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# Microbiology

W Matthew Sattley, *Division of Natural Sciences, Indiana Wesleyan University, Marion, Indiana, USA*

Michael T Madigan, *Department of Microbiology, Southern Illinois University, Carbondale, Illinois, USA*

## Introductory article

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**Microbiology is the study of microorganisms – biological entities too small to be seen with the unaided eye. Most major advances in microbiology have occurred within the past 150 years, and several important subdisciplines of microbiology have developed during this time, including microbial ecology, molecular biology, immunology, industrial microbiology and biotechnology. Microorganisms of various types exist in all three domains of life (the *Bacteria*, *Archaea* and *Eukarya*), and they are by far the most abundant life forms on Earth. Microscopic biological agents include bacteria, archaea, protists (protozoa and algae), fungi, parasitic worms (helminths) and viruses. Although a small percentage of microorganisms are harmful to certain plants and animals and may cause serious disease in humans, the vast majority of microorganisms provide beneficial services, such as assisting in water purification and the production of certain foods, and many are essential for the proper functioning of Earth's ecosystems.**

## Microbiology and its Historical Roots

Microbiology is the study of microorganisms, microscopic organisms that include in particular the bacteria, a large group of very small cells that have enormous basic and practical significance (Madigan *et al.*, 2015). Microbiology considers all aspects of microbial cells, including their structure, metabolism, diversity, genetics and evolution, ecology and roles in infectious diseases. Microbiology is composed of several subdisciplines, each of which is focused on part of the broader science. Scientists

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who study microorganisms, called microbiologists, typically specialise in one or more of these areas (Table 1).

The science of microbiology developed later than other biological sciences, primarily because needed tools, such as the microscope, had to be developed to convincingly prove that microorganisms (also called microbes) exist. Following early microscopic discoveries, methods for the culture and identification of microorganisms were developed, and from these, our understanding of the enormous beneficial and detrimental effects of microbes began to unfold. We review some historical highlights in microbiology now.

## The discovery of microorganisms

The English naturalist Robert Hooke (1635–1703) was an early microscopist and published the first book devoted entirely to microscopic observations of microorganisms. Hooke prepared detailed and quite accurate drawings of moulds (fungi) and many other microbes, and these were the first known description of microorganisms.

The first person to see bacteria, which are typically much smaller than moulds, was the Dutch amateur microscopist Antoni van Leeuwenhoek (1632–1723). van Leeuwenhoek constructed simple microscopes that contained a single lens and used them to examine various natural substances. These microscopes were crude by today's standards, but by careful manipulation and focusing, van Leeuwenhoek was able to see a wide variety of microorganisms, including bacteria. van Leeuwenhoek reported his discoveries in a series of letters to the Royal Society of London, which were then published in the *Philosophical Transactions of the Royal Society*, one of the most prestigious scientific journals of the era and the first in the world exclusively devoted to science. His communications revealed a previously hidden microbial world that existed in water, nutrient solutions, the oral cavity and virtually anywhere one could imagine. van Leeuwenhoek's discoveries also boosted the long held belief that invisible agents of some sort were the cause of infectious diseases, a belief that was not scientifically confirmed until nearly 200 years later. **See also: Leeuwenhoek, Antoni van; Light Microscopy; History of Bacteriology**

## The golden age of microbiology

Major advances in microbiology in the nineteenth and early twentieth centuries surrounded four major scientific questions of that

**Table 1** Selected major subdisciplines of microbiology

Subdiscipline	Focus
Agricultural/soil microbiology	Microbial diversity and processes in soils
Aquatic microbiology	Microbial processes in water and wastewaters
Biotechnology	Production of high-value products by genetically engineered microorganisms
Genomics	Genome sequencing and analyses
Immunology	The immune response
Industrial microbiology	Large-scale production of antibiotics and commodity chemicals
Medical microbiology	Nature and control of infectious diseases
Microbial biochemistry	Enzymes, chemical reactions in cells, structural biology
Microbial ecology	Microbial diversity and activity in natural habitats, biogeochemistry
Microbial genetics	Genes, heredity and genetic variation
Microbial physiology	Nutrition, metabolism and bioenergetics
Microbial systematics	Classification and nomenclature
Molecular biology	Nucleic acids and proteins, genetic information processing
Virology	Viruses and subviral particles

period: (1) can life emerge from nonlife, (2) do microorganisms cause infectious diseases, (3) how diverse is the microbial world and (4) do soil and water microbes carry out any beneficial activities? These questions were addressed, respectively, through the research of four giants in the then growing field of microbiology: the French chemist Louis Pasteur (1822–1895), the German physician Robert Koch (1843–1910), the Dutch microbiologist Martinus Beijerinck (1851–1931) and the Russian microbiologist Sergei Winogradsky (1856–1953).

Pasteur initiated studies on the mechanism of the alcoholic fermentation, which in the mid-nineteenth century was assumed to be a strictly chemical process. Through microscopic observations and other rigorous experiments, Pasteur showed that the fermentation was actually caused by the metabolic activities of yeast cells. Pasteur then used these insights to design a series of classic experiments to disprove the theory of spontaneous generation, the widely held belief at the time that living organisms could arise from nonliving matter. Pasteur showed that if nutrient solutions are freed of all microorganisms (typically by heating) and protected from airborne contamination, they remain microbe-free unless and until microorganisms are introduced. Pasteur's work on spontaneous generation forced him to develop effective sterilisation procedures, many of which have remained mainstays in microbiology and clinical medicine to this day.

