component of ribosomes and plays a part in protein synthesis.

rumen (pl. rumina or rumens)

One of the four chambers of the stomach of a cud-chewing mammal (ruminant) in which storage and initial digestion of food occurs.

S**sagenogen**

See *bothrosome*.

saprophyte

Osmotroph; organism that excretes extracellular digestive enzymes and absorbs dead organic matter.

sclerotium (pl. sclerotia)

Mass of hyphae, usu. with a darkened rind, that is capable of surviving unfavorable environmental conditions, characteristic of fungi.

sedentary (adj.)

Bottom-dwelling animal capable of limited locomotion. Compare *sessile*.

sediment

(1) Matter that settles to the bottom of a liquid. (2) Material that is deposited by wind, water, or glaciers.

seed

Propagule of a seed plant; ripened ovule that contains a plant embryo.

seed coat

In seed, outer layer that develops from integument of the ovule.

septate junction

Specialized area of adjoining cell membranes that show partitions in animal tissue.

septum (pl. septa)

Dividing wall or membrane.

serial endosymbiosis theory (abbr. SET)

Theory that all eukaryotic cells evolved from mergers among prokaryotes. According to the theory, undulipodia, mitochondria, and plastids began as swimming, respiring, and photosynthetic free-living bacteria that, in this order, established symbioses with *Thermoplasma*-like, fermenting bacteria.

sessile (adj.)

Attached; not free to move about.

seta (pl. setae)

Bristle.

sex

Formation of a new organism from more than a single genetic source, usu. from the genetic endowment of two parents.

soredium (pl. soredia)

Propagule; asexual reproductive structure of lichens; fragment containing fungal hyphae and algal cells.

sorocarp

Multicellular, aerial, stalked structure derived from the aggregation of many individual cells; characteristic of slime molds.

sorus (pl. sori)

Cluster of spores, sporangia, or similar structures in which spores are formed.

species

Taxonomic level below genus that contains organisms that resemble each other greatly. Animal (and plant) populations that interbreed readily with one another under natural conditions are grouped in the same species.

sperm

Male gamete of animal or plant, which is motile and usu. smaller than the female gamete.

spermatophore

Capsule or packet that contains sperm.

spermatozoan

Sperm; motile, undulipodiated male gamete of animals and some plants and protocists.

spicule

Small spine; slender, typically needle-shaped cell process.

spirillum (pl. spirilla)

Flagellated bacterium with a helical form in which the flagella are external to the membrane.

sporangiophore

Propagule-bearing structure; branch bearing one or more sporangia.

sporangium (pl. sporangia)

Hollow, unicellular or multicellular structure in which propagules (cysts or spores) are produced and from which propagules are released.

spore

Small or microscopic propagule, often dark, desiccation- and heat-resistant, that contains at least one genome and is capable of further growth and eventual maturation. Spores occur in bacteria, Protocista, Fungi, and Plantae kingdoms.

spore stalk

Propagule-bearing, multicellular, aerial, stalked structure derived from the aggregation of many individual cells; sporocarp; sorocarp.

sporocarp

Propagule-bearing structure, usu. stalked, spore-bearing structure in which one initial cell is the source of all the spores.

sporogony

Multiple-fission process of protocists, esp. apicomplexans; multiple mitoses of a spore or zygote with no increase in cell size, producing sporozoites.

sporophore

Propagule-bearing structure; protocist stalk that bears spores.

sporophyll

Plant leaf that bears sporangia.

sporophyte

Spore-producing diploid plant. Compare *gametophyte*.

sporoplasm

Propagule of symbiotrophic protists; infective body; ameboid organism within a spore.

sporozoan

Informal name of a member of the animal class Sporozoa (in phylum Protozoa) in the traditional two-kingdom classification system; ambiguous former name for apicomplexans, which included the spore-forming parasites: myxozoans and microsporans. (Obsolete term.)

sporozoite

Trophic propagule; motile, usu. infective product of multiple mitoses (sporogony) of a zygote or spore, characteristic of apicomplexans.

starch

Complex, insoluble polysaccharide carbohydrate of some algae and green plants that constitutes one of their main energy reserve materials.

statoblast

Propagule; asexually formed resistant internal bud of an ectoproct that, under severe conditions, is disseminated and grows into a new individual.

statolith (otolith)

