Prokaryote Organisms

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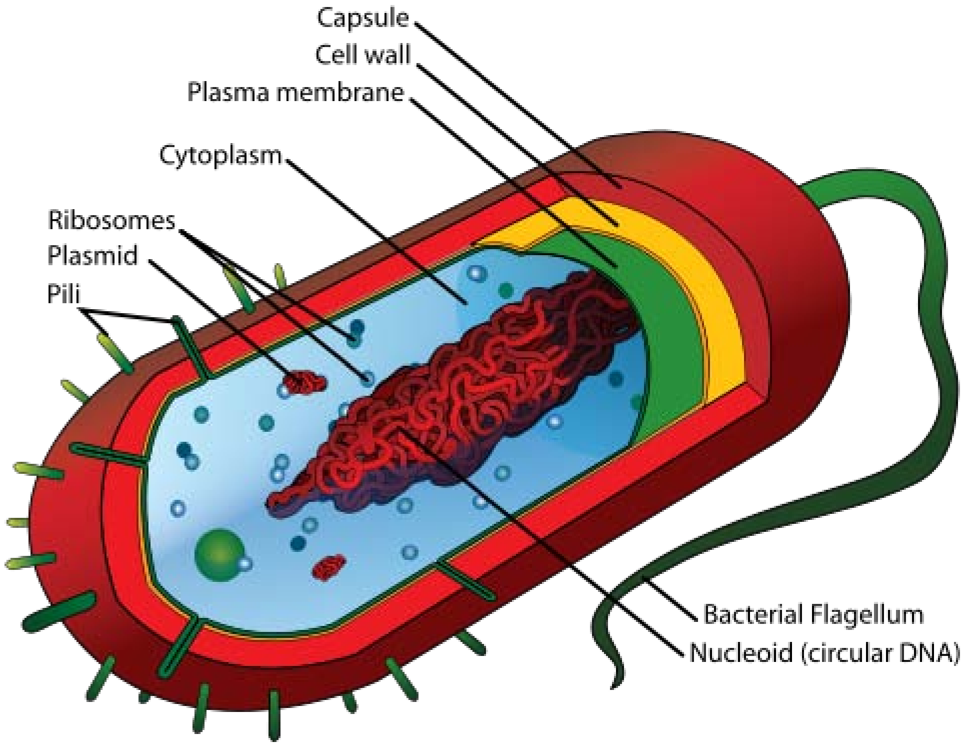
Prokaryote



Cell structure of a bacterium, one of the two domains of prokaryotic life.

The **prokaryotes** are a group of organisms that lack a cell nucleus (= karyon), or any other membrane-bound organelles. The organisms that have a cell nucleus are called eukaryotes. Most prokaryotes are unicellular, but a few such as myxobacteria have multicellular stages in their life cycles. The word *prokaryote* comes from the Greek *πρό- (pro-)* "before" + *καρυόν (karyon)* "nut or kernel".

It is generally agreed that prokaryotes as a group do not have taxonomic value. They comprehend two domains: the bacteria and the archaea. Archaea were recognized as a domain of life in 1990. These organisms were originally thought to live only in inhospitable conditions such as extremes of temperature, pH, and radiation but have since been found in all types of habitats.

Relationship to eukaryotes

Prokaryotes are single-cell organisms that do not have a nucleus, mitochondria, or any other membrane-bound organelles. In other words, neither their DNA nor any of their other sites of metabolic activity are collected together in a discrete membrane-enclosed area. Instead, everything is openly accessible within the cell, some of which is free-floating.

A distinction between prokaryotes and eukaryotes (meaning true kernel, also spelled "eucaryotes") is that eukaryotes do have "true" nuclei containing their DNA. Unlike prokaryotes, eukaryotic organisms may be unicellular, as in amoebae, or multicellular, as in plants and animals. The difference between the structure of prokaryotes and eukaryotes is so great that it is sometimes considered to be the most important distinction among groups of organisms.

The cell structure of prokaryotes differs greatly from that of eukaryotes. The defining characteristic is the absence of a nucleus. Also the size of Ribosomes in prokaryotes is smaller than that in eukaryotes, which is now where respiration takes place. The genomes of prokaryotes are held within an irregular DNA/protein complex in the cytosol called the nucleoid, which lacks a nuclear envelope. In general, prokaryotes lack the following membrane-bound cell compartments: mitochondria and chloroplasts. Instead, processes such as oxidative phosphorylation and photosynthesis take place across the prokaryotic plasma membrane. However, prokaryotes do possess some internal structures, such as cytoskeletons, and the bacterial order Planctomycetes have a membrane around their nucleoid and contain other membrane-bound cellular structures. Both eukaryotes and prokaryotes contain large RNA/protein structures called ribosomes, which produce protein. Prokaryotes are usually much smaller than eukaryotic cells.

Prokaryotes also differ from eukaryotes in that they contain only a single loop of stable chromosomal DNA stored in an area named the nucleoid, whereas eukaryote DNA is found on tightly bound and organized chromosomes. Although some eukaryotes have satellite DNA structures called plasmids, in general these are regarded as a prokaryote feature, and many important genes in prokaryotes are stored on plasmids.

Prokaryotes have a larger surface-area-to-volume ratio giving them a higher metabolic rate, a higher growth rate, and, as a consequence, a shorter generation time compared to Eukaryotes.

A criticism of this classification is that the word "prokaryote" is based on what these organisms are not (they are not eukaryotic), rather than what they are (either archaea or bacteria).

In 1977, Carl Woese proposed dividing prokaryotes into the Bacteria and Archaea (originally Eubacteria and Archaebacteria) because of the major differences in the structure and genetics between the two groups of organisms. This arrangement of Eukaryota (also called "Eukarya"), Bacteria, and Archaea is called the three-domain system, replacing the traditional two-empire system.

Sociality

While prokaryotes are still commonly imagined to be strictly unicellular, most are capable of forming stable aggregate communities. When such communities are encased in a stabilizing polymer matrix (“slime”), they may be called “biofilms”. Cells in biofilms often show distinct patterns of gene expression (phenotypic differentiation) in time and space. Also, as with multicellular eukaryotes, these changes in expression appear to often result from cell-to-cell signaling, a phenomenon known as quorum sensing.

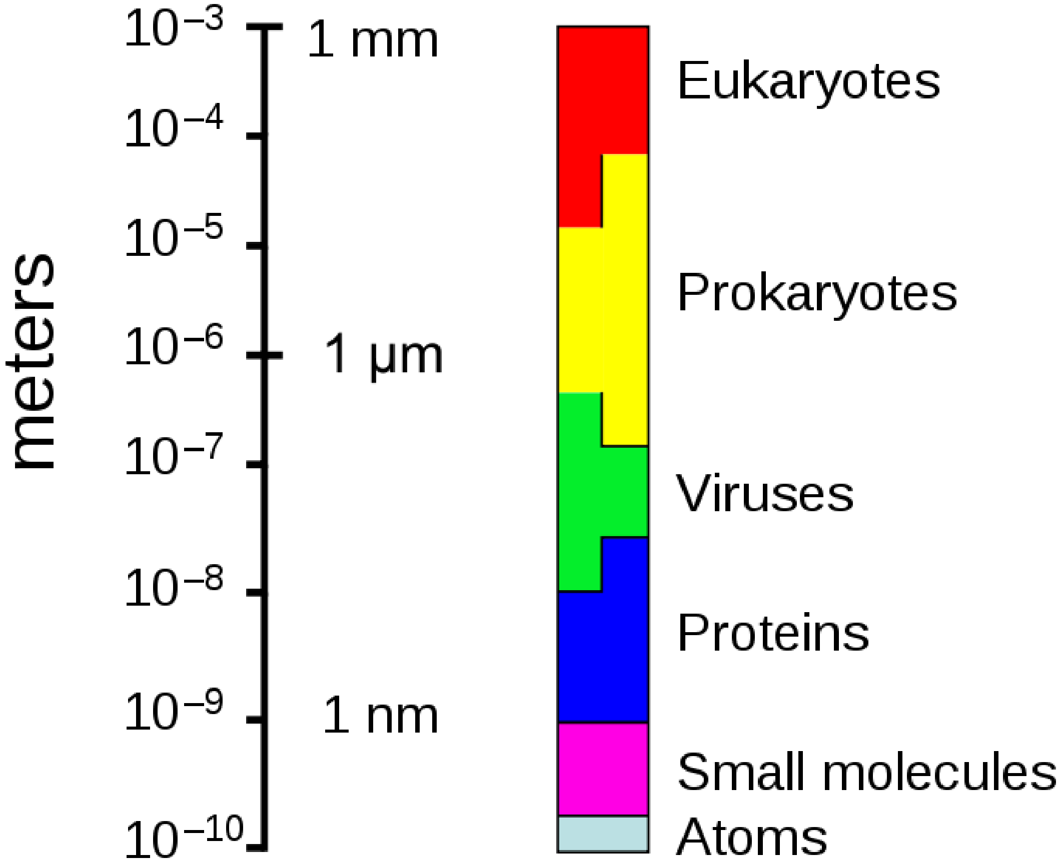
Biofilms may be highly heterogeneous and structurally complex and may attach to solid surfaces, or exist at liquid-air interfaces, or potentially even liquid-liquid interfaces. Bacterial biofilms are often made up of microcolonies (approximately dome-shaped masses of bacteria and matrix) separated by “voids” through which the medium (e.g., water) may flow relatively uninhibited. The microcolonies may join together above the substratum to form a continuous layer, closing the network of channels separating microcolonies. This structural complexity — combined with observations that oxygen limitation (a ubiquitous challenge for anything growing in size beyond the scale of diffusion) is at least partially eased by movement of medium throughout the biofilm — has led some to speculate that this may constitute a circulatory system and many researchers have started calling prokaryotic communities multicellular (for example). Differential cell expression, collective behavior, signaling, programmed cell death, and (in some cases) discrete biological dispersal events all seem to point in this direction. However, these colonies are seldom if ever founded by a single founder (in the way that animals and plants are founded by single cells), which presents a number of theoretical issues. Most explanations of co-operation and the evolution of multicellularity have focused on high relatedness between members of a group (or colony, or whole organism). If a copy of a gene is present in all members of a group, behaviors that promote cooperation between members may permit those members to have (on average) greater fitness than a similar group of selfish individuals.

Should these instances of prokaryotic sociality prove to be the rule rather than the exception, it would have serious implications for the way we view prokaryotes in general and the way we deal with them in medicine. Bacterial biofilms may be 100 times more resistant to antibiotics than free-living unicells and may be nearly impossible to remove from surfaces once they have colonized them. Other aspects of bacterial cooperation — such as bacterial conjugation and quorum-sensing-mediated pathogenicity — present additional challenges to researchers and medical professionals seeking to treat the associated diseases.

Reproduction

Bacteria and archaea reproduce through asexual reproduction, usually by binary fission or budding. Genetic exchange and recombination still occur, but this is a form of horizontal gene transfer and is not a replicative process, simply involving the transference of DNA between two cells, as in bacterial conjugation.

Structure



The sizes of prokaryotes relative to other organisms and biomolecules

Recent research indicates that all prokaryotes actually do have cytoskeletons, albeit more primitive than those of eukaryotes. Besides homologues of actin and tubulin (MreB and FtsZ), the helically arranged building-block of the flagellum, flagellin, is one of the most significant cytoskeletal proteins of bacteria, as it provides structural backgrounds of chemotaxis, the basic cell physiological response of bacteria. At least some prokaryotes also contain intracellular structures that can be seen as primitive organelles. Membranous organelles (a.k.a. intracellular membranes) are known in some groups of prokaryotes, such as vacuoles or membrane systems devoted to special metabolic properties, e.g., photosynthesis or chemolithotrophy. In addition, some species also contain protein-enclosed microcompartments, which have distinct physiological roles (e.g., carboxysomes or gas vacuoles).