Pasteur went on from his seminal work on spontaneous generation to a series of triumphs in medical microbiology. These included the development of a vaccine against the otherwise fatal disease rabies and the demonstration that attenuated vaccines, made from noninfectious but still active microbes, are safe and typically more effective than killed vaccines. These were some of the first practical successes in the field of infectious disease microbiology. However, despite the extensive work of Pasteur with various pathogenic agents (see also: **Pasteur, Louis**), definitive proof of cause and effect with any infectious disease remained elusive until the work of Robert Koch.

Robert Koch was a medical doctor primarily interested in infectious diseases and, in particular, the clear identification of causative agents of infectious diseases. Koch surmised that such studies would require the development of methods to

obtain laboratory cultures of suspected disease-causing microbes (pathogens), and many of the procedures he devised to do this, such as the use of Petri plates, remain standards in the microbiology laboratory today. From experimental studies on the disease anthrax and, later, tuberculosis, Koch developed a set of criteria (known today as Koch's postulates) that, when faithfully executed, unequivocally link a specific microbe to a specific infectious disease.

To fulfil his postulates, Koch and his associates devised methods to isolate suspected pathogens from diseased animals and grow them in pure cultures (containing only a single kind of microbe) in the laboratory. The ability to transmit an infectious disease by injecting the laboratory-cultured pathogen into a healthy animal was the linchpin in Koch's postulates and supplied the definitive proof needed to join cause and effect. In his greatest medical triumph, Koch used his newly developed laboratory methods to link the bacterium *Mycobacterium tuberculosis* with the disease tuberculosis, and for this monumental achievement, Koch was awarded a Nobel Prize in 1905. See also: **Koch, Heinrich Hermann Robert**

As microbiology entered the twentieth century, its initial focus on basic principles, methods and medical aspects broadened to include studies of the microbial diversity of soil and water and the metabolic processes that microorganisms carry out in these habitats. Notable microbiologists of this era were Martinus Beijerinck and Sergei Winogradsky. Beijerinck's greatest contribution was his development of the enrichment culture technique, a process in which highly selective nutrient and incubation conditions are used to isolate microbes from nature whose metabolism and other properties are best suited to the conditions employed and thus give them a competitive advantage. Using this technique, Beijerinck isolated the first pure cultures of many common soil and aquatic microorganisms we know today. See also: **Beijerinck, Martinus Willem**

Sergei Winogradsky was also interested in the microbial diversity of soils and waters but was particularly interested in the metabolic reactions carried out by bacteria. Winogradsky was the first to show that bacteria can oxidise inorganic nitrogen and sulphur compounds and that the organisms that oxidised

nitrogen compounds differed from those that oxidised sulphur compounds. Further, Winogradsky's brilliant insight into the metabolism of these organisms led him to propose the concept of chemolithotrophy, the oxidation of inorganic compounds for the purpose of obtaining the energy necessary for growth (Winogradsky, 1949). Winogradsky went on to show that these organisms – the chemolithotrophs – were widespread in nature and shared with plants the ability to use CO<sub>2</sub> as their sole carbon source. Winogradsky was thus the first to demonstrate that autotrophy occurred in nonphotosynthetic organisms, a property that we now know is widespread in the microbial world. **See also: Winogradsky, Sergei Nikolaevitch; Chemolithotrophy; Microbial Inorganic Carbon Fixation**

## The modern era of microbiology

The field of microbiology developed quickly in the twentieth century in step with the many new powerful laboratory tools that became available. During this period, microbiology as a science matured, spawning several new subdisciplines rooted in genetics and molecular biology (**Table 1**). Much of the science of microbiology today is fueled by genomics: the mapping, sequencing and analysis of genes and genomes. New and faster methods of deoxyribonucleic acid (DNA) sequencing coupled with robust computer analyses are being used to attack some of the greatest challenges in medicine, agriculture and the environment, and they have revealed the true extent and diversity of the microbial world (López-García and Moreira, 2008). **See also: Genome Sequencing; Genome Mapping**

Along with the suite of foundational techniques developed by early microbiologists, molecular microbiologists today are on track to understanding how cells work in unprecedented detail. This knowledge will help humans better exploit the beneficial effects and control the potentially devastating effects of microbial activities. However, before we consider some of these activities,

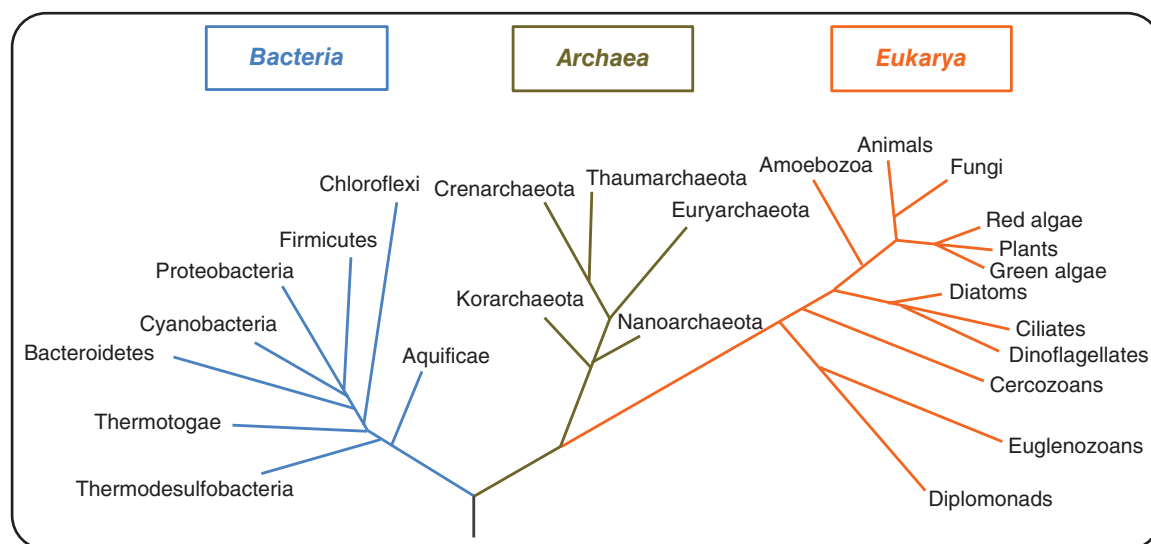
we need to compare and contrast the major microbial groups that compose the microbial world, and we focus on this topic now.