Small movable concretion composed of calcium carbonate in statocysts (balance organ of marine animals that stimulates undulipodia [cilia] when the animal moves).

steroids

Saturated hydrocarbons that contain seventeen carbon atoms arranged in a system of four fused rings. The hormones of the gonads and adrenal cortex, the bile acids, vitamin D, digitalis, and certain carcinogens are steroids.

stigma (pl. stigmata or stigmas)

(1) In plants, the female flower part that is the receptive surface upon which pollen germinates. (2) In protocists, an eyespot.

stolon

Horizontal stalk near the base of a plant or colonial animal that produces new individuals by budding.

stomate (pl. stomata)

One of many minute openings bordered by guard cells in the epidermis of leaves and stems; route of gas exchange between air and the plant.

striated (adj.)

Striped; referring to muscle marked by light and dark bands and made up of elongated, multinucleate fibers.

strobilus (pl. strobili)

Modified ovule-bearing leaves or scales grouped together on an axis; cone.

stromatolite

Laminated carbonate or silicate rocks, organosedimentary structures produced by growth, metabolism, trapping, binding, and/or precipitating of sediment by communities of microorganisms, principally microbial-mat-forming cyanobacteria.

style

Rigid, elongated organ (female flower part) or appendage (e.g., crystalline style).

stylet

Rigid, elongated organ or appendage.

substrate

(1) Foundation to which an organism is attached (e.g., a rock). (2) Compound acted upon by an enzyme.

sulfuretum

Marine habitat in which the sand smells of rotten eggs because of the bacterial reduction of sulfate to hydrogen sulfide.

suspension feeding

Mode of heterotrophic nutrition; process of eating by filtering particles suspended in water.

swarmer cell

See *zoospore*.

symbiogenesis

The appearance in evolution of new forms of life resulting from symbioses, such as lichens from associations between algae and fungi; the fusion of lines on a phylogeny that represents new forms of life.

symbiont

Member of a symbiosis.

symbiosis

Intimate and protracted physical association between two or more organisms of different species.

symbiotrophy

Mode of nutrition in which a heterotrophic symbiont derives both its carbon and its energy from a living partner.

synangium (pl. synangia)

Organ; two or three sporangia joined together.

T**taxonomy**

Science of identifying, naming, and classifying organisms.

tentacle

Elongate, flexible, usu. tactile appendage.

terrestrial (adj.)

Dwelling on land.

test

Shell, hard covering, valve, or theca.

thallus (pl. thalli or thalluses)

Simple, flat, leaflike body of alga or plant undifferentiated into organs such as leaves or roots.

theca (pl. thecae)

Test; shell; hard covering.

thylakoid membrane

Photosynthetic membrane, lamella, or sac that bears chlorophylls, carotenoids, and their associated proteins usu. stacked in layers.

tissue

Aggregation of similar cells organized into a structural and functional unit; component of organs.

tornaria

Larva; immature, ciliated form of certain hemichordates.

trachea

Air-conducting tube.

tracheophyte

Vascular plant; plant that contains xylem and phloem.

trichocyst

Organelle underlying the surface of many ciliates and some mastigotes that is capable of sudden discharge to sting prey.

trochophore

Free-swimming, ciliated, marine larva.

trophic (adj.)

Of or relating to nutrition; referring to feeding form in life-history stage.

trophomere

Reproductive structure of ellobiopsids that bears gonameres, which contain spores.

trophosome

Digestive organ of submarine tube worms; midgut of vestimentiferans packed with symbiotrophic sulfide-oxidizing bacteria.

trophozoite

Growing, feeding life-history stage of symbiotrophic protists.

tuber

Fleshy, enlarged underground stem.

tumor

Amorphous swelling caused by uncontrolled growth of tissue cells with no apparent physiological function.

tun

Cryptobiotic form of tardigrades that is shaped like a wine cask.

U**ultrastructure**

Detailed structure of cells and organs that is visible by transmission electron microscopy.

undulipodium (pl. undulipodia)

Cilium or eukaryotic "flagellum"; the long, fine, intrinsically motile, intracellular structure of eukaryotes that is used for locomotion or for feeding. Undulipodia are underlain by [9(3)+0] microtubular kinetosomes from which they grow, as well as shaft microtubules in the [9(2)+2] array, and are composed of tubulin and other proteins (but not flagellin).

unicellular (adj.)