Most prokaryotes are between 1 µm and 10 µm, but they can vary in size from 0.2 µm to 750 µm (Thiomargarita namibiensis).

Prokaryotic cell Structure

Flagellum
Cell membrane
Cell wall (except genus Mycoplasma)
Cytoplasm
Ribosome
Nucleoid
Glycocalyx
Inclusions

Morphology of prokaryotic cells

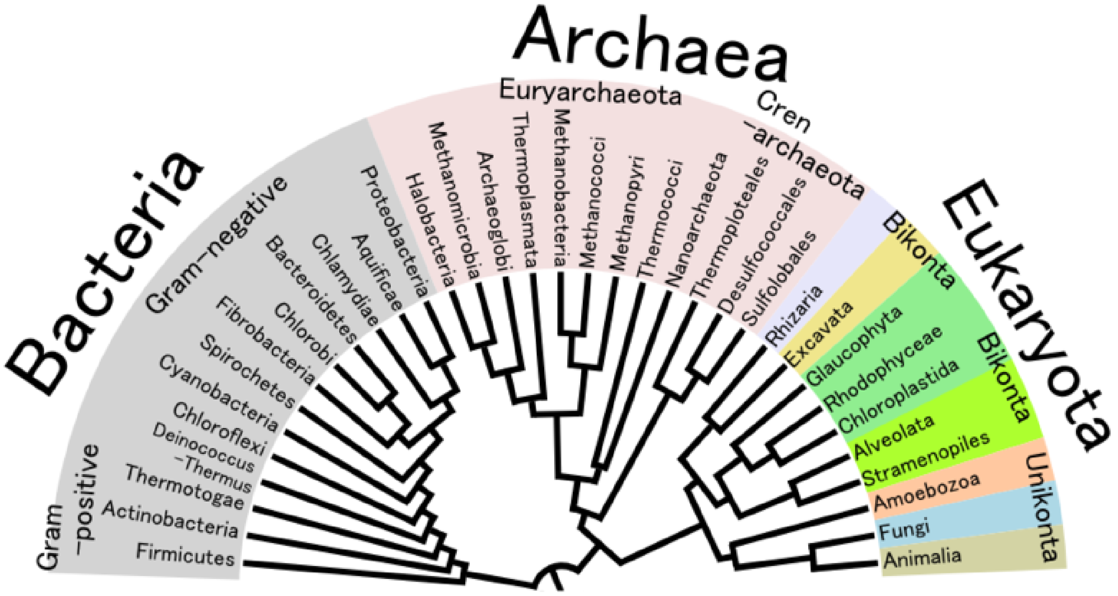
Prokaryotic cells have various shapes; the four basic shapes are:

- Cocci - spherical
- Bacilli - rod-shaped
- Spirochaete - spiral-shaped
- Vibrio - comma-shaped

Environment

Prokaryotes live in nearly all environments on earth where there is liquid water. Some archaea and bacteria thrive in harsh conditions, such as high temperatures (thermophiles) or high salinity (halophiles). Organisms such as these are referred to as extremophiles. Many archaea grow as plankton in the oceans. Symbiotic prokaryotes live in or on the bodies of other organisms, including humans.

Evolution of prokaryotes



Phylogenetic tree showing the diversity of prokaryotes, compared to eukaryotes.

The current model of the evolution of the first living organisms is that these were some form of prokaryotes, which may have evolved out of protobionts. In general, the eukaryotes are thought to have evolved later in the history of life. However, some authors have questioned this conclusion, arguing that the current set of prokaryotic species may have evolved from more complex eukaryotic ancestors through a process of simplification. Others have argued that the three domains of life arose simultaneously, from a set of varied cells that formed a single a gene pool. This controversy was summarized in 2005:

There is no consensus among biologists concerning the position of the eukaryotes in the overall scheme of cell evolution. Current opinions on the origin and position of eukaryotes span a broad spectrum including the views that eukaryotes arose first in evolution and that prokaryotes descend from them, that eukaryotes arose contemporaneously with eubacteria and archeabacteria and hence represent a primary line of descent of equal age and rank as the prokaryotes, that eukaryotes arose through a symbiotic event entailing an endosymbiotic origin of the nucleus, that eukaryotes arose without endosymbiosis, and that eukaryotes arose through a symbiotic event entailing a simultaneous endosymbiotic origin of the flagellum and the nucleus, in addition to many other models, which have been reviewed and summarized elsewhere.

The oldest known fossilized prokaryotes were laid down approximately 3.5 billion years ago, only about 1 billion years after the formation of the Earth's crust. Even today, prokaryotes are perhaps the most successful and abundant life-forms. Eukaryotes only appear in the fossil record later, and may have formed from endosymbiosis of multiple prokaryote ancestors. The oldest known fossil eukaryotes are about 1.7 billion years old.

However, some genetic evidence suggests eukaryotes appeared as early as 3 billion years ago.

While Earth is the only place in the universe where life is known to exist, some have suggested that there is evidence on Mars of fossil or living prokaryotes; but this possibility remains the subject of considerable debate and skepticism.

Prokaryotes have diversified greatly throughout their long existence. The metabolism of prokaryotes is far more varied than that of eukaryotes, leading to many highly distinct prokaryotic types. For example, in addition to using photosynthesis or organic compounds for energy, as eukaryotes do, prokaryotes may obtain energy from inorganic compounds such as hydrogen sulfide. This enables prokaryotes to thrive in harsh environments as cold as the snow surface of Antarctica, and as hot as undersea hydrothermal vents and land-based hot springs.

Chapter 2

Archaea

Archaea
Temporal range: Paleoarchean – Recent

Halobacteria sp. strain NRC-1, each cell about 5 µm long

Scientific classification

Domain: **Archaea** Woese, Kandler & Wheelis, 1990

Kingdoms and phyla

Crenarchaeota
Euryarchaeota
Korarchaeota
Nanoarchaeota
Thaumarchaeota
Aigarchaeota

The **Archaea** are a group of single-celled microorganisms. A single individual or species from this domain is called an *archaeon* (sometimes spelled "archeon"). They have no cell nucleus nor any other membrane-bound organelles within their cells. In the past they were viewed as an unusual group of bacteria and named **archaebacteria**, but the Archaea have an independent evolutionary history and show many differences in their biochemistry from other forms of life, and so they are now classified as a separate domain in the three-domain system. In this system the phylogenetically distinct branches of evolutionary descent are the Archaea, Bacteria and Eukaryota. Archaea are divided into four recognized phyla, but many more phyla may exist. Of these groups, the Crenarchaeota and the Euryarchaeota are most intensively studied. Classification is still difficult, because the vast majority have never been studied in the laboratory and have only been detected by analysis of their nucleic acids in samples from the environment. Although archaea have, in the past, been classed with bacteria as *prokaryotes* (or Kingdom Monera), this classification is regarded by some as outdated.

Archaea and bacteria are quite similar in size and shape, although a few archaea have very unusual shapes, such as the flat and square-shaped cells of *Haloquadratum walsbyi*. Despite this visual similarity to bacteria, archaea possess genes and several metabolic pathways that are more closely related to those of eukaryotes: notably the enzymes involved in transcription and translation. Other aspects of archaean biochemistry are unique, such as their reliance on ether lipids in their cell membranes. Archaea use a much greater variety of sources of energy than eukaryotes: ranging from familiar organic compounds such as sugars, to ammonia, metal ions or even hydrogen gas. Salt-tolerant archaea (the Halobacteria) use sunlight as an energy source and other species of archaea fix carbon; however, unlike plants and cyanobacteria, no species of archaea is known to do both. Archaea reproduce asexually and divide by binary fission, fragmentation, or budding; unlike bacteria and eukaryotes, no known species form spores.

Initially, archaea were seen as extremophiles that lived in harsh environments, such as hot springs and salt lakes, but they have since been found in a broad range of habitats, including soils, oceans, and marshlands. Archaea are particularly numerous in the oceans, and the archaea in plankton may be one of the most abundant groups of organisms on the planet. Archaea are now recognized as a major part of Earth's life and may play roles in both the carbon cycle and the nitrogen cycle. No clear examples of archaeal pathogens or parasites are known, but they are often mutualists or commensals. One example is the methanogens that inhabit the gut of humans and ruminants, where their vast numbers aid digestion. Methanogens are used in biogas production and sewage treatment, and enzymes from extremophile archaea that can endure high temperatures and organic solvents are exploited in biotechnology.

Classification

New domain

For much of the 20th century, prokaryotes were regarded as a single group of organisms and classified based on their biochemistry, morphology and metabolism. For example, microbiologists tried to classify microorganisms based on the structures of their cell walls, their shapes, and the substances they consume. However, a new approach was proposed in 1965, using the sequences of the genes in these organisms to work out which prokaryotes are genuinely related to each other. This approach, known as phylogenetics, is the main method used today.

Archaea were first found in extreme environments, such as volcanic hot springs.

Archaea were first classified as a separate group of prokaryotes in 1977 by Carl Woese and George E. Fox in phylogenetic trees based on the sequences of ribosomal RNA (rRNA) genes. These two groups were originally named the Archaebacteria and Eubacteria and treated as kingdoms or subkingdoms, which Woese and Fox termed *Urkingdoms*. Woese argued that this group of prokaryotes is a fundamentally different sort of life. To emphasize this difference, these two domains were later renamed Archaea and Bacteria. The word *archaea* comes from the Ancient Greek ἀρχαῖα, meaning "ancient things".

At first, only the methanogens were placed in this new domain, and the archaea were seen as extremophiles that exist only in habitats such as hot springs and salt lakes. By the end of the 20th century, microbiologists realized that archaea is a large and diverse group of organisms that are widely distributed in nature and are common in much less extreme habitats, such as soils and oceans. This new appreciation of the importance and ubiquity of archaea came from using the polymerase chain reaction to detect prokaryotes in samples of water or soil from their nucleic acids alone. This allows the detection and identification of organisms that cannot be cultured in the laboratory, which generally remains difficult.

Current classification

The classification of archaea, and of prokaryotes in general, is a rapidly moving and contentious field. Current classification systems aim to organize archaea into groups of organisms that share structural features and common ancestors. These classifications rely heavily on the use of the sequence of ribosomal RNA genes to reveal relationships between organisms (molecular phylogenetics). Most of the culturable and well-investigated species of archaea are members of two main phyla, the Euryarchaeota and Crenarchaeota. Other groups have been tentatively created. For example, the peculiar species *Nanoarchaeum equitans*, which was discovered in 2003, has been given its own phylum, the Nanoarchaeota. A new phylum Korarchaeota has also been proposed. It contains a small group of unusual thermophilic species that shares features of both of the main phyla, but is most closely related to the Crenarchaeota. Other recently detected species of archaea are only distantly related to any of these groups, such as the Archaeal Richmond Mine Acidophilic Nanoorganisms (ARMAN), which were discovered in 2006 and are some of the smallest organisms known.

The ARMAN are a new group of archaea recently discovered in acid mine drainage.