## Classification and Basic Characteristics of Microorganisms

Microorganisms encompass an enormous diversity of microscopic life forms, each with distinct characteristics. On the basis of their genotypic (genetic) and phenotypic (observed) properties, all organisms are classified into one of three domains – the *Bacteria*, *Archaea* or *Eukarya* – and numerous examples of microorganisms are found in all three (**Figure 1**; Woese *et al.*, 1990). The comparison of ribosomal ribonucleic acid (rRNA) gene sequences has been especially important in determining the evolutionary, or phylogenetic, relationships of organisms. Although very different on a phylogenetic level, the *Bacteria* and *Archaea* (traditionally called prokaryotes) are structurally similar in that cells of these groups do not typically contain membrane-bound organelles and, therefore, show a lesser degree of cellular compartmentalisation than organisms belonging to the *Eukarya* (the eukaryotes). The presence of membrane-bound organelles, including a defined nucleus, is the hallmark of eukaryotic cells, and microbial *Eukarya* include fungi, protists and certain helminths, especially the parasitic worms. An overview discussion of microbiology must also include a consideration of viruses, even though they are not cellular and thus are not included in the three-domain tree of life. We now consider each of these groups in more detail. **See also: Cell Structure; The Cell Nucleus; Phylogeny Based on 16S rRNA/DNA**

### The *Bacteria* and *Archaea*

The *Bacteria* and *Archaea* are vast groups of microorganisms consisting of potentially hundreds of thousands to millions of



**Figure 1** Universal phylogenetic tree showing relationships between major lineages of the three domains of life (*Bacteria*, *Archaea* and *Eukarya*). Tree topology and branch lengths were determined by comparative small subunit (SSU) rRNA gene sequence analysis.

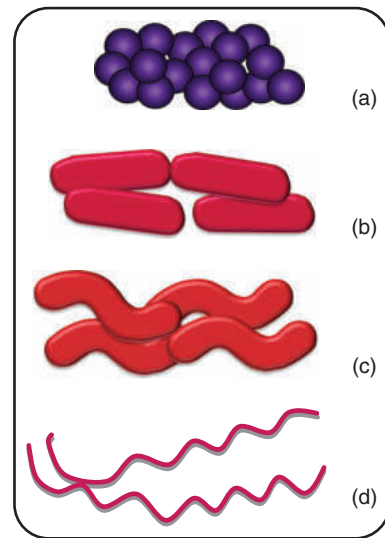
species, most of which remain uncharacterised. These microbes are ubiquitous, inhabiting and subsist in nearly every imaginable environment on Earth. Various species thrive on or within every plant and animal, within and underneath massive glaciers, in hypersaline waters of the Great Salt Lake and the Dead Sea, and even in boiling hot springs and deep sea volcanic (hydrothermal) vents. Many microorganisms, called extremophiles, are able to thrive in environmental conditions that humans would consider punishingly harsh, and numerous members of the *Archaea*, in particular, excel in this lifestyle. **See also: Archaea**

*Bacteria* and *Archaea* are classified based on (1) phylogenetic distinctions, (2) structural and morphological characteristics, such as cell shape, size and arrangement and (3) biochemical and physiological traits, such as growth factor requirements, range of carbon and energy sources and end products of metabolism. For example, the *Cyanobacteria* are a large phylum of physiologically and phylogenetically related *Bacteria* that carry out oxygenic ( $O_2$ -producing) photosynthesis using chlorophyll-based pigments.

The classification of *Bacteria* and *Archaea* into various taxonomic groups is rapidly undergoing revision and modification as novel species continue to be discovered and as insights from the field of genomics (a discipline in which the total genetic makeup of organisms is determined and studied) provide more accurate information of phylogenetic relationships. Molecular tools have become essential for classifying *Bacteria* and *Archaea* that resist laboratory culture and thus can only be identified by analysing sequences of DNA or RNA isolated from natural samples. Once determined, taxonomic conclusions are published in peer-reviewed journals and organised into reference manuals, such as *Bergey's Manual of Systematic Bacteriology* and *The Prokaryotes*. **See also: Semantides and Modern Bacterial Systematics; Bacterial Cells; Archaeal Cells; Bacteriology**

Cells of *Bacteria* and *Archaea* exist in three major morphological forms: spherical (coccus), rod-shaped (bacillus) and spiral-shaped (spirillum) (**Figure 2a–c**). Less common cell morphologies also exist, such as tightly coiled (spirochete; **Figure 2d**), appendaged and filamentous. All of these cell types are generally very small; most rods are 0.5–1  $\mu\text{m}$  wide and 1–4  $\mu\text{m}$  long, and a typical coccus has a diameter of 0.6–1  $\mu\text{m}$  (about one-tenth the diameter of a human red blood cell). Many of these cells are motile by means of one or more rotating appendages called flagella. And unlike animal cells and protozoa, most species of *Bacteria* and *Archaea* have a cell wall, a strong layer of material located outside the cell membrane that confers structural integrity and shape to the cell. **See also: Bacterial Flagella; Archaeal Flagella; Bacterial Cell Wall; Archaeal Cell Walls**