Having or consisting of only one cell.

uninucleate (adj.)

Having only one nucleus.

V**vacuole**

Space or cavity surrounded by a membrane in cell cytoplasm that contains fluid or air.

valve

Test, shell, or hard covering.

vascular (adj.)

Concerning vessels that conduct fluid (blood, lymph, sap, water) in a body.

vasoconstrictor

Chemical or pharmaceutical (e.g., ergot) that reduces or constricts vertebrate blood vessels.

vegetative (adj.)

(1) Resulting from mitotic cell divisions. (2) Of or relating to a growing and feeding stage of an organism's life history.

ventral (adj.)

On or toward the belly or undersurface; in humans, the front of the body. Compare *dorsal*.

vermiform (adj.)

Resembling a worm in shape.

vertebra (pl. vertebrae or vertebrae)

One of the bony or cartilaginous segments that make up the spinal column.

vertebrate (adj. and n.)

Animal having a spinal column.

vibrio

Bacterium shaped like a comma.

virus

Protein-coated genetic material that is capable of growth and replication only within a living cell.

X**xanthin**

Yellow or orange carotenoid that is soluble in alcohol.

xanthophyll

One of several yellow or orange oxygenated carotenoid pigments.

xanthoplast

Plastid that contains xanthophylls.

xenoma

Symbiotic aggregate formed by multiplying intracellular symbiotrophs within growing tissue cells, the whole structure increasing in size, as in the single-celled tumors formed by microsporans.

xylem

Vascular tissue of plants that conducts water and minerals from the roots to other parts of the plant, xylem constitutes the wood of trees, woody vines, and shrubs.

Z**zooecium (pl. zooecia)**

Shelter made of calcium carbonate skeleton overlaid with chitin and within which ectoprocts are anchored.

zooplankton

Free-floating heterotrophic microorganisms.

zoospore

Undulipodiated, motile cell capable of germinating into a different developmental stage without being fertilized.

zygosporangium (pl. zygosporangia)

Sporangium in which zygospores are produced.

zygospore

Large, multinucleate, resistant structure (resting spore) that results from the fusion of two gametangia.

zygote

Diploid nucleus or cell produced by the fusion of two haploid cells and with the potential to develop into a new organism.

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Resources

We have included here references to the biology literature on biodiversity at levels from high school to professional and from classics to contemporary writings. This enables you to sample of the richness of published materials about life on Earth. These references link you to additional material that limitations of space make impossible to list here. All of the sources on this list are in the English language. In addition, much of the literature on natural history and science is published in other languages.

Internet sites that provide further information on organisms are listed as Virtual Field Trips in Margulis and Schwartz (1998).

Listed alphabetically by author, the works listed below have extensive bibliographies of their own, enabling the curious reader to delve even deeper into the literature. We list works by the following categories: (1) books, (2) articles, (3) classroom and laboratory teaching materials, (4) audiovisual materials, and (5) citation services. We describe briefly the contents of many entries. If illustrations are not mentioned, assume that the work has few or none. Each work is also identified by one of the following codes: AT (adult trade), ATX (adult text or reference, nonspecialized), ATX-S (adult text or reference that assumes readers have considerable previous experience in the subject matter), and YA (young adult readers).

Information about obtaining specific material is available from the publisher, the distributor, librarians, and bookshop keepers. These people can assist you in obtaining books and articles no longer in print and/or not in your local library. Useful search tools include SciDex, the Electronic Index to articles in *Scientific American*; a reference set called Books in Print (the list of paperback and hardcover books currently being published by many but not all publishers); the biological or chemical abstracting services; and ISI (Institute for Scientific Information (see page 227), which maintains on computer a huge data base of scientific publications that is available in many forms (e.g., print, floppy disk, magnetic tape, or compact disc).

Books

Balows, A., H. G. Trüper, M. Dworkin, W. Harder, and K.-H. Schleifer, eds. 1991. *The Prokaryotes. A Handbook on the Biology of Bacteria: Ecophysiology, Isolation, Identifi-*

cation, Applications. 4 volumes. Second edition. Springer-Verlag, New York. This exhaustive illustrated listing of bacterial groups is in large format with professional references. ATX-S.

Balick, M. J., and P. S. Cox. 1996. *Plants, People, and Culture: The Science of Ethnobotany*. Scientific American Library, W. H. Freeman, New York. Plant diversity related to people of a variety of cultures. Illustrated Maps. AT.