Species

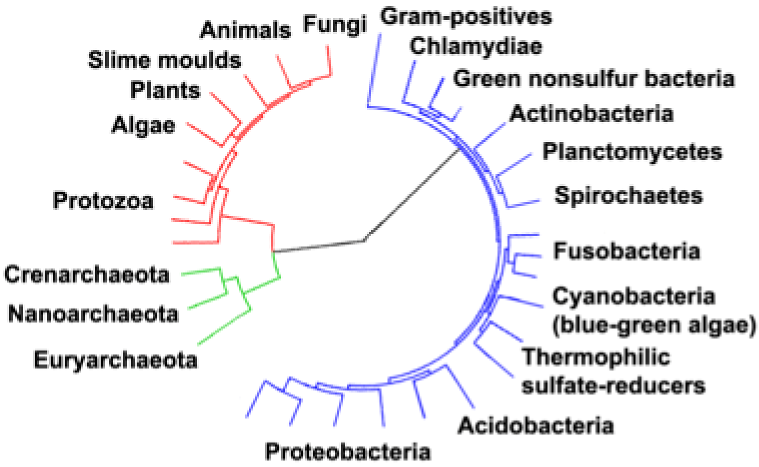
The classification of archaea into species is also controversial. Biology defines a species as a group of related organisms. The familiar exclusive breeding criterion (organisms that can breed with each other but not with others), is of no help because archaea reproduce asexually.

Archaea show high levels of horizontal gene transfer between lineages. Some researchers suggest that individuals can be grouped into species-like populations given highly similar genomes and infrequent gene transfer to/from cells with less-related genomes, as in the genus *Ferroplasma*. On the other hand, studies in *Halorubrum* found significant genetic transfer to/from less-related populations, limiting the criterion's applicability. A second concern is to what extent such species designations have practical meaning.

Current knowledge on genetic diversity is fragmentary and the total number of archaean species cannot be estimated with any accuracy. Estimates of the number of phyla range from 18 to 23, of which only 8 have representatives that have been cultured and studied directly. Many of these hypothesized groups are known from a single rRNA sequence, indicating that the diversity among these organisms remains obscure. The Bacteria also contain many uncultured microbes with similar implications for characterization.

Origin and evolution

Although probable prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies and fossil shapes cannot be used to identify them as Archaea. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in shales dating from 2.7 billion years ago; such data have since been questioned. Such lipids have also been detected in Precambrian formations. The oldest such traces come from the Isua district of west Greenland, which include Earth's oldest sediments, formed 3.8 billion years ago. The archaeal lineage may be the most ancient that exists on Earth.



Phylogenetic tree showing the relationship between the archaea and other forms of life. Eukaryotes are colored red, archaea green and bacteria blue. Adapted from Ciccarelli *et al.*

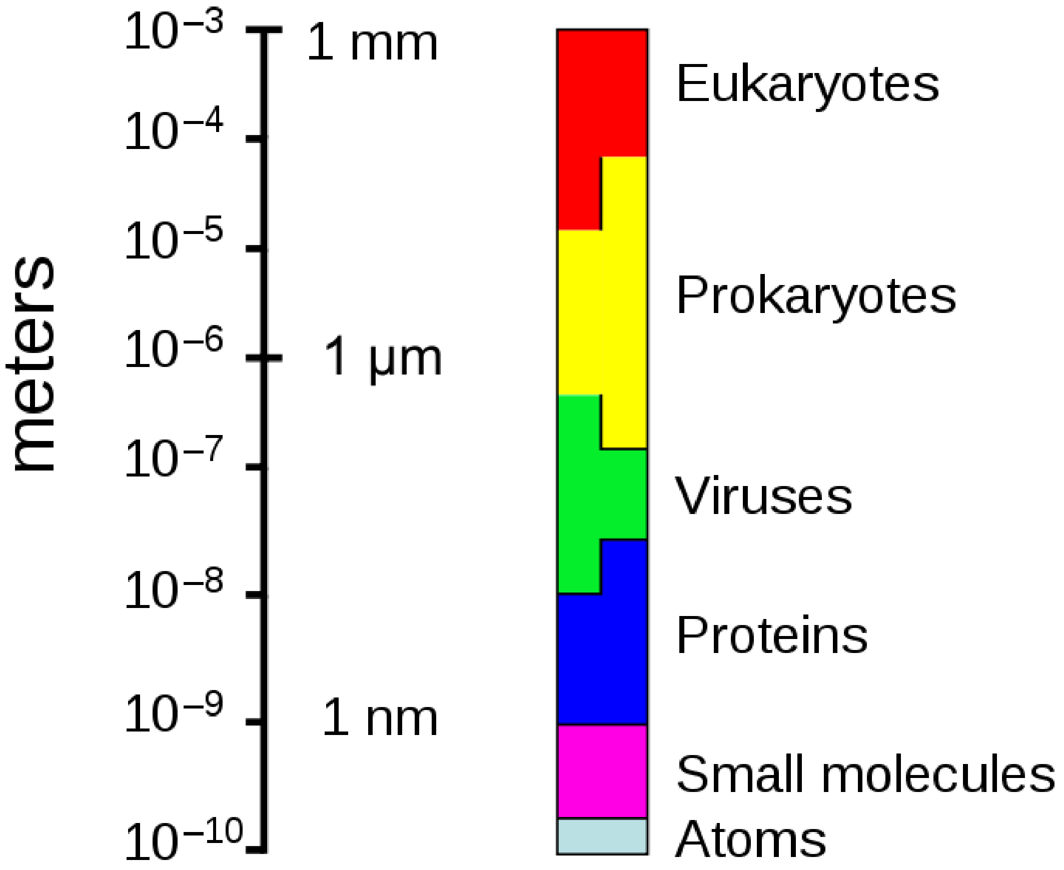
Woese argued that the bacteria, archaea, and eukaryotes represent separate lines of descent that diverged early on from an ancestral colony of organisms. However, a few biologists argue that the Archaea and Eukaryota arose from a group of bacteria. In any case, it is thought that viruses and archaea began relationships approximately two billion years ago, and that co-evolution may have been occurring between members of these groups. It is possible that the last common ancestor of the bacteria and archaea was a thermophile, which raises the possibility that lower temperatures are "extreme environments" in archaeal terms, and organisms that live in cooler environments appeared only later. Since the Archaea and Bacteria are no more related to each other than they are to eukaryotes, the term *prokaryote*'s only surviving meaning is "not a eukaryote", limiting its value.

Relation to eukaryotes

The evolutionary relationship between archaea and eukaryotes remains unclear. Aside from the similarities in cell structure and function that are discussed below, many genetic trees group the two.

Complicating factors include claims that the relationship between eukaryotes and the archaeal phylum Euryarchaeota is closer than the relationship between the Euryarchaeota and the phylum Crenarchaeota and the presence of archaean-like genes in certain bacteria, such as *Thermotoga maritima*, from horizontal gene transfer. The leading hypothesis is that the ancestor of the eukaryotes diverged early from the Archaea, and that eukaryotes arose through fusion of an archaean and eubacterium, which became the nucleus and cytoplasm; this explains various genetic similarities but runs into difficulties explaining cell structure.

Morphology



The sizes of prokaryotic cells relative to other cells and biomolecules (logarithmic scale)

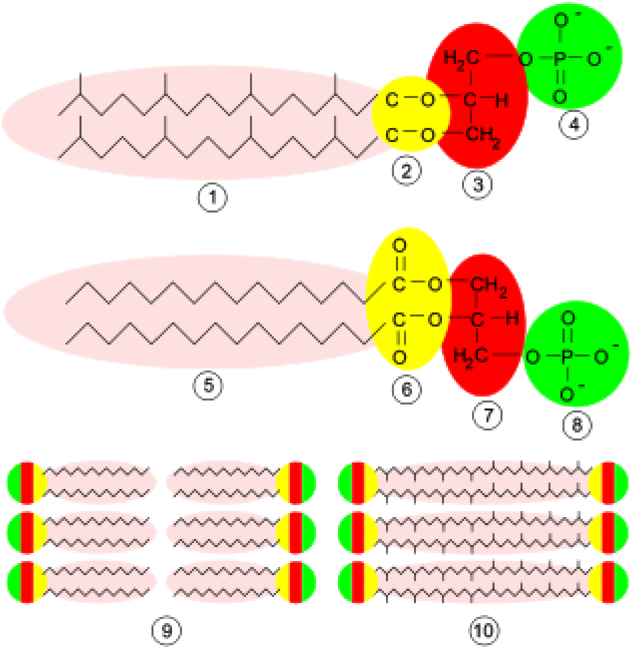
Individual archaea range from 0.1 micrometers (μm) to over 15 μm in diameter, and occur in various shapes, commonly as spheres, rods, spirals or plates. Other morphologies in the Crenarchaeota include irregularly shaped lobed cells in *Sulfolobus*, needle-like filaments that are less than half a micrometer in diameter in *Thermofilum*, and almost perfectly rectangular rods in *Thermoproteus* and *Pyrobaculum*. *Haloquadratum walsbyi* are flat, square archaea that live in hypersaline pools. These unusual shapes are probably maintained both by their cell walls and a prokaryotic cytoskeleton. Proteins related to the cytoskeleton components of other organisms exist in archaea, and filaments form within their cells, but in contrast to other organisms, these cellular structures are poorly understood. In *Thermoplasma* and *Ferroplasma* the lack of a cell wall means that the cells have irregular shapes, and can resemble amoebae.

Some species form aggregates or filaments of cells up to 200 μm long. These organisms can be prominent in biofilms. Notably, aggregates of *Thermococcus coalescens* cells fuse together in culture, forming single giant cells. Archaea in the genus *Pyrodictium* produce an elaborate multicell colony involving arrays of long, thin hollow tubes called *cannulae* that stick out from the cells' surfaces and connect them into a dense bush-like agglomeration. The function of these cannulae is not settled, but they may allow communication or nutrient exchange with neighbors. Multi-species colonies exist, such as the "string-of-pearls" community that was discovered in 2001 in a German swamp. Round whitish colonies of a novel Euryarchaeota species are spaced along thin filaments that can range up to 15 centimetres (5.9 in) long; these filaments are made of a particular bacteria species.

Structure, composition development, operation

Archaea and bacteria have generally similar cell structure, but cell composition and organization set the archaea apart. Like bacteria, archaea lack interior membranes and organelles. Like bacteria, archaea cell membranes are usually bounded by a cell wall and they swim using one or more flagella. Structurally, archaea are most similar to gram-positive bacteria. Most have a single plasma membrane and cell wall, and lack a periplasmic space; the exception to this general rule is *Ignicoccus*, which possess a particularly large periplasm that contains membrane-bound vesicles and is enclosed by an outer membrane.

Membranes



Membrane structures. **Top**, an archaeal phospholipid: **1**, isoprene chains; **2**, ether linkages; **3**, L-glycerol moiety; **4**, phosphate group. **Middle**, a bacterial or eukaryotic phospholipid: **5**, fatty acid chains; **6**, ester linkages; **7**, D-glycerol moiety; **8**, phosphate group. **Bottom**: **9**, lipid bilayer of bacteria and eukaryotes; **10**, lipid monolayer of some archaea.

Archaeal membranes are made of molecules that differ strongly from those in other life forms, showing that archaea are related only distantly to bacteria and eukaryotes. In all organisms cell membranes are made of molecules known as phospholipids. These molecules possess both a polar part that dissolves in water (the phosphate "head"), and a "greasy" non-polar part that does not (the lipid tail). These dissimilar parts are connected by a glycerol moiety. In water, phospholipids cluster, with the heads facing the water and the tails facing away from it. The major structure in cell membranes is a double layer of these phospholipids, which is called a lipid bilayer.