Most species of *Bacteria* and *Archaea* divide by binary fission, a process in which one cell divides into two identical daughter cells following replication of the parental cell's DNA. Bacterial and archaeal genomes are usually organised into a single, circular chromosome, and many species also have small, extra-chromosomal, circular pieces of DNA called plasmids, which often carry genes for antibiotic resistance, toxin production or specialised metabolisms. The chromosome is densely coiled in



**Figure 2** Major morphological forms of bacterial cells. (a) coccus (plural, cocci); (b) rod (bacillus; plural, bacilli); (c) spirillum (plural, spirilla) and (d) spirochete.

the cytoplasm to create a nucleoid, which is analogous to the nucleus of a eukaryotic cell but differs in that it is not bound by a membrane. **See also: Binary Fission in Bacteria; Bacterial Reproduction and Growth; Bacterial Chromosome; Bacterial Plasmids; Archaeal Plasmids**

## Microorganisms of the domain *Eukarya*

Like *Bacteria* and *Archaea*, eukaryotic microorganisms are remarkably diverse, consisting of hundreds of thousands of species of fungi, protozoa and algae, as well as hundreds of species of parasitic worms (Crompton, 1999). Fungi are a major component of soil ecosystems. Similar to plants, cells of fungi have rigid cell walls and are nonmotile, but unlike plants, they lack chlorophyll and are nonphotosynthetic. Instead, fungi subsist by degrading dead plant and animal matter, and therefore, along with bacteria, play a key role in the decomposition and recycling of nutrients. **See also: Fungal Ecology**

Fungi exist in two basic forms: moulds, which consist of filaments called hyphae that can form into masses known as mycelia, and yeasts, which are unicellular and typically oval-shaped. Some fungi are dimorphic in that they can assume either morphology depending on environmental conditions. Fungi are capable of sexual reproduction or asexual reproduction, both of which may result in the production of spores that can germinate to form new hyphae. In addition, yeasts often reproduce asexually by budding, a process in which a new daughter cell develops on the surface of a parent cell before eventually breaking away. **See also: Hyphae; Fungal Cells; Fungal Spores**

Protozoa are unicellular, mostly nonphotosynthetic protists that lack cell walls. Some protozoa are large enough to be seen with the unaided eye, although most are microscopic. Many protozoa are capable of reproducing sexually or asexually. Depending



on the species, asexual reproduction may occur through any of several mechanisms, including budding, spore formation or mitotic fission. A common mechanism of sexual reproduction in protozoa is conjugation, in which two cells join, exchange genetic material and produce progeny by budding or fission. **See also:** **Protozoan Asexuality**

Protozoa are diverse in their habitats and distribution. Most protozoa obtain energy by breaking down ingested foods via aerobic respiration, but some species are anaerobes that lack mitochondria (the energy-generating organelle of eukaryotic cells) and instead obtain their energy through fermentation. Fermentative protozoa inhabit anoxic environments, such as the digestive tract of certain animals, where they often establish symbiotic relationships that may be either beneficial or harmful to their host. Some protozoa cause devastating human diseases, such as malaria (caused by species of *Plasmodium*), while others (e.g. *Paramecium*) are innocuous members of the biosphere, where they exist as important components of the food chain. **See also:** **Protozoan Ecology; Protozoan Symbioses**

Algae are plant-like protists that are distinguished from fungi and most protozoa by their ability to perform photosynthesis using chlorophyll pigments, and they comprise much of the basis of the food chain in marine and freshwater environments. Algae exhibit a variety of morphological forms, including unicellular, filamentous, colonial and large multicellular aggregates called kelps or 'seaweeds' that can attain lengths of up to 50 m. Some algae have become increasingly important sources of food or food additives for humans. For example, the red alga *Porphyra*, known as nori, is popular in sushi preparation, and other red algae are the source of agar, a polysaccharide used as a solidifying agent to make Petri plate culture media as or as a thickener for a variety of foods. Most algae reproduce asexually, whereas others form spores or reproduce by fragmentation of cells from larger aggregates. Some algae reproduce sexually by forming diploid zygotes from haploid gametes. **See also:** **Algal Ecology; Algal Photosynthesis**

The helminths are a group of multicellular animals that includes roundworms and flatworms. Even though some of these organisms are visible to the naked eye, they are important topics of study for microbiologists because (1) they often have microscopic larval forms as part of their life cycles and (2) many species of helminths are parasitic and cause important infectious diseases. Helminth life cycles can be complex and often require multiple hosts for the different stages. In addition to humans, these hosts may include other mammals, insects (e.g. flies and mosquitoes), various fish species and certain aquatic invertebrates, such as squid, snails and crustaceans.