Balick, M. J., E. Elizabetsky, and S. A. Laird, eds. 1996. *Medicinal Resources of the Tropical Forest: Biodiversity and its Importance to Human Health*. Columbia University Press, New York. Illustrated. AT.

Barlow, C., ed. 1991. *From Gaia to Selfish Genes: Selected Writings in the Life Sciences*. MIT Press, Cambridge, MA. Sparsely but artistically illustrated, this book gives a wonderful flavor of the nature of the debate among life scientists and others about what life is and how life works. Insightful comments by the editor establish a context for a wide range of well-stated opinions. AT.

Baskin, Y. 1997. *The Work of Nature: How the Diversity of Life Sustains Us*. Island Press, Washington, DC. Human ecology, biodiversity, and conservation of natural resources. Elegantly illustrated. AT.

Brightman, F. H. 1966. *Oxford Book of Flowerless Plants*. Oxford University Press, New York. Diversity of fungi, ferns, mosses, liverworts, lichens, and seaweeds with exquisite watercolor illustrations. AT.

Callenbach, E. 1998. *Ecology: A Pocket Guide*. University of California Press, Berkeley, CA. This dictionary of ecological concepts is written in jargon-free prose, making it ideal for novices. YA.

Carpenter, P. L., T. D. Walker, and F. O. Lanphear. 1989. Second edition. *Plants in the Landscape*. W. H. Freeman, New York. Illustrated. AT.

Cloud, P. 1988. *Oasis in Space: Earth History from the Beginning*. W. W. Norton, New York. Profusely illustrated with maps, charts, diagrams, and photographs, this book is the master work of a great geologist who understood the first 80 percent of Earth's record, the pre-Phanerozoic time division during which life evolved and developed most of its tricks of planetary modification. Through this tour of the Hadean, Archean, and Proterozoic eons, we realize that the beginning of the story of biodiversity and environment is far too interesting to miss. ATX.

Dewdney, A. K. 1998. *Hungry Hollow: The Story of a Natural Place*. Copernicus, Springer-Verlag, New York. Biodiversity of the eastern deciduous North American forest under threat from humanity. Delightful voyage into the local microcosm. AT, YA.

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Eldredge, N. 1998. *Life in the Balance: Humanity and the Biodiversity Crisis*. Peter N. Nevraumont Book/Princeton University Press, Princeton, New Jersey. AT.

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Groombridge, B., ed. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. A report compiled by the World Conservation Monitoring Centre. Chapman & Hall, London. This large book, which contains colored biodiversity maps, is a report developed in collaboration with the Natural History Museum, London; the World Conservation Union; the United Nations Environment Program; the World Wildlife Fund for Nature; and the World Resources Institute. With no index and a limited glossary, it is still an up-to-date tabulation of the flora and fauna of the world. Although discussion of the microbiota is weak, the book is extremely useful for an international perspective on biodiversity. ATX-S.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L-A. C. Hayek, and M. S. Foster, eds. 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, DC. Diversity of amphibians, their natural histories, and how diversity is measured. Cloth and paper. ATX-S.

Hudson, H. J. 1986. *Fungal Biology*. Cambridge University Press, New York. Fungal ecology—biodiversity of the 60,000 or so fungal species. ATX.

International Union for the Conservation of Nature and Natural Resources. 1963-. *Animals and Plants Threatened with Extinction*. Morges, Switzerland. IUCN publishes the Red Data Book, a continuing series that lists rare and endangered mammals, reptiles, amphibians, birds, fishes, invertebrates, and plants. Compiled by various authors. ATX-S.

Joseph, L. E. 1990. *Gaia: The Growth of an Idea*. St. Martin's Press, New York. This story of how the idea of Gaia originated and was contested and co-opted by nonscientists gives the reader great insight into the relationship between specialist science and the ideas of the society that supports it. AT.

Kendrick, B. 1992. *The Fifth Kingdom*. Second edition. Mycologue Publications, Waterloo, Ontario, and Focus Information Group, Newburyport, MA. Illustrated with simple diagrams and black-and-white drawings, this book describes fungal diversity in taxonomic order. ATX.