These phospholipids are unusual in four ways:

- Bacteria and eukaryotes have membranes composed mainly of glycerol-ester lipids, whereas archaea have membranes composed of glycerol-ether lipids. The difference is the type of bond that joins the lipids to the glycerol moiety; the two types are shown in yellow in the figure at the right. In ester lipids this is an ester bond, whereas in ether lipids this is an ether bond. Ether bonds are chemically more resistant than ester bonds. This stability might help archaea to survive extreme temperatures and very acidic or alkaline environments. Bacteria and eukaryotes do contain some ether lipids, but in contrast to archaea these lipids are not a major part of their membranes.

- The stereochemistry of the glycerol moiety is the reverse of that found in other organisms. The glycerol moiety can occur in two forms that are mirror images of one another, called the right-handed and left-handed forms; in chemistry these are called *enantiomers*. Just as a right hand does not fit easily into a left-handed glove, a right-handed glycerol molecule generally cannot be used or made by enzymes adapted for the left-handed form. This suggests that archaea use entirely different enzymes for synthesizing phospholipids than do bacteria and eukaryotes. Such enzymes developed very early in life's history, suggesting an early split from the other two domains.

- Archaeal lipid tails are chemically different from other organisms. Archaeal lipids are based upon the isoprenoid sidechain and are long chains with multiple side-branches and sometimes even cyclopropane or cyclohexane rings. This is in contrast to the fatty acids found in other organisms' membranes, which have straight chains with no branches or rings. Although isoprenoids play an important role in the biochemistry of many organisms, only the archaea use them to make phospholipids. These branched chains may help prevent archaean membranes from leaking at high temperatures.

- In some archaea the lipid bilayer is replaced by a monolayer. In effect, the archaea fuse the tails of two independent phospholipid molecules into a single molecule with two polar heads; this fusion may make their membranes more rigid and better able to resist harsh environments. For example, the lipids in *Ferroplasma* are of this type, which is thought to aid this organism's survival in its highly acidic habitat.

Wall and flagella

Most archaea (but not *Thermoplasma* and *Ferroplasma*) possess a cell wall. In most archaea the wall is assembled from surface-layer proteins, which form an S-layer. An S-layer is a rigid array of protein molecules that cover the outside of the cell (like chain mail). This layer provides both chemical and physical protection, and can prevent macromolecules from contacting the cell membrane. Unlike bacteria, archaea lack peptidoglycan in their cell walls. Methanobacteriales do have cell walls containing pseudopeptidoglycan, which resembles eubacterial peptidoglycan in morphology, function, and physical structure, but pseudopeptidoglycan is distinct in chemical structure; it lacks D-amino acids and N-acetylmuramic acid.

Archaea flagella operate like bacterial flagella—their long stalks are driven by rotatory motors at the base. These motors are powered by the proton gradient across the membrane. However, archaeal flagella are notably different in composition and development. The two types of flagella evolved from different ancestors. The bacterial flagellum shares a common ancestor with the type III secretion system, while archaeal flagella appear to have evolved from bacterial type IV pili. In contrast to the bacterial flagellum, which is hollow and is assembled by subunits moving up the central pore to the tip of the flagella, archaeal flagella are synthesized by adding subunits at the base.

Metabolism

Archaea exhibit a great variety of chemical reactions in their metabolism and use many sources of energy. These reactions are classified into nutritional groups, depending on energy and carbon sources. Some archaea obtain energy from inorganic compounds such as sulfur or ammonia (they are lithotrophs). These include nitrifiers, methanogens and anaerobic methane oxidisers. In these reactions one compound passes electrons to another (in a redox reaction), releasing energy to fuel the cell's activities. One compound acts as an electron donor and one as an electron acceptor. The energy released generates adenosine triphosphate (ATP) through chemiosmosis, in the same basic process that happens in the mitochondrion of eukaryotic cells.

Other groups of archaea use sunlight as a source of energy (they are phototrophs). However, oxygen–generating photosynthesis does not occur in any of these organisms. Many basic metabolic pathways are shared between all forms of life; for example, archaea use a modified form of glycolysis (the Entner–Doudoroff pathway) and either a complete or partial citric acid cycle. These similarities to other organisms probably reflect both early origins in the history of life and their high level of efficiency.

Nutritional types in archaeal metabolism

Nutritional type	**Source of energy**	**Source of carbon**	**Examples**
Phototrophs	Sunlight	Organic compounds	*Halobacteria*
Lithotrophs	Inorganic compounds	Organic compounds or carbon fixation	*Ferroglobus*, *Methanobacteria* or *Pyrolobus*
Organotrophs	Organic compounds	Organic compounds or carbon fixation	*Pyrococcus*, *Sulfolobus* or *Methanosarcinales*

Some Euryarchaeota are methanogens living in anaerobic environments such as swamps. This form of metabolism evolved early, and it is even possible that the first free-living organism was a methanogen. A common reaction involves the use of carbon dioxide as an electron acceptor to oxidize hydrogen. Methanogenesis involves a range of coenzymes that are unique to these archaea, such as coenzyme M and methanofuran. Other organic compounds such as alcohols, acetic acid or formic acid are used as alternative electron acceptors by methanogens. These reactions are common in gut-dwelling archaea. Acetic acid is also broken down into methane and carbon dioxide directly, by *acetotrophic* archaea. These acetotrophs are archaea in the order Methanosarcinales, and are a major part of the communities of microorganisms that produce biogas.

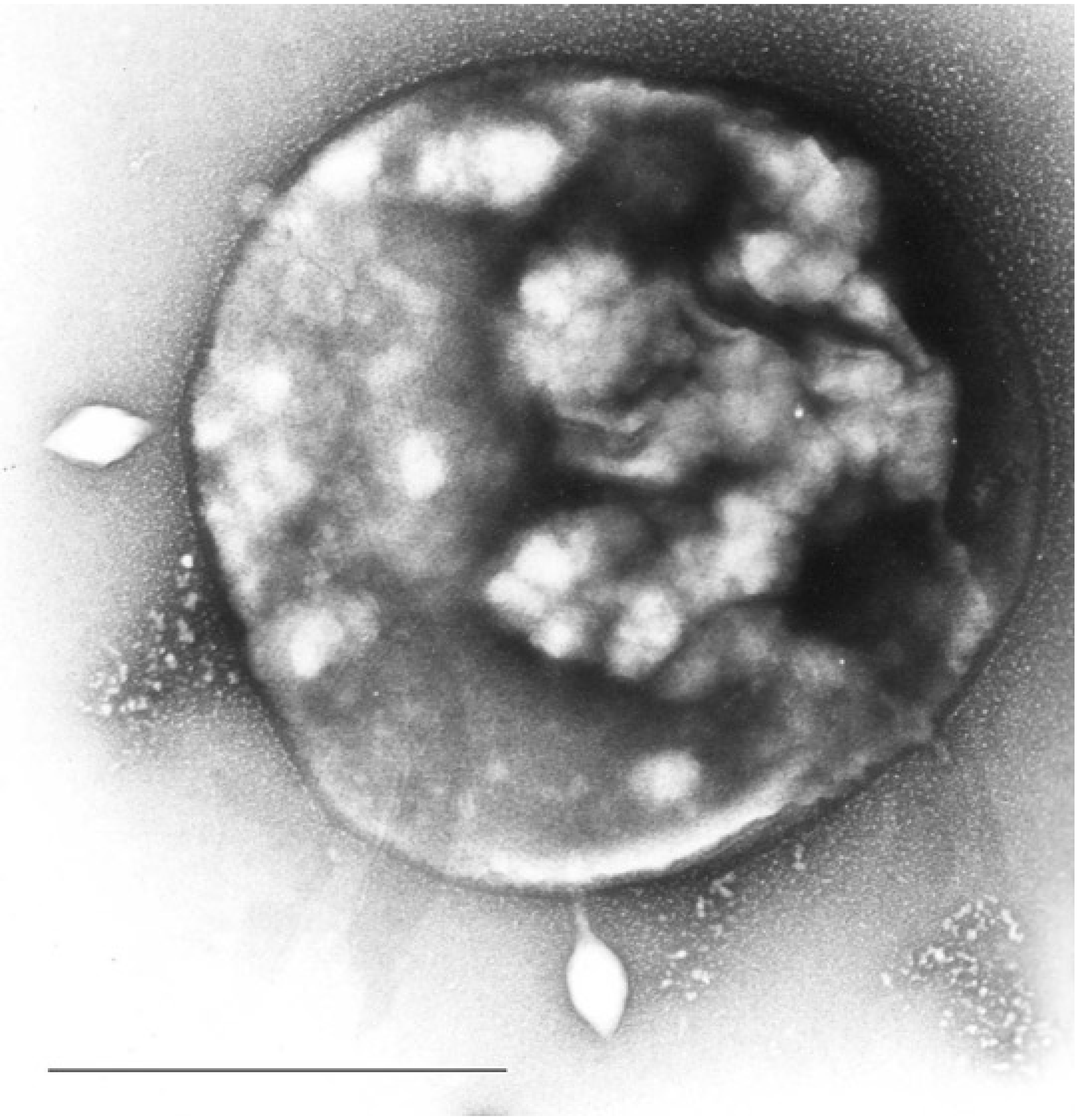
Bacteriorhodopsin from *Halobacterium salinarum*. The retinol cofactor and residues involved in proton transfer are shown as ball-and-stick models.

Other archaea use CO_2 in the atmosphere as a source of carbon, in a process called carbon fixation (they are autotrophs). This process involves either a highly modified form of the Calvin cycle or a recently discovered metabolic pathway called the 3-hydroxypropionate/4-hydroxybutyrate cycle. The Crenarchaeota also use the reverse Krebs cycle while the Euryarchaeota also use the reductive acetyl-CoA pathway. Carbon–fixation is powered by inorganic energy sources. No known archaea carry out photosynthesis. Archaeal energy sources are extremely diverse, and range from the oxidation of ammonia by the Nitrosopumilales to the oxidation of hydrogen sulfide or elemental sulfur by species of *Sulfolobus*, using either oxygen or metal ions as electron acceptors.

Phototrophic archaea use light to produce chemical energy in the form of ATP. In the Halobacteria, light-activated ion pumps like bacteriorhodopsin and halorhodopsin generate ion gradients by pumping ions out of the cell across the plasma membrane. The energy stored in these electrochemical gradients is then converted into ATP by ATP synthase. This process is a form of photophosphorylation. The ability of these light-driven pumps to move ions across membranes depends on light-driven changes in the structure of a retinol cofactor buried in the center of the protein.

Genetics

Archaea usually have a single circular chromosome, the size of which may be as great as 5,751,492 base pairs in *Methanosarcina acetivorans*, the largest known archaean genome. One-tenth of this size is the tiny 490,885 base-pair genome of *Nanoarchaeum equitans*, the smallest archaean genome known; it is estimated to contain only 537 protein-encoding genes. Smaller independent pieces of DNA, called *plasmids*, are also found in archaea. Plasmids may be transferred between cells by physical contact, in a process that may be similar to bacterial conjugation.



Sulfolobus infected with the DNA virus STSV1. Bar is 1 micrometer.

Archaea can be infected by double-stranded DNA viruses that are unrelated to any other form of virus and have a variety of unusual shapes, including bottles, hooked rods, or teardrops. These viruses have been studied in most detail in thermophilics, particularly the orders Sulfolobales and Thermoproteales. A single-stranded DNA virus that infects halophilic archaea was identified in 2009. Defenses against these viruses may involve RNA interference from repetitive DNA sequences that are related to the genes of the viruses.