A helminth infection usually begins with either an insect bite or an accidental ingestion of worm eggs or larvae. However, a few worm species, such as those that cause hookworm and schistosomiasis, are capable of burrowing directly through the skin. The most important means of preventing parasitic worm infections include thoroughly cooking foods, drinking only purified or boiled water and employing repellents or physical barriers to prevent insect bites. Effective treatment of established infections is often possible using antihelminthic drugs. **See also:** **Schistosomiasis and Other Trematode Infections**

## Viruses and virology

Viruses are acellular microbes that require living host cells to multiply; thus, they are obligate intracellular parasites. Structurally, viruses are quite simple, often consisting of only DNA or RNA (the viral genome) surrounded by a simple protein coat having either a helical or icosahedral morphology (**Figure 3**). Viruses that infect bacteria, called bacteriophages, often have a complex morphology in that they exhibit a combination of these two forms (**Figure 3**). Most viruses are too small to be seen with even the best light microscopes, and because of their tiny size and dependence on host cells, their genomes are typically quite small, in some cases consisting of only two genes (Faurez *et al.*, 2009; Niagro *et al.*, 1998)! **See also:** **Viruses; Virus Structure; Bacteriophages**

Viruses replicate within an infected cell by commandeering the host's enzymatic machinery, which may include use of the host cell's nucleic acid polymerases (enzymes that make DNA or RNA) and/or ribosomes. Following viral replication, progeny viruses are released, either by lysis of the host cell or by budding from the host cell's membrane. Therefore, in many cases, viral infections lead to death of the host cell, either abruptly or eventually. Viruses cause many serious diseases, including acquired immunodeficiency syndrome (AIDS), influenza, measles, poliomyelitis, rabies and haemorrhagic fevers, such as Ebola. **See also:** **Virus Replication**

With a broad overview of microbial diversity in place, we can now explore the crucial role that microorganisms play in the environment around us.

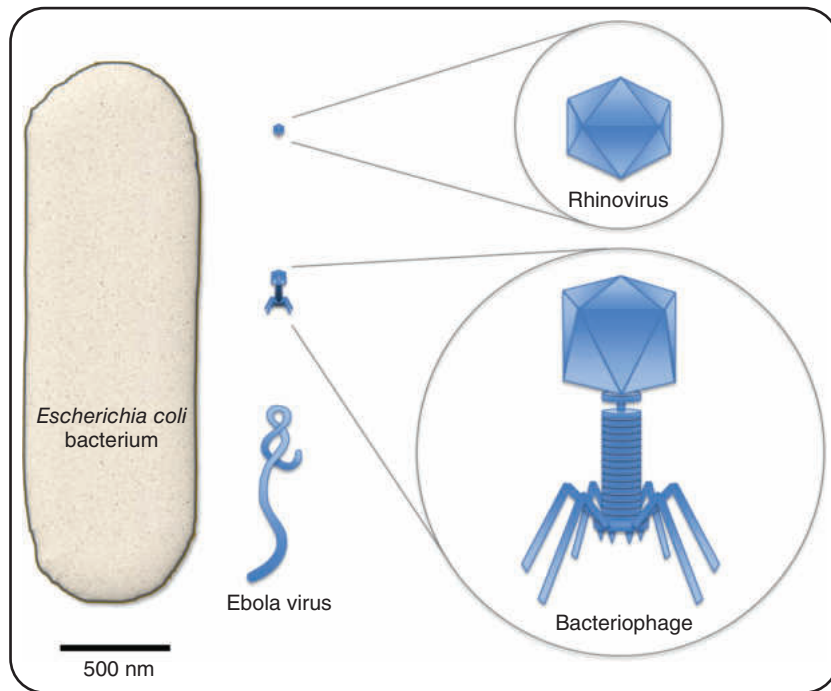
## Microbial Ecology

Microbial ecology is focused on how microbial communities interact with each other and their environments. A microbial community is an assembly of one or more populations of cells, each population composed of a single kind or species of microbe. An ecosystem is a dynamic complex of living organisms and their abiotic surroundings, all of which interact as a functional unit.

In terrestrial and aquatic ecosystems, microorganisms interact with each other and with the plants and animals in the ecosystem. Microbes play essential roles in these ecosystems by cycling inorganic nutrients and both producing and consuming organic matter. Associations of specific microbes with specific plants or animals are also quite common, and many of these associations are essential for the health and well-being of the plant or animal. We briefly consider the roles of microorganisms in some major ecosystems now.

### Soil, water and higher organisms as homes for microbial communities

Soil is the loose outer material that comprises much of Earth's surface and forms over long periods of time from a combination of biological and chemical processes. Soils often contain large numbers of microorganisms, and depending on the amount of organic matter present and the soil pH, salinity, degree of aeration and other abiotic factors, soil microbial communities can be



**Figure 3** Major morphological forms of viruses. Most viruses are considerably smaller than cells (a representation of an *Escherichia coli* cell is shown for size comparison). Viruses of eukaryotes typically have either icosahedral (e.g. rhinoviruses) or helical (e.g. ebola virus) symmetry, whereas viruses that infect bacteria (bacteriophages) often exhibit a complex 'head-and-tail' combination of these forms.

relatively simple or highly complex. In addition to soil, however, microbial communities also exist deep underground in the Earth's subsurface, fed by nutrients transported by groundwater.

In soils, microbial numbers are typically greatest in and around plant roots, a zone called the rhizosphere. It is here that organic matter excreted from the roots and from dead plant material greatly stimulates the activities of microbial communities. Temporal changes in the abundance and composition of soil microbial communities occur from variations in moisture, organic matter inputs and temperature. In contrast to surface soil, subsurface microbial communities are less dynamic due to more predictable conditions. Various *Bacteria*, *Archaea*, microbial eukaryotes and viruses inhabit soils and the deep subsurface, and many important nutrient cycling reactions occur there, including major transformations of the elements C, N and S, key constituents of living organisms.

Aerobic bacteria and fungi in soils consume oxygen in their respiratory activities. Many bacteria are anaerobes, carrying out various types of fermentation or anaerobic respiration (a form of respiration in which an oxidant other than  $O_2$  is used). However, in the final analysis, aerobic and anaerobic respiration and fermentation all accomplish the same thing; these metabolisms oxidise organic carbon, returning it to  $CO_2$ . Many anoxic ( $O_2$ -free) zones exist in soils and thus aerobes and anaerobes coexist there.