Krieg, N. R., and J. G. Holt, eds. 1984–1989. *Bergey's Manual of Systematic Bacteriology*, 4 volumes, Williams & Wilkins, Baltimore and London. Nicknamed the microbiologist's "Bible," this standard reference now includes cyanobacteria and archaeobacteria—in fact all formally recognized bacteria—and now occupies four volumes. Reflecting the point of view of the professional microbiologist, the work's main purpose is to identify bacteria important to medicine, food processing, soil science, and other practices. ATX-S.

Lederberg, J., ed. 1992. *Encyclopedia of Microbiology*. Academic Press, San Diego. A four-volume, multi-authored work on topics ranging from AIDS in Africa to alkaliphilic bacteria, refrigerated foods, and wine, this text is less an encyclopedia than it is a smorgasbord of essays that give the reader a good idea of the current state of microbiology. ATX-S.

Lee, J. J., S. H. Hutner, and E. C. Bovee. 1985. *An Illustrated Guide to the Protozoa*. Society of Protozoologists, Lawrence, KS. Profusely illustrated primarily with drawings and scanning electron micrographs, this book is particularly good for the lower taxa of ciliates, dinomastigotes, and other small heterotrophic protocists. The protozoa are classified here in the animal kingdom, so the occasional inclusion of algae, slime molds, and other protocists that traditionally have been classified as plants or fungi is inadequate, as their treatment is prejudicially zoological. ATX-S.

Lincoff, G. 1981. *Audubon Society Field Guide to North American Mushrooms*. Knopf, New York. Illustrated guide to fungi in forests and fields of North America. AT.

Lovelock, J. E. 1988. *The Ages of Gaia: A Biography of Our Living Earth*. W. W. Norton, New York. The most articulate and riveting description of the idea that life, a planetary-level phenomenon, creates and alters its own habitat was written by the inventor of the idea that Earth is alive. Because Lovelock traces the planetary-level influence of life and its history both from its beginning and from his beginning as a student of the process, the book speaks in a personal way to the reader. AT.

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Margulis, L. 1992. *Diversity of Life: The Five Kingdoms*. Enslow, Hillside, NJ. With many black-and-white illustrations, this small book details the major features, members, and history of the five kingdoms and provides the background for the five-kingdoms poster classroom activities (see page 224). YA.

Margulis, L., J. O. Corliss, M. Melkonian, and D. J. Chapman. 1990. *Handbook of Protocista: The Structure, Cultivation, Habitats and Life Histories of the Eukaryotic Microorganisms and Their Descendants Exclusive of Animals, Plants and Fungi*. Jones and Bartlett, Boston. The "Bergey's Manual" (see Krieg and Holt, 1984) of the eukaryotic microorganisms, this large-format, profusely illustrated book, the work of fifty authors, integrates information on acquisition, culture, structure and classification, the fossil record, the literature, and other aspects of these organisms. ATX-S.

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Margulis, L., and K. V. Schwartz. 1998. Third edition. *Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth*. W. H. Freeman, New York. A photograph with size scale and a labeled drawing illustrate the structure of a typical member of each phylum of bacteria, protocists, fungi, animals, and plants with a description of

major features. In this book, which succinctly describes the highest taxa, all phyla are represented, about 100 inclusive groups of organisms. New discoveries about archaeobacteria are integrated into the rest of biology. The section Field Trips Through Time lists museums and parks that depict prehistoric life. ATX. Also available in translation.

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National Research Council. Committee on Research Opportunities in Biology. 1989. *Opportunities in Biology*. National Academy Press, Washington, DC. About 450 well-indexed pages explain the new, chemically based biology, cell and development study, medically oriented biology, evolution and diversity, ecology and ecosystems, plant biology, and agriculture as the professional views these subfields. This book is ideal for anyone studying biology, no matter at what level, especially for those who wish to enter the field. YA.

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Oldfield, M. L. 1989b. *The Value of Conserving Genetic Resources*. Sinauer, Sunderland, MA. Conservation of the diversity of life. Photographic illustrations. AT.

Pechenik, J. A. 1996. Third edition. *Biology of the Invertebrates*. Wm. C. Brown, Dubuque, IA. This college text of zoology depicts all major groups of aquatic and terrestrial animals, exclusive of the vertebrates, in their evolutionary context. Illustrated. ATX.