Archaea are genetically distinct from bacteria and eukaryotes, with up to 15% of the proteins encoded by any one archaeal genome being unique to the domain, although most of these unique genes have no known function. Of the remainder of the unique proteins that have an identified function, most are involved in methanogenesis. The proteins that archaea, bacteria and eukaryotes share form a common core of cell function, relating mostly to transcription, translation, and nucleotide metabolism. Other characteristic archaean features are the organization of genes of related function—such as enzymes that catalyze steps in the same metabolic pathway into novel operons, and large differences in tRNA genes and their aminoacyl tRNA synthetases.

Transcription and translation in archaea resemble these processes in eukaryotes more than in bacteria, with the archaean RNA polymerase and ribosomes being very close to their equivalents in eukaryotes. Although archaea only have one type of RNA polymerase, its structure and function in transcription seems to be close to that of the eukaryotic RNA polymerase II, with similar protein assemblies (the general transcription factors) directing the binding of the RNA polymerase to a gene's promoter. However, other archaean transcription factors are closer to those found in bacteria. Post-transcriptional modification is simpler than in eukaryotes, since most archaean genes lack introns, although there are many introns in their transfer RNA and ribosomal RNA genes, and introns may occur in a few protein-encoding genes.

Reproduction

Archaea reproduce asexually by binary or multiple fission, fragmentation, or budding; meiosis does not occur, so if a species of archaea exists in more than one form, all have the same genetic material. Cell division is controlled in a cell cycle; after the cell's chromosome is replicated and the two daughter chromosomes separate, the cell divides. Details have only been investigated in the genus *Sulfolobus*, but here that cycle has characteristics that are similar to both bacterial and eukaryotic systems. The chromosomes replicate from multiple starting-points (origins of replication) using DNA polymerases that resemble the equivalent eukaryotic enzymes. However, the proteins that direct cell division, such as the protein FtsZ, which forms a contracting ring around the cell, and the components of the septum that is constructed across the center of the cell, are similar to their bacterial equivalents.

Both bacteria and eukaryotes, but not archaea, make spores. Some species of Haloarchaea undergo phenotypic switching and grow as several different cell types, including thick-walled structures that are resistant to osmotic shock and allow the archaea to survive in water at low salt concentrations, but these are not reproductive structures and may instead help them reach new habitats.

Ecology

Habitats

Archaea exist in a broad range of habitats, and as a major part of global ecosystems, may contribute up to 20% of earth's biomass. The first-discovered archaeans were extremophiles. Indeed, some archaea survive high temperatures, often above 100 °C (212 °F), as found in geysers, black smokers, and oil wells. Other common habitats include very cold habitats and highly saline, acidic, or alkaline water. However, archaea include mesophiles that grow in mild conditions, in marshland, sewage, the oceans, and soils.

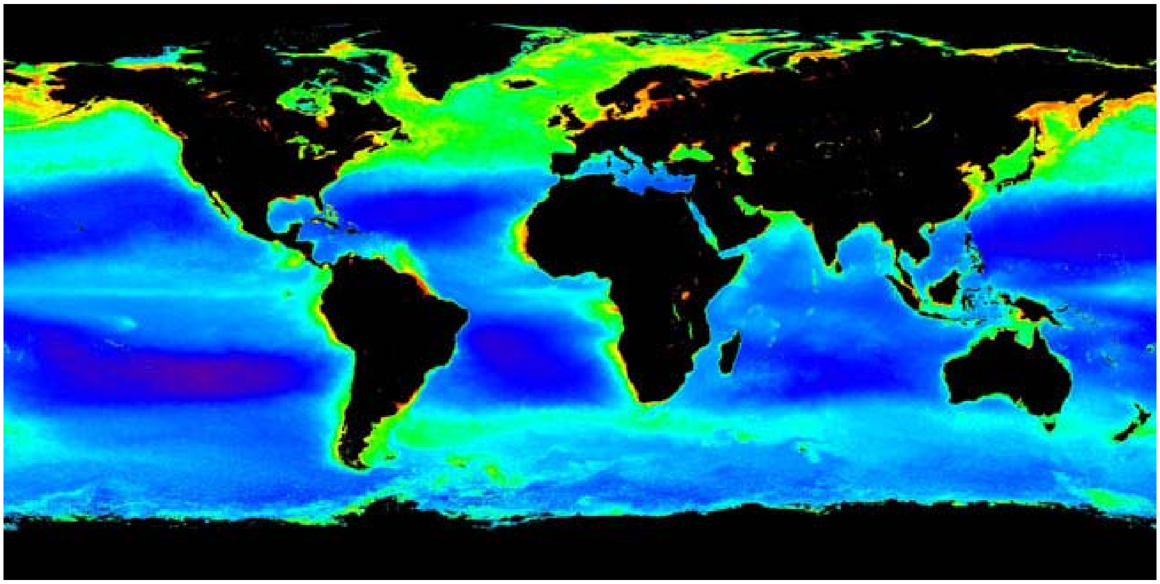


Image of plankton (light green) in the oceans; archaea form a major part of oceanic life.

Extremophile archaea are members of four main physiological groups. These are the halophiles, thermophiles, alkaliphiles, and acidophiles. These groups are not comprehensive or phylum-specific, nor are they mutually exclusive, since some archaea belong to several groups. Nonetheless, they are a useful starting point for classification.

Halophiles, including the genus *Halobacterium*, live in extremely saline environments such as salt lakes and outnumber their bacterial counterparts at salinities greater than 20–25%. Thermophiles grow best at temperatures above 45 °C (113 °F), in places such as hot springs; *hyperthermophilic* archaea grow optimally at temperatures greater than 80 °C (176 °F). The archaeal *Methanopyrus kandleri* Strain 116 grows at 122 °C (252 °F), the highest recorded temperature of any organism.

Other archaea exist in very acidic or alkaline conditions. For example, one of the most extreme archaean acidophiles is *Picrophilus torridus*, which grows at pH 0, which is equivalent to thriving in 1.2 molar sulfuric acid.

This resistance to extreme environments has made archaea the focus of speculation about the possible properties of extraterrestrial life. Some extremophile habitats are not dissimilar to those on Mars, leading to the suggestion that viable microbes could be transferred between planets in meteorites.

Recently, several studies have shown that archaea exist not only in mesophilic and thermophilic environments but are also present, sometimes in high numbers, at low temperatures as well. For example, archaea are common in cold oceanic environments such as polar seas. Even more significant are the large numbers of archaea found throughout the world's oceans in non-extreme habitats among the plankton community (as part of the picoplankton). Although these archaea can be present in extremely high numbers (up to 40% of the microbial biomass), almost none of these species have been isolated and studied in pure culture. Consequently, our understanding of the role of archaea in ocean ecology is rudimentary, so their full influence on global biogeochemical cycles remains largely unexplored. Some marine Crenarchaeota are capable of nitrification, suggesting these organisms may affect the oceanic nitrogen cycle, although these oceanic Crenarchaeota may also use other sources of energy. Vast numbers of archaea are also found in the sediments that cover the sea floor, with these organisms making up the majority of living cells at depths over 1 meter below the ocean bottom.

Role in chemical cycling

Archaea recycle elements such as carbon, nitrogen and sulfur through their various habitats. Although these activities are vital for normal ecosystem function, archaea can also contribute to human-made changes, and even cause pollution.

Archaea carry out many steps in the nitrogen cycle. This includes both reactions that remove nitrogen from ecosystems, such as nitrate-based respiration and denitrification, as well as processes that introduce nitrogen, such as nitrate assimilation and nitrogen fixation. Archaean involvement in ammonia oxidation reactions was recently discovered. These reactions are particularly important in the oceans. The archaea also appear to be crucial for ammonia oxidation in soils. They produce nitrite, which other microbes then oxidize to nitrate. Plants and other organisms consume the latter.

In the sulfur cycle, archaea that grow by oxidizing sulfur compounds release this element from rocks, making it available to other organisms. However, the archaea that do this, such as *Sulfolobus*, produce sulfuric acid as a waste product, and the growth of these organisms in abandoned mines can contribute to acid mine drainage and other environmental damage.

In the carbon cycle, methanogen archaea remove hydrogen and are important in the decay of organic matter by the populations of microorganisms that act as decomposers in anaerobic ecosystems, such as sediments, marshes and sewage treatment works. However, methane is one of the most abundant greenhouse gases in Earth's atmosphere, constituting 18% of the global total. It is 25 times more potent as a greenhouse gas than carbon dioxide. Methanogens are the primary source of atmospheric methane, and are responsible for most of the world's yearly methane emissions. As a consequence, these archaea contribute to global greenhouse gas emissions and global warming.

Interactions with other organisms

Methanogenic archaea form a symbiosis with termites.

The well-characterized interactions between archaea and other organisms are either mutual or commensal. As of 2007, no clear examples of archaeal pathogens or parasites were known. However, a relationship has been proposed between some species of methanogens and infections in the mouth, and *Nanoarchaeum equitans* may be a parasite of another species of archaea, since it only survives and reproduces within the cells of the Crenarchaeon *Ignicoccus hospitalis*, and appears to offer no benefit to its host.

Mutualism

One well-understood example of mutualism is the interaction between protozoa and methanogenic archaea in the digestive tracts of animals that digest cellulose, such as ruminants and termites. In these anaerobic environments, protozoa break down plant cellulose to obtain energy. This process releases hydrogen as a waste product, but high levels of hydrogen reduce energy production. When methanogens convert hydrogen to methane, protozoa benefit from more energy.

In anaerobic protozoa such as *Plagiopyla frontata*, archaea reside inside the protozoa and consume hydrogen produced in their hydrogenosomes. Archaea also associate with larger organisms. For example, the marine archaean *Cenarchaeum symbiosum* lives within (is an endosymbiont of) the sponge *Axinella mexicana*.

Commensalism

Archaea can also be commensals, benefiting from an association without helping or harming the other organism. For example, the methanogen *Methanobrevibacter smithii* is by far the most common archaean in the human flora, making up about one in ten of all the prokaryotes in the human gut. In termites and in humans, these methanogens may in fact be mutualists, interacting with other microbes in the gut to aid digestion. Archaean communities also associate with a range of other organisms, such as on the surface of corals, and in the region of soil that surrounds plant roots (the rhizosphere).

Significance in technology and industry

Extremophile archaea, particularly those resistant either to heat or to extremes of acidity and alkalinity, are a source of enzymes that function under these harsh conditions. These enzymes have found many uses. For example, thermostable DNA polymerases, such as the Pfu DNA polymerase from *Pyrococcus furiosus*, revolutionized molecular biology by allowing the polymerase chain reaction to be used in research as a simple and rapid technique for cloning DNA. In industry, amylases, galactosidases and pullulanases in other species of *Pyrococcus* that function at over 100 °C (212 °F) allow food processing at high temperatures, such as the production of low lactose milk and whey. Enzymes from these thermophilic archaea also tend to be very stable in organic solvents, allowing their use in environmentally friendly processes in green chemistry that synthesize organic compounds. This stability makes them easier to use in structural biology. Consequently the counterparts of bacterial or eukaryotic enzymes from extremophile archaea are often used in structural studies.