Aquatic microbial ecosystems include both freshwaters and ocean waters. These two environments differ in many ways, including salinity, average temperature, depth and nutrient levels. Photosynthetic microbial communities play important roles in aquatic ecosystems. The  $CO_2$ -fixing (autotrophic) activities of

these organisms provide not only the organic carbon needed for their own metabolism and growth but also the organic matter and oxygen needed by heterotrophic microbes present in the aquatic microbial community. Photosynthetic microbes are indeed the base of the aquatic food chain and thus are critical components of aquatic ecosystems.

The sediments of fresh and marine waters are hotbeds of distinctly different anaerobic metabolisms. In freshwater sediments, the bulk of organic carbon is eventually degraded to  $CH_4$  (methane). Methane is formed by methanogenic *Archaea* that reduce  $CO_2$  to  $CH_4$  using hydrogen ( $H_2$ ) as reductant in the anaerobic respiration called methanogenesis. In contrast to freshwater sediments, marine sediments contain large amounts of salts, including sulphate ( $SO_4^{2-}$ ). Sulphate respiration, whereby  $SO_4^{2-}$  is reduced to  $H_2S$ , is the dominant form of anaerobic respiration in marine sediments because it is more energetically favourable than methanogenesis (the low levels of  $SO_4^{2-}$  in most freshwater sediments limits sulphate reduction and favours methanogenesis) (Widdel and Bak, 1992).

Many microorganisms form relationships with other organisms, which can include other microbes, plants or animals. Such associations are called symbioses (literally, 'living together'). Plants interact with microorganisms through their roots and leaf surfaces, but in some cases, the association becomes highly specific and intimate, including actual growth within the plant tissue. Such is the case with the legume–root nodule symbiosis, an association in which tumour-like nodules form on the roots of leguminous plants (plants that bear their seeds in pods), such as soybeans and peanuts. The root nodules provide a habitat for

bacteria that fix atmospheric nitrogen into ammonia ( $\text{N}_2 + 6\text{H} \rightarrow 2\text{NH}_3$ ). The plant then uses the ammonia as a source of nitrogen to make proteins and nucleic acids, allowing it to thrive in nitrogen-poor soils.

Animal–microbe symbioses are also quite common. The human large intestine, for example, contains enormous numbers of bacterial cells that form a huge microbial community, the human gut microbiome, the composition of which varies from person to person and is influenced by diet, health and other factors (The Human Microbiome Project Consortium, 2012). As more is learned about the microbiomes of different animals, it has become clear that any perturbations in this species-specific microbial community can affect an animal's physical condition and susceptibility to disease. In some cases, the microbiome is essential for the very nutrition of the animal. For example, in the rumen (forestomach) of animals such as cows and sheep, bacteria and protozoa digest cellulose and ferment the released glucose to fatty acids, which are taken up by the animal. This allows the ruminant to subsist on a diet of plant matter, which is primarily cellulose.

## Microbial nutrient cycling

The key nutrients for life are cycled by both microorganisms and by plants and animals, but for any given nutrient, it is microbial activities that dominate. The major nutrient cycles include those of carbon, nitrogen and sulphur (Figure 4). Carbon is cycled primarily through  $\text{CO}_2$  (carbon dioxide) and the large pool of organic compounds present in living organisms (Figure 4a).  $\text{CO}_2$  is reduced to organic compounds by plants but also by many different microorganisms, both photosynthetic and chemolithotrophic. Organic matter, either excreted by living organisms or released from dead organisms, is eventually oxidised to  $\text{CO}_2$  or is converted to methane ( $\text{CH}_4$ ) by methanogenic archaea and later oxidised to  $\text{CO}_2$  by methane-consuming bacteria. **See also: Global Carbon Cycle**

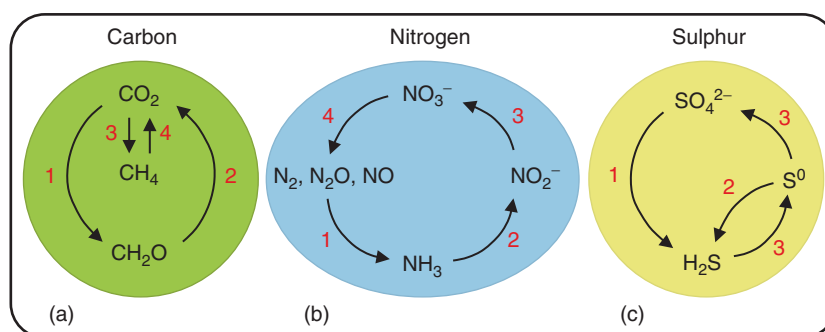
Nitrogen compounds can be either oxidised or reduced by microbes depending on the compound. Ammonia ( $\text{NH}_3$ ) is oxidised to nitrate ( $\text{NO}_3^-$ ) by a group of chemolithotrophs called

the nitrifying bacteria. Nitrate is then reduced to atmospheric nitrogen ( $\text{N}_2$ ) by nitrate-respiring anaerobic bacteria (denitrifiers) or to  $\text{NH}_3$  by ammonifying bacteria. The major remaining link in the nitrogen cycle is the reduction of  $\text{N}_2$  to  $\text{NH}_3$  by the nitrogen-fixing bacteria (Figure 4b). This process is an important means of enriching soils in usable nitrogen and is the key to the soybean–root nodule symbiosis mentioned earlier. **See also: Nitrogen Fixation; Nitrification**