Perlman, D. L., and G. Adelson. 1997. *Biodiversity: Exploring Values and Priorities in Conservation*. Blackwell Science, Cambridge, MA. Defining biodiversity and practical problems in the protection of biodiversity. AT.

Rainis, K. G., and B. J. Russell. 1996. *Guide to Microlife*. Franklin Watts, New York. Microscopic animals, fungi, protists, and bacteria—their natural history, classification, and collecting. Color photos. YA.

Raven, P. H., R. F. Evert, and S. E. Eichhorn. 1999. Sixth edition. *Biology of Plants*. Worth/W. H. Freeman and Company, New York. Clearly written and elegantly illus-

trated, this description of all major groups of plants (and protocists traditionally classified with plants), their structures, life cycles, and likely evolutionary histories, is especially suited for college students seeking botanical knowledge. If you have one book about plants, this is an excellent choice. ATX.

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Simon, N. 1966-. *Mammalia*. IUCN, Lausanne, Switzerland. Rare mammals. Continuing.

Sneath, P. H., N. S. Mair, M. E. Sharpe, and J. G. Holt. 1986. *Bergey's Manual of Systematic Bacteriology*, volume 2. Williams & Wilkins, Baltimore. See Krieg and Holt (1984). Volumes 3 and 4 have now also appeared. ATX-S.

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Wilson, D. E., F. R. Cole, J. D. Nichols, R. Rudran, and M. S. Foster, eds. 1996. *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*. Smithsonian Institution Press, Washington, DC. Diversity and natural histories of all twenty-six orders of extant mammals and how biodiversity is sampled. ATX-S.

Wilson, E. O., ed. 1988. *Biodiversity*. National Academy Press, Washington, DC. Available in softcover, this book is the report of a symposium on the loss of diversity due primarily to the expansion of human ecosystems. Forests, coastal zones, "deep ecology," the monitoring of diversity and its value, attempts to restore lost ecosystems, and the varying views of nature are discussed in short papers by many well-qualified authors. A video of a portion of this symposium is available from the National Academy of Sciences. ATX.

Wilson, E. O. 1992. *The Diversity of Life*. Belknap Press of Harvard University Press, Cambridge, MA, and Norton (paper), New York. A moving and authoritative work on the value of nature in the fragility and splendor of its diversity, written by a master of biodiversity and arthropod expert. Charming, beautifully drawn, black-and-white illustrations and color photographs document the seriousness of species loss by habitat disturbance and destruction. AT.

Articles

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Classroom and Laboratory Teaching Materials

Teacher's Guides

Armstrong, L., and L. Margulis. 1992. *Teacher's Guide to the Five Kingdom Poster*. Ward's Natural Science Establishment, Rochester, NY. This guide describes class-

room activities to accompany the *Five Kingdoms* poster (drawings by Christie Lyons based on design by Dorion Sagan). YA.

Margulis, L., et al. 1992. *What Happens to Trash and Garbage? An Introduction to the Carbon Cycle*. Ward's Natural Science Establishment, Rochester, NY, which includes Margulis, L., and L. Olendzenski. 1991. *Common Fungi: Teacher's Guide* [videocassette]. This boxed unit provides from one lesson to several weeks of activities that link our ordinary experience with waste materials to the movement of matter, especially inorganic and organic carbon, through the biosphere, atmosphere, and soil, focusing especially on the roles of fungi and people in the carbon recycling process. A poster of the carbon cycle, photographs to be matched with appropriate captions, and other materials for associated activities come with the unit. YA.

Margulis, L., and D. Sagan. 1988. *The Microcosmos Coloring Book*. Harcourt Brace Jovanovich, Boston. With labeled drawings and explanation in the text, this entry into the strange world of the subvisible illustrates microbes of the seashore, forest, karst, and park (i.e., those living on people). YA.

Margulis, L., and L. Brynes. 1999. *Living sands: Using forams to map time and space*. Teacher's guide and student booklets. Ward's Natural History Establishment, Rochester, New York.

Margulis, L., and K. V. Schwartz. 1998. Third edition. *Five Kingdoms*. This newly revised edition includes a list of science museums, national parks, and state parks that feature animals, plants, seaweeds, and other ancestors in actual fossil deposits, dioramas, interpretive walks, and models—a glimpse of origins of biodiversity. A list of web sites directs anyone interested in biodiversity to additional information about organisms in all of the kingdoms of organisms.