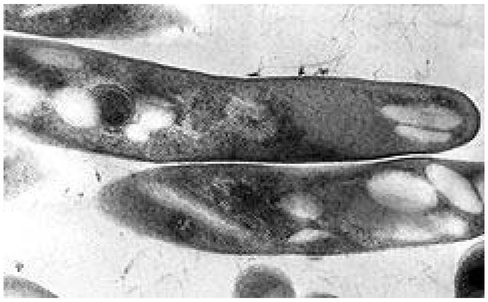
In contrast to the range of applications of archaean enzymes, the use of the organisms themselves in biotechnology is less developed. Methanogenic archaea are a vital part of sewage treatment, since they are part of the community of microorganisms that carry out anaerobic digestion and produce biogas. In mineral processing, acidophilic archaea display promise for the extraction of metals from ores, including gold, cobalt and copper.

Archaea host a new class of potentially useful antibiotics. A few of these archaeocins have been characterized, but hundreds more are believed to exist, especially within *Haloarchaea* and *Sulfolobus*. These compounds differ in structure from bacterial antibiotics, so they may have novel modes of action. In addition, they may allow the creation of new selectable markers for use in archaeal molecular biology.

Chapter 3

Mycobacterium

Mycobacterium	

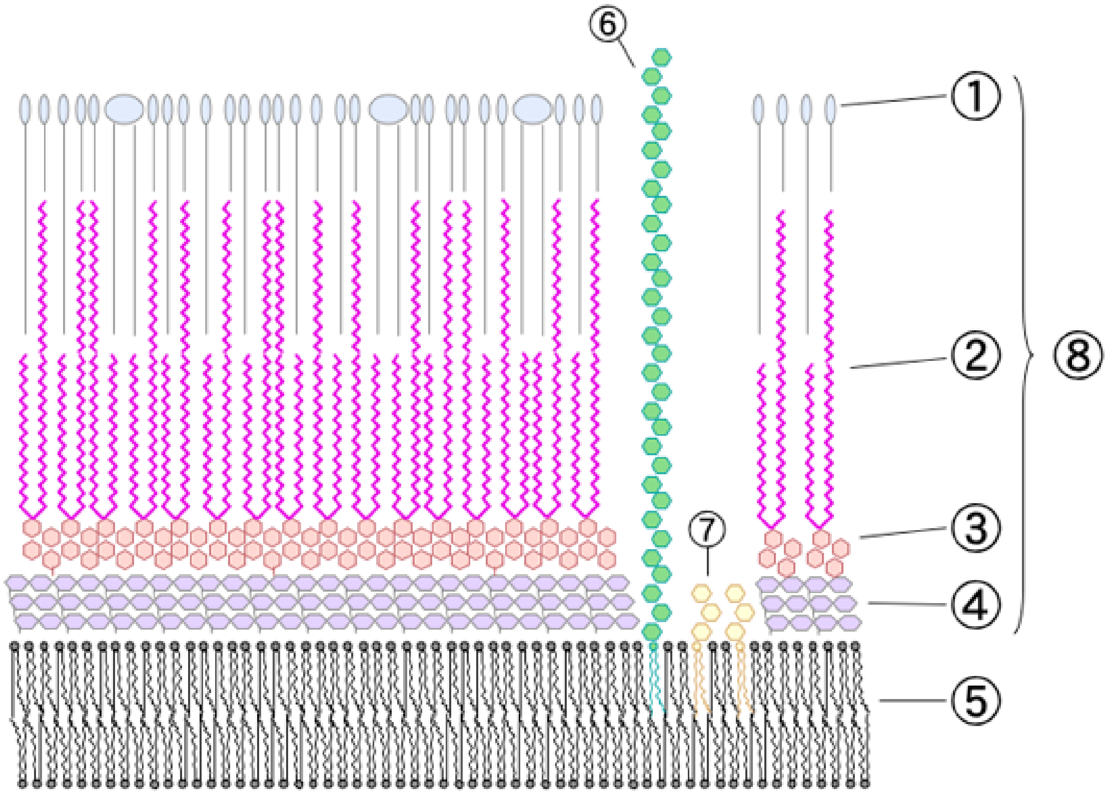


TEM micrograph of *M. tuberculosis*.

Scientific classification	
Kingdom:	Bacteria
Phylum:	Actinobacteria
Order:	Actinomycetales
Suborder:	Corynebacterineae
Family:	**Mycobacteriaceae**
Genus:	***Mycobacterium*** Lehmann & Neumann 1896

Mycobacterium is a genus of Actinobacteria, given its own family, the Mycobacteriaceae. The genus includes pathogens known to cause serious diseases in mammals, including tuberculosis (*Mycobacterium tuberculosis*) and leprosy (*Mycobacterium leprae*). The Latin prefix *"myco—"* means both *fungus* and *wax*; its use here reflects the "waxy" compounds that compose parts of the cell wall**.**

Microbiologic characteristics



Mycobacterial cell wall: 1-outer lipids, 2-mycolic acid, 3-polysaccharides (arabinogalactan), 4-peptidoglycan, 5-plasma membrane, 6-lipoarabinomannan (LAM), 7-phosphatidylinositol mannoside, 8-cell wall skeleton

Mycobacteria are aerobic and nonmotile bacteria (except for the species *Mycobacterium marinum*, which has been shown to be motile within macrophages) that are characteristically acid-alcohol fast. Mycobacteria do not contain endospores or capsules and are usually considered Gram-positive. A recent paper in PNAS showed sporulation in *Mycobacterium marinum* and perhaps in *M. bovis* . However, this has been strongly argued by other scientists . While mycobacteria do not seem to fit the Gram-positive category from an empirical standpoint (i.e. they generally do not retain the crystal violet stain well), they are classified as an acid-fast Gram-positive bacterium due to their lack of an outer cell membrane. All *Mycobacterium* species share a characteristic cell wall, thicker than in many other bacteria, which is hydrophobic, waxy, and rich in mycolic acids/mycolates. The cell wall consists of the hydrophobic mycolate layer and a peptidoglycan layer held together by a polysaccharide, arabinogalactan. The cell wall makes a substantial contribution to the hardiness of this genus. The biosynthetic pathways of cell wall components are potential targets for new drugs for tuberculosis.

Many *Mycobacterium* species adapt readily to growth on very simple substrates, using ammonia or amino acids as nitrogen sources and glycerol as a carbon source in the presence of mineral salts. Optimum growth temperatures vary widely according to the species and range from 25 °C to over 50 °C.

Some species can be very difficult to culture (i.e. they are fastidious), sometimes taking over two years to develop in culture. Further, some species also have extremely long reproductive cycles — *M. leprae*, may take more than 20 days to proceed through one division cycle (for comparison, some *E. coli* strains take only 20 minutes), making laboratory culture a slow process. In addition, the availability of genetic manipulation techniques still lags far behind that of other bacterial species.

A natural division occurs between slowly– and rapidly–growing species. Mycobacteria that form colonies clearly visible to the naked eye within seven days on subculture are termed rapid growers, while those requiring longer periods are termed slow growers. Mycobacteria cells are straight or slightly curved rods between 0.2-0.6 µm wide by 1.0-10 µm long.

Pigmentation

Some mycobacteria produce carotenoid pigments without light. Others require photoactivation for pigment production.

Photochromogens (Group I)

Produce nonpigmented colonies when grown in the dark and pigmented colonies only after exposure to light and reincubation.

- Ex: *M. kansasii*, *M. marinum*, *M. simiae*.

Scotochromogens (Group II)

Produce deep yellow to orange colonies when grown in the presence of either the light or dark.

- Ex: *M. scrofulaceum*, *M. gordonae*, *M. xenopi*, *M. szulgai*.

Non-chromogens (Groups III & IV)

Nonpigmented in the light and dark or have only a pale yellow, buff or tan pigment that does not intensify after light exposure.

- Ex: *M. tuberculosis*, *M. avium-intra-cellulare*, *M. bovis*, *M. ulcerans*
- Ex: *M. fortuitum*, *M. chelonae*

Staining characteristics

Mycobacteria are classical acid-fast organisms. Stains used in evaluation of tissue specimens or microbiological specimens include Fite's stain, Ziehl-Neelsen stain, and Kinyoun stain.

Mycobacteria appear phenotypically most closely related to members of *Nocardia*, *Rhodococcus* and *Corynebacterium*.

Ecological characteristics

Mycobacteria are widespread organisms, typically living in water (including tap water treated with chlorine) and food sources. Some, however, including the tuberculosis and the leprosy organisms, appear to be obligate parasites and are not found as free-living members of the genus.

Pathogenicity

Mycobacteria can colonize their hosts without the hosts showing any adverse signs. For example, billions of people around the world have asymptomatic infections of *M. tuberculosis*.

Mycobacterial infections are notoriously difficult to treat. The organisms are hardy due to their cell wall, which is neither truly Gram negative nor positive. Additionally, they are naturally resistant to a number of antibiotics that disrupt cell-wall biosynthesis, such as penicillin. Due to their unique cell wall, they can survive long exposure to acids, alkalis, detergents, oxidative bursts, lysis by complement, and many antibiotics. Most mycobacteria are susceptible to the antibiotics clarithromycin and rifamycin, but antibiotic-resistant strains have emerged.

As with other bacterial pathogens, surface and secreted proteins of *M. tuberculosis* contribute significantly to the virulence of this organism. There is an increasing list of extracytoplasmic proteins proven to have a function in the virulence of *M. tuberculosis*.

Medical classification

Mycobacteria can be classified into several major groups for purpose of diagnosis and treatment: *M. tuberculosis* complex, which can cause tuberculosis: *M. tuberculosis, M. bovis, M. africanum, and M. microti*; *M. leprae*, which causes Hansen's disease or leprosy; Nontuberculous mycobacteria **(NTM)** are all the other mycobacteria, which can cause pulmonary disease resembling tuberculosis, lymphadenitis, skin disease, or disseminated disease.

Phenotypic testing

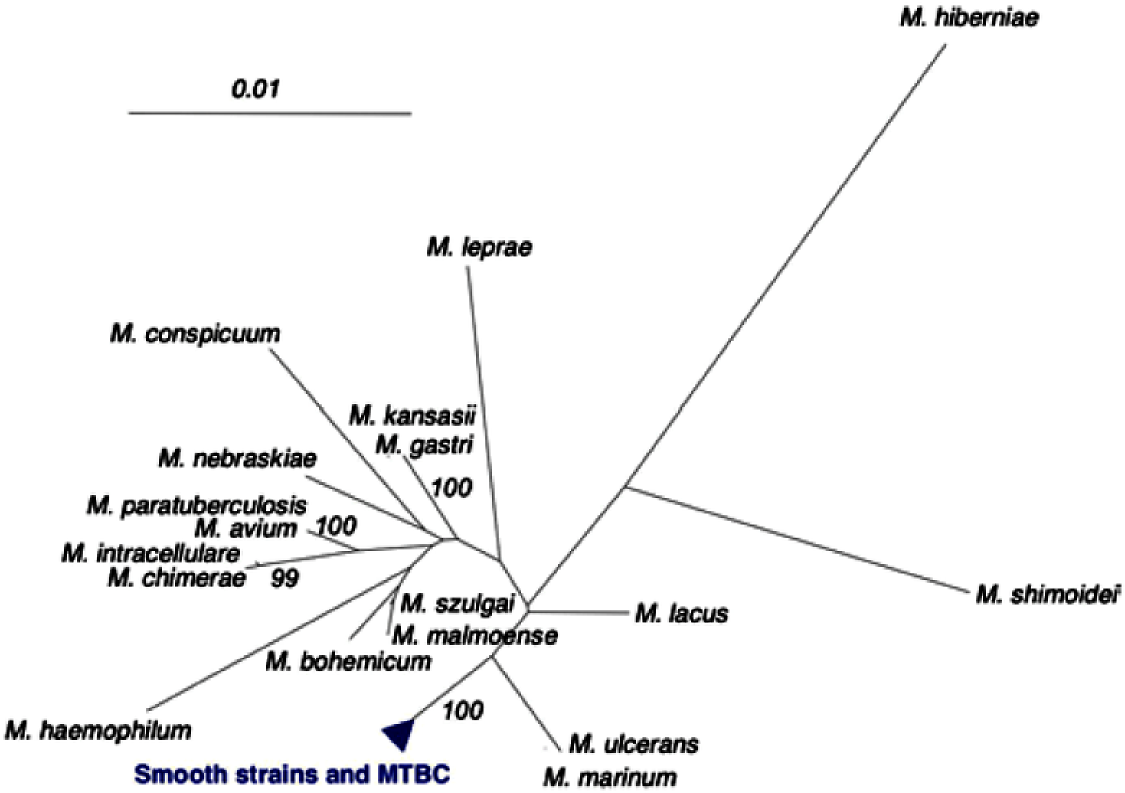
Various phenotypic tests can be used to identify and distinguish different Mycobacteria species and strains.