Sulphur is cycled primarily between  $\text{SO}_4^{2-}$  and sulphide ( $\text{H}_2\text{S}$ ) through the activities of sulphate-reducing (sulphate-respiring) bacteria and chemolithotrophic sulphide-oxidising bacteria. Elemental sulphur ( $\text{S}^0$ ) is often an intermediate product in these metabolisms and can be either oxidised to sulphate or reduced to sulphide (Figure 4c). Sulphur-oxidising bacteria are primarily aerobes and participate in the sulphur cycle by consuming sulphide – a toxic substance for higher organisms – and generating sulphate, a key plant nutrient. By contrast, sulphate-reducing bacteria are anaerobes and oxidise organic matter to  $\text{CO}_2$  in anoxic environments, generating sulphide (Figure 4c). Some photosynthetic bacteria can also oxidise sulphide to support autotrophic growth ( $\text{CO}_2 + \text{H}_2\text{S} \rightarrow \text{Organic matter} + \text{SO}_4^{2-}$ ) (Gregersen *et al.*, 2011). Other key elements, such as P and Fe, are also cycled in nature, and like the C, N and S cycles, the cycling of these nutrients is driven primarily by the activities of microorganisms. **See also: Sulfur Oxidation in Prokaryotes; Biogeochemical Cycles**

## Medical Microbiology

While the vast majority of microorganisms provide beneficial services to humans, a few species (<1%), called pathogens, are potentially harmful. When pathogens successfully invade, multiply and cause damage to the host, disease ensues. Pathogens can damage the host in two ways: toxicity and invasiveness. Several pathogens produce toxins that can harm or even be lethal to humans. Some toxins, called exotoxins, are proteins secreted by the pathogen once established in the host. By contrast, endotoxins make up part of the outer layer (cell wall) of the cell itself. Bacterial exotoxins are among the most potent toxins known.



**Figure 4** Key elemental cycles driven predominantly by the activity of microorganisms. (a) Carbon is cycled between inorganic ( $\text{CO}_2$ ) and organic ( $\text{CH}_2\text{O}$ ) forms by the actions of autotrophs (1) and heterotrophs (2). In addition, methane ( $\text{CH}_4$ ) is produced (3) or consumed (4) by methanogens or methanotrophs, respectively. (b) Nitrogen compounds are cycled by nitrogen-fixing (1), nitrosifying (2), nitrifying (3) and denitrifying (4) bacteria. (c) In the sulphur cycle, sulphide is produced by sulphate- and sulphur-reducing bacteria (1 and 2, respectively). Sulphur chemolithotrophic bacteria oxidise sulphide to sulphate through an elemental sulphur intermediate (3).



For example, just 1 µg (one-millionth of a gram) of botulinum exotoxin can kill an adult human (Arnon *et al.*, 2001). **See also: Botulinum Toxin; Toxin Action: Molecular Mechanisms**

Invasive pathogens harm the host by directly damaging tissues or depriving them of nutrients. Bacterial invasion begins with attachment to host cells, which is facilitated by cellular appendages, such as fimbriae or pili. Tissue destruction occurs through the secretion of enzymes, such as leukocidins, which destroy white blood cells, and collagenases, which erode collagen, a fibrous protein found in various connective tissues. Some bacteria produce dense polymer coatings outside their cell walls called capsules that protect the invading pathogen from the host's immune response. Hosts respond to microbial invasion and the presence of toxins by producing protective antibodies that bind to and neutralise the microbe or toxin and by amassing white blood cells to attack invading pathogens by either consuming them or producing toxic agents to kill them. **See also: Bacterial Pili and Fimbriae; Bacterial Capsules and Evasion of Immune Responses**

Human hosts acquire infectious diseases by different routes, including the respiratory tract, the oral cavity and digestive system and the skin and genitourinary system. In some cases, pathogens are transmitted person-to-person, as in sexually transmitted infections (e.g. gonorrhoea and syphilis) or respiratory diseases (e.g. tuberculosis and influenza). In other instances, pathogens are transmitted indirectly through inanimate objects, such as clothing or towels, or through vectors, animals that carry pathogens between susceptible hosts. Lyme disease and malaria are examples of diseases that are transmitted indirectly to humans by arthropod vectors, the deer tick and *Anopheles* mosquito, respectively. After a pathogen is transmitted to a susceptible host, an incubation period occurs in which the pathogen multiplies and becomes established in the host before signs and symptoms of disease appear. **See also: Syphilis: Epidemiological Aspects; Tuberculosis; Malaria; Respiratory System: Bacterial Infections**

Antibiotics are antimicrobial chemicals produced by various microorganisms. Antibiotics are often administered to help fight infectious microorganisms and kill or inhibit pathogens by disrupting nucleic acid or protein synthesis, damaging the plasma membrane, preventing cell wall synthesis or interfering with cellular metabolism. Viruses, which replicate only inside a host cell, are not affected by antibiotics and must therefore be treated by other chemical compounds that block viral enzymes or alter viral nucleic acids. The indiscriminate use of antibiotics in humans and other animals in recent years has led to the development of microorganisms that are resistant to many of these drugs. These antibiotic-resistant microbes challenge conventional chemotherapy and are of major concern to medical professionals.

An alternative strategy to combating microbial infections is to employ vaccines to prevent pathogens from becoming established in the body in the first place. Vaccines induce an immune response in the host, and this triggers the production of protective antibodies that provide immunity against specific infectious agents and other foreign antigens. Vaccines have been particularly helpful in preventing common childhood diseases, including diphtheria, whooping cough (pertussis), poliomyelitis, measles and mumps.