Smithsonian Chart of Animal Evolution. Smithsonian Institution Press, Washington, DC 20560. Poster depicting relationships of extant and extinct terrestrial and aquatic animals with geological time scale that marks major events.

Projection Slides

The following slide sets, in color, are accompanied by teacher's guides that include worksheets. Single sets are packed in translucent, plastic sheets; the entire set of six comes in a notebook that includes pockets for the printed materials.

Margulis, L., and K. V. Schwartz. 1987. *Introduction to the Five Kingdoms* [20 35-mm slides and teacher's guide]. Ward's Natural Science Establishment, Rochester, NY. The history, distribution, and examples of the five kinds of life, as well as cell and virus structure, are illustrated.

Margulis, L., and K. V. Schwartz. 1987. *Monera* [40 35-mm slides]. Ward's Natural Science Establishment, Rochester, NY. The diversity of bacterial life, prokaryotic cell structure, and environmental effects of bacteria are explored. Teacher's guide included.

Margulis, L., and K. V. Schwartz. 1988. *Protoctista* [40 35-mm slides]. Ward's Natural Science Establishment, Rochester, NY. Examples of each major type of protist—algae, slime molds, ciliates, amoebas, and others—photographed live are shown. With teacher's guide.

Margulis, L., and K. V. Schwartz. 1987. *Fungi* [20 35-mm slides]. Ward's Natural Science Establishment, Rochester, NY. From mating hyphae of basidiomycetes through the resulting mushrooms to lichens and their components, this slide set shows the major features of fungi, their life cycles, beauty, and phylogeny. With teacher's guide.

Margulis, L., and K. V. Schwartz. 1988. *Animals* [40 35-mm slides]. Ward's Natural Science Establishment, Rochester, NY. An example of a member of each phylum of animals is shown alive in its habitat. Animal phylogeny, origin of domesticated animals, and teacher's guide.

Margulis, L., and K. V. Schwartz. 1987. *Plants* [40 35-mm slides]. Ward's Natural Science Establishment, Rochester, NY. An example of a member of each phylum (division) of plants is shown. Plant biodiversity and origin of domesticated plants are illustrated. With teacher's guide.

Audiovisual Materials

Margulis, L., and L. Olendzenski. 1991. *Common Fungi: Teacher's Guide* [videocassette]. Ward's Natural Science Establishment, Rochester, NY. The development of *Rhizopus* on bread, *Fusarium*, *Alternaria*, and *Coprinus* from spores is depicted. Hyphae, mycelia, growth rings, pigments, and other features of live fungi are illustrated. Each numbered scene via time-lapse photography is described in film notes. 16 minutes; silent.

Margulis, L., and D. Sagan. 1996. *Gaia to Microcosm* vol. 1. Kendall/Hunt Publishing Co., Dubuque, Iowa. Four part videocassette with 108 page booklet explaining each video sequence. Bacteria to Biosphere (14 minutes); Photosynthetic Bacteria—Sunlight Transformers (4 minutes); *Spirosymplokos deltaeiberi*—Microbial Mats and Mud Puddles (8 minutes); *Ophrydium versatile*—What Is an individual? (9 minutes).

Our Living Planet series [videocassette]. 1993. Ward's Natural Science Establishment, Rochester, NY. YA.

Part I: *Origins of Life*. Music and graphics are included in this explanation of modern ideas of how life began and what life is. 10 minutes; color.

Part II: *Five Kingdoms of Life*. With the help of live examples, models, and graphics and accompanied by music, this video reviews members of the five kingdoms and their interactions. 10 minutes; color.

Part III: *People Are . . . Mammals*. On a journey beginning at the level of kingdom (the animals) and traveling through the chordates, vertebrates, tetrapods, mammals, and primates to *Homo sapiens*, this video explains why people are classified as they are. 10 minutes; color.

Olendzenski, L., L. Margulis, S. Goodwin 1998. *Looking at Microbes: The Microbiology Laboratory for Students*. Jones and Bartlett Publishers, Sudbury, MA.

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SciDex 2.0, the *Scientific American electronic index*. Index to all articles in *Scientific American* magazine from 1948 to 1996. Easy access by author, title, and subject to articles regarding all facets of biodiversity from individual species to the facets of ecology and evolution that generate diversity. CD-ROM or 3.5" HD diskettes.

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