Phenotypic testing of Mycobacteria

Mycosides

Mycosides are phenolic alcohols (such as phenolphthiocerol) that were shown to be components of mycobacterium glycolipids that are termed glycosides of phenolphthiocerol dimycocerosate (Smith DW et al., Nature 1960, 186, 887) There are 18 and 20 carbon atoms in mycosides A, and B, respectively.

Species



Phylogenetic Position of the Tubercle Bacilli within the Genus Mycobacterium The blue triangle corresponds to tubercle bacilli sequences that are identical or differing by a single nucleotide. The sequences of the genus Mycobacterium that matched most closely to those of M. tuberculosis were retrieved from the BIBI database and aligned with those obtained for 17 smooth and MTBC strains. The unrooted neighbor-joining tree is based on 1,325 aligned nucleotide positions of the 16S rRNA gene. The scale gives the pairwise distances after Jukes-Cantor correction. Bootstrap support values higher than 90% are indicated at the nodes.

In older systems, mycobacteria are grouped based upon their appearance and rate of growth. However, these are symplesiomorphies, and more recent classification is based upon cladistics.

Slowly growing

Mycobacterium tuberculosis complex

- *Mycobacterium tuberculosis complex* (MTBC) members are causative agents of human and animal tuberculosis. Species in this complex include:

  M. tuberculosis, the major cause of human tuberculosis
  M. bovis
  M. bovis BCG
  M. africanum
  M. canetti
  M. caprae
  M. microti
  M. pinnipedii

Mycobacterium avium complex

- *Mycobacterium avium complex (MAC),* is a group of species that, in a disseminated infection but not lung infection, used to be a significant cause of death in AIDS patients. Species in this complex include:

  M. avium
  M. avium paratuberculosis, which has been implicated in Crohn's disease in humans and Johne's disease in cattle and sheep
  M. avium silvaticum
  M. avium "hominissuis"
  M. colombiense

Mycobacterium gordonae clade

- *M. asiaticum*
- *M. gordonae*

Mycobacterium kansasii clade

- *M. gastri*
- *M. kansasii*

Mycobacterium nonchromogenicum/terrae clade

- *M. hiberniae*
- *M. nonchromogenicum*
- *M. terrae*
- *M. triviale*

Mycolactone-producing mycobacteria

- *M. ulcerans*, which causes the "Buruli", or "Bairnsdale, ulcer"
- *M. pseudoshottsii*
- *M. shottsii*

Mycobacterium simiae clade

- *M. triplex*
- *M. genavense*
- *M. florentinum*
- *M. lentiflavum*
- *M. palustre*
- *M. kubicae*
- *M. parascrofulaceum*
- *M. heidelbergense*
- *M. interjectum*
- *M. simiae*

Ungrouped

- *M. branderi*
- *M. cookii*
- *M. celatum*
- *M. bohemicum*
- *M. haemophilum*
- *M. malmoense*
- *M. szulgai*
- *M. leprae*, which causes leprosy
- *M. lepraemurium*
- *M. lepromatosis*, another (less significant) cause of leprosy, described in 2008
- *M. africanum*
- *M. botniense*
- *M. chimaera*
- *M. conspicuum*
- *M. doricum*
- *M. farcinogenes*
- *M. heckeshornense*
- *M. intracellulare*
- *M. lacus*
- *M. marinum*
- *M. monacense*
- *M. montefiorense*
- *M. murale*
- *M. nebraskense*
- *M. saskatchewanense*

- *M. scrofulaceum*
- *M. shimoidei*
- *M. tusciae*
- *M. xenopi*

Intermediate growth rate

- *M. intermedium*

Rapidly growing

Mycobacterium chelonae clade

- *M. abscessus*
- *M. chelonae*
- *M. bolletii*

Mycobacterium fortuitum clade

- *M. fortuitum*
- *M. fortuitum subsp. acetamidolyticum*
- *M. boenickei*
- *M. peregrinum*
- *M. porcinum*
- *M. senegalense*
- *M. septicum*
- *M. neworleansense*
- *M. houstonense*
- *M. mucogenicum*
- *M. mageritense*
- *M. brisbanense*
- *M. cosmeticum*

Mycobacterium parafortuitum clade

- *M. parafortuitum*
- *M. austroafricanum*
- *M. diernhoferi*
- *M. hodleri*
- *M. neoaurum*
- *M. frederiksbergense*

Mycobacterium vaccae clade

- *M. aurum*
- *M. vaccae*

CF

- *M. chitae*
- *M. fallax*

Ungrouped

- *M. confluentis*
- *M. flavescens*
- *M. madagascariense*
- *M. phlei*
- *M. smegmatis*
    - *M. goodii*
    - *M. wolinskyi*
- *M. thermoresistibile*
- *M. gadium*
- *M. komossense*
- *M. obuense*
- *M. sphagni*
- *M. agri*
- *M. aichiense*
- *M. alvei*
- *M. arupense*
- *M. brumae*
- *M. canariasense*
- *M. chubuense*
- *M. conceptionense*
- *M. duvalii*
- *M. elephantis*
- *M. gilvum*
- *M. hassiacum*
- *M. holsaticum*
- *M. immunogenum*
- *M. massiliense*
- *M. moriokaense*
- *M. psychrotolerans*
- *M. pyrenivorans*
- *M. vanbaalenii*
- *M. pulveris*

Ungrouped

- *M. arosiense*
- *M. aubagnense*
- *M. caprae*
- *M. chlorophenolicum*

- *M. fluoroanthenivorans*
- *M. kumamotonense*
- *M. novocastrense*
- *M. parmense*
- *M. phocaicum*
- *M. poriferae*
- *M. rhodesiae*
- *M. seoulense*
- *M. tokaiense*

Chapter 4

Cell Wall

The **cell wall** is the tough, usually flexible but sometimes fairly rigid layer that surrounds some types of cells. It is located outside the cell membrane and provides these cells with structural support and protection, and also acts as a filtering mechanism. A major function of the cell wall is to act as a pressure vessel, preventing over-expansion when water enters the cell. They are found in plants, bacteria, fungi, algae, and some archaea. Animals and protozoa do not have cell walls.

The materials in a cell wall vary between species, and in plants and fungi also differ between cell types and developmental stages. In plants, the strongest component of the complex cell wall is a carbohydrate called cellulose, which is a polymer of glucose. In bacteria, peptidoglycan forms the cell wall. Archaean cell walls have various compositions, and may be formed of glycoprotein S-layers, pseudopeptidoglycan, or polysaccharides. Fungi possess cell walls made of the glucosamine polymer chitin, and algae typically possess walls made of glycoproteins and polysaccharides. Unusually, diatoms have a cell wall composed of silicic acid. Often, other accessory molecules are found anchored to the cell wall.

Properties

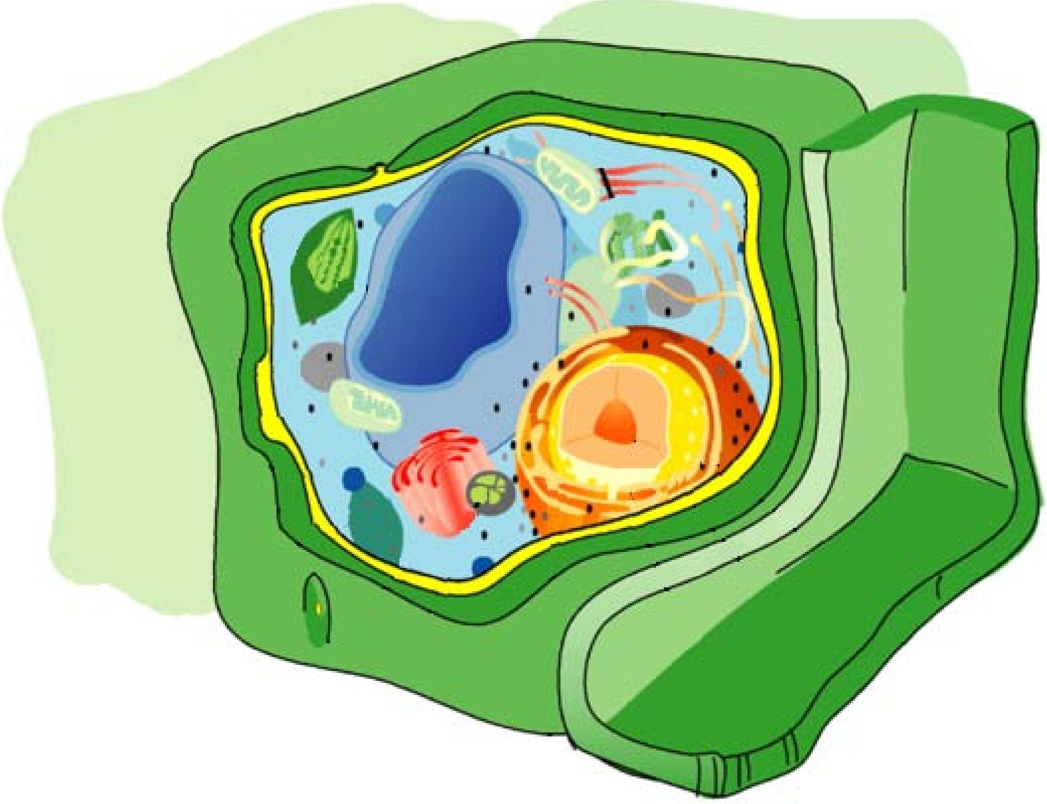


Diagram of the plant cell, with the cell wall in green.

The cell wall serves a similar purpose in those organisms that possess them. The wall gives cells rigidity and strength, offering protection against mechanical stress. In multicellular organisms, it permits the organism to build and hold its shape (morphogenesis). The cell wall also limits the entry of large molecules that may be toxic to the cell. It further permits the creation of a stable osmotic environment by preventing osmotic lysis and helping to retain water. The composition, properties, and form of the cell wall may change during the cell cycle and depend on growth conditions.

Rigidity of cell walls

The rigidity of the cell walls is often over-estimated. In most cells, the cell wall is flexible, meaning that it will bend rather than holding a fixed shape, but has considerable tensile strength. The apparent rigidity of primary plant tissues is enabled by cell walls, but not due to the walls' strength. Hydraulic turgor pressure creates this rigidity, along with the wall structure. The flexibility of the cell walls is seen when plants wilt, so that the stems and leaves begin to droop, or in seaweeds that bend in water currents. As John Howland states it:

Think of the cell wall as a wicker basket in which a balloon has been inflated so that it exerts pressure from the inside. Such a basket is very rigid and resistant to mechanical damage. Thus does the prokaryote cell (and eukaryotic cell that possesses a cell wall) gain strength from a flexible plasma membrane pressing against a rigid cell wall.

The rigidity of the cell wall thus results in part from inflation of the cell contained. This inflation is a result of the passive uptake of water.

In plants, a **secondary cell wall** is a thicker additional layer of cellulose which increases wall rigidity. Additional layers may be formed containing lignin in xylem cell walls, or containing suberin in cork cell walls. These compounds are rigid and waterproof, making the secondary wall stiff. Both wood and bark cells of trees have secondary walls. Other parts of plants such as the leaf stalk may acquire similar reinforcement to resist the strain of physical forces.

Certain single-cell protists and algae also produce a rigid wall. Diatoms build a **frustule** from silica extracted from the surrounding water; radiolarians also produce a **test** from minerals. Many green algae, such as the Dasycladales encase their cells in a secreted skeleton of calcium carbonate. In each case, the wall is rigid and essentially inorganic.

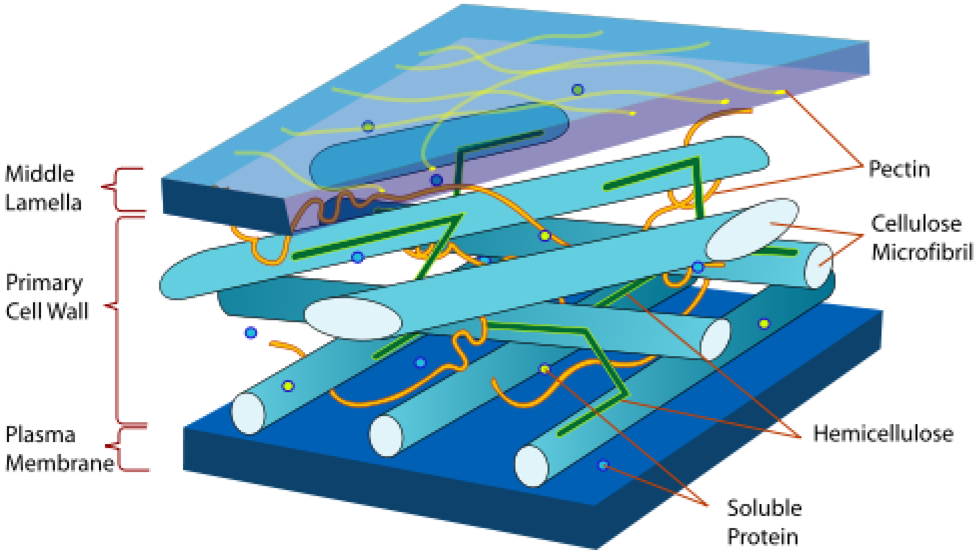
Permeability

The primary cell wall of most plant cells is semi-permeable and permit the passage of small molecules and small proteins, with size exclusion estimated to be 30-60 kDa. Key nutrients, especially water and carbon dioxide, are distributed throughout the plant from cell wall to cell wall in apoplastic flow. The pH is an important factor governing the transport of molecules through cell walls.

Plant cell walls

Many plant cells have walls that are strong enough to withstand the osmotic pressure from the difference in solute concentration between the cell interior and distilled water.

Layers



Molecular structure of the primary cell wall in plants.

Up to three strata or layers may be found in plant cell walls:

- The **middle lamella**, a layer rich in pectins. This outermost layer forming the interface between adjacent plant cells and glues them together.
- The **primary cell wall**, generally a thin, flexible and extensible layer formed while the cell is growing.
- The **secondary cell wall**, a thick layer formed inside the primary cell wall after the cell is fully grown. It is not found in all cell types. In some cells, such as found xylem, the secondary wall contains lignin, which strengthens and waterproofs the wall.

Composition

In the primary (growing) plant cell wall, the major carbohydrates are cellulose, hemicellulose and pectin. The cellulose microfibrils are linked via hemicellulosic tethers to form the cellulose-hemicellulose network, which is embedded in the pectin matrix. The most common hemicellulose in the primary cell wall is xyloglucan. In grass cell walls, xyloglucan and pectin are reduced in abundance and partially replaced by glucuronarabinoxylan, a hemicellulose. Primary cell walls characteristically extend (grow) by a mechanism called acid growth, which involves turgor-driven movement of the strong cellulose microfibrils within the weaker hemicellulose/pectin matrix, catalyzed by expansin proteins. The outer part of the primary cell wall of the plant epidermis is usually impregnated with cutin and wax, forming a permeability barrier known as the plant cuticle.

Secondary cell walls contain a wide range of additional compounds that modify their mechanical properties and permeability. The major polymers that make up wood (largely secondary cell walls) include:

- cellulose, 35-50%
- xylan, 20-35%, a type of hemicellulose
- lignin, 10-25%, a complex phenolic polymer that penetrates the spaces in the cell wall between cellulose, hemicellulose and pectin components, driving out water and strengthening the wall.

Additionally, structural proteins (1-5%) are found in most plant cell walls; they are classified as hydroxyproline-rich glycoproteins (HRGP), arabinogalactan proteins (AGP), glycine-rich proteins (GRPs), and proline-rich proteins (PRPs). Each class of glycoprotein is defined by a characteristic, highly repetitive protein sequence. Most are glycosylated, contain hydroxyproline (Hyp) and become cross-linked in the cell wall. These proteins are often concentrated in specialized cells and in cell corners. Cell walls of the epidermis and endodermis may also contain suberin or cutin, two polyester-like polymers that protect the cell from herbivores. The relative composition of carbohydrates, secondary compounds and protein varies between plants and between the cell type and age.

Plant cells walls also contain numerous enzymes, such as hydrolases, esterases, peroxidases, and transglycosylases, that cut, trim and cross-link wall polymers.

The walls of cork cells in the bark of trees are impregnated with suberin, and suberin also forms the permeability barrier in primary roots known as the Casparian strip. Secondary walls - especially in grasses - may also contain microscopic silica crystals, which may strengthen the wall and protect it from herbivores.

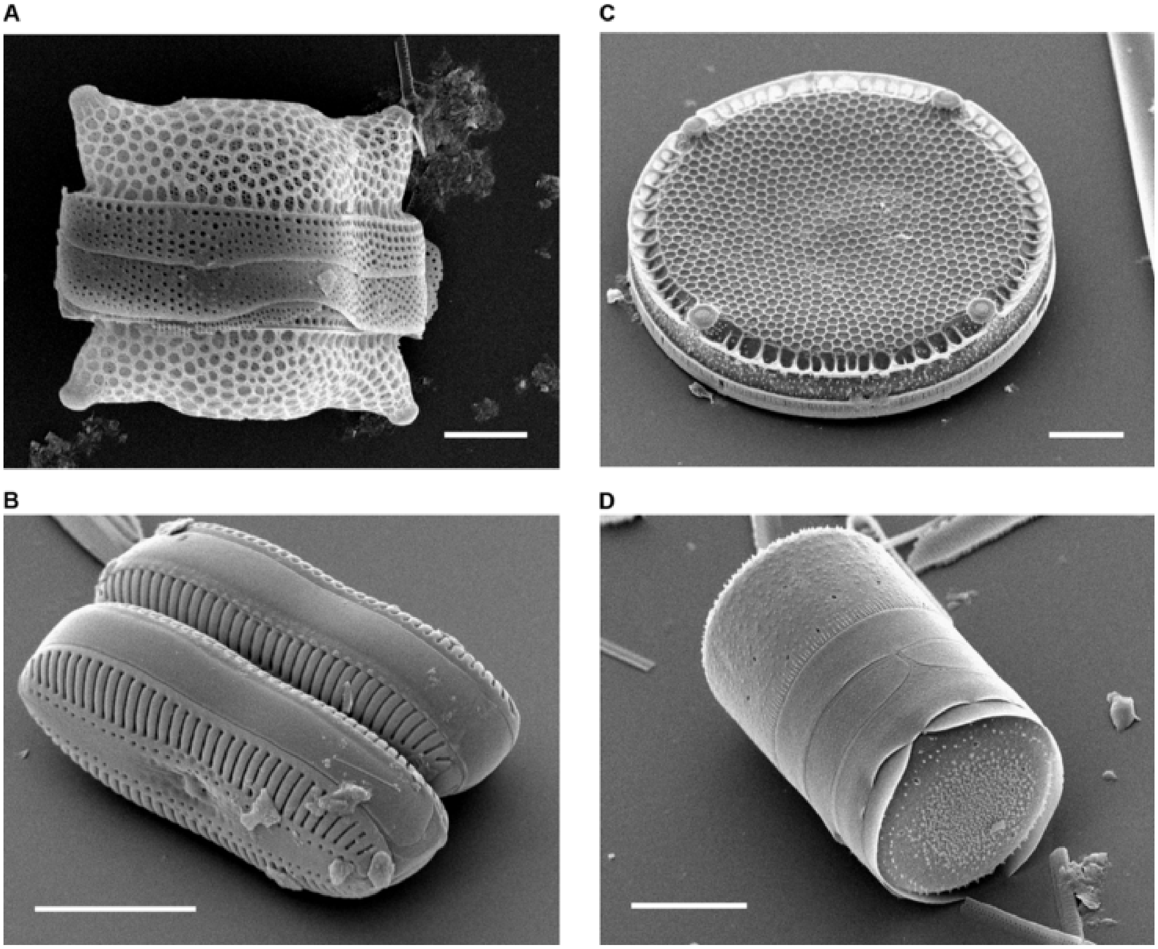
Cell walls in some plant tissues also function as storage depots for carbohydrates that can be broken down and resorbed to supply the metabolic and growth needs of the plant. For example, endosperm cell walls in the seeds of cereal grasses, nasturtium, and other species, are rich in glucans and other polysaccharides that are readily digested by enzymes during seed germination to form simple sugars that nourish the growing embryo. Cellulose microfibrils are not readily digested by plants, however.

Formation

The middle lamella is laid down first, formed from the cell plate during cytokinesis, and the primary cell wall is then deposited inside the middle lamella. The actual structure of the cell wall is not clearly defined and several models exist - the covalently linked cross model, the tether model, the diffuse layer model and the stratified layer model. However, the primary cell wall, can be defined as composed of cellulose microfibrils aligned at all angles. Microfibrils are held together by hydrogen bonds to provide a high tensile strength. The cells are held together and share the gelatinous membrane called the *middle lamella*, which contains magnesium and calcium pectates (salts of pectic acid). Cells interact though plasmodesma(ta), which are inter-connecting channels of cytoplasm that connect to the protoplasts of adjacent cells across the cell wall.

In some plants and cell types, after a maximum size or point in development has been reached, a *secondary wall* is constructed between the plant cell and primary wall. Unlike the primary wall, the microfibrils are aligned mostly in the same direction, and with each additional layer the orientation changes slightly. Cells with secondary cell walls are rigid. Cell to cell communication is possible through *pits* in the secondary cell wall that allow plasmodesma to connect cells through the secondary cell walls.

Algal cell walls



Scanning electron micrographs of diatoms showing the external appearance of the cell wall