**See also: Antiviral Drugs; Antibiotics and the Evolution of Antibiotic Resistance; Vaccination of Humans**

## Applications in Microbiology

### Commercial products from microorganisms

Microorganisms can be harnessed to make many valuable products, and industrial microbiology and biotechnology are the sub-disciplines of microbiology focused on these tasks (**Table 1**). Industrial microbiology uses microorganisms to synthesise products in large amounts. This is done by taking microbes that naturally produce some substance of relatively low value – for example, an antibiotic or alcohol – and selecting for ‘overproducing strains’ that can be grown on a huge scale; the resulting product may be made by tons or thousands of litres. Biotechnology, by contrast, employs genetically engineered microbes to synthesise small amounts of very high-value products that the microbes are otherwise unable to make, such as a human protein. Some major products of industrial microbiology and biotechnology are listed in **Table 2**.

### Food and mining microbiology

Food production and mining are obviously quite different activities but both owe their success to the microbial world. Certain microbes are used in the preparation of common food products while others are used in the mining industry to extract valuable minerals from crude ores.

Yeast is the key catalyst in the production of baked goods and alcoholic beverages. The fermentative metabolism of yeasts (glucose → 2 ethanol + 2 CO<sub>2</sub>) generates key products for the baker (CO<sub>2</sub> to raise the dough) and the brewer (ethyl alcohol). Many cheeses owe their characteristic flavours to the activities of fermentative microbes. For example, the key components in Swiss

**Table 2** Selected products of industrial microbiology and biotechnology

Product	Example
<i>Industrial microbiology</i>	
Antibiotics	Penicillin, tetracycline
Enzymes	Laundry proteases and lipases, glucose isomerase
Food additives	Vitamins, amino acids, citric acid
Alcohol/chemicals	Ethanol in alcoholic beverages and gasohol, butanol, biodiesel and steroids
<i>Biotechnology</i>	
Human hormones	Insulin, somatotropin
Blood proteins	Tissue plasminogen activator
Immune modulators	Interferons, tumour necrosis factor
Therapeutic enzymes	DNase

cheese – propionic acid and CO<sub>2</sub> – are responsible for the distinctive nutty taste and characteristic holes (eyes), respectively, of this popular cheese. Other major food products of microbial origin include fermented milks (e.g. buttermilk and yogurt), meats (e.g. salami and summer sausage) and vegetables (e.g. sauerkraut and pickles).

The mining of copper, gold and a few other metals relies on the leaching properties of bacteria. These valuable metals are typically present in low amounts in complex mineral ores that contain large amounts of iron. The metabolic activities of various acid-tolerant, iron-oxidising bacteria release these metals from the ores and generate acidic solutions (the leachate) from which the now solubilised metals can be concentrated and harvested by chemical treatment. Copper, widely used in electrical equipment, piping and the brewing industry, is the most commonly leached metal. The strategic element uranium is also mined by microbial leaching processes.

## Environmental applications of microorganisms

Microorganisms play critically important roles in the environment. We have already considered the key roles that microbes play in nature's major nutrient cycles. But in addition to these more or less continuous activities, microorganisms have been exploited for purifying wastewaters and for cleaning pollution in the environment, a process called bioremediation.

Sewage and other wastewaters must be treated before they can be released into natural waterways. This is because without treatment, the massive influx of organic matter and mineral nutrients would trigger extensive microbial growth and O<sub>2</sub> consumption, causing die-offs of plants and animals and diminishing the aesthetic and recreational value of the water. To deal with the high nutrient load of wastewaters, elaborate treatment facilities are used to stimulate the activities of complex microbial communities to remove as much organic carbon and other polluting nutrients (such as nitrates and phosphates) from the wastewaters as possible. Following treatment, the water can then be safely released into rivers or other bodies of water. **See also: Eutrophication of Lakes and Rivers**

To produce potable drinking water, additional treatment is necessary to remove as many potentially pathogenic microorganisms and remaining toxic substances as possible. Drinking water production includes the coagulation and filtration of already high-quality surface or subsurface waters followed by disinfection with chlorine and transport of the water through water mains to the consumer. The entire process of drinking water production must be carefully performed and monitored to prevent breakdowns that can lead to incidents of serious waterborne illness, such as cholera or typhoid fever.

When pollution of the environment occurs, either from natural events or from the activities of humans, microorganisms can be harnessed to clean up the mess. Microbial bioremediation is typically the most cost-effective method of removing environmental pollutants and, in many cases, it is the only practical way to accomplish the job. Bioremediation is grounded in the astounding diversity of metabolic reactions capable in the microbial world.

Thus, if some pollutant, such as crude oil, is spilled in the environment, oil-consuming microbes applied to the spill site can clean up the mess by oxidising hydrocarbons in the oil to CO<sub>2</sub>. **See also: Bioremediation**

In a similar manner, microbes that can degrade pesticides, such as insecticides and herbicides, are beneficial in keeping these poisonous substances from accumulating in the environment and damaging plants and animals that were not the original targets of these agents. Although not every substance that humans have created is biodegradable (e.g. teflon is not), the vast majority of pollutants are, and it is through the activities of microorganisms that these undesirable substances are converted into compounds that can enter the natural nutrient cycles (**Figure 4**).

Humans owe a considerable debt to the microbial world for keeping planet Earth habitable and healthy. If cyanobacteria had never become established on Earth, then the oxygen we breathe and depend on would never have been produced. And if it were not for microbes today, the everyday activities of humans would eventually damage the environment beyond its capacity to sustain human life. The microbial world is clearly the foundation of the biosphere, and thus the science of microbiology, which attempts to understand this unusual world, may be our most relevant biological science today.

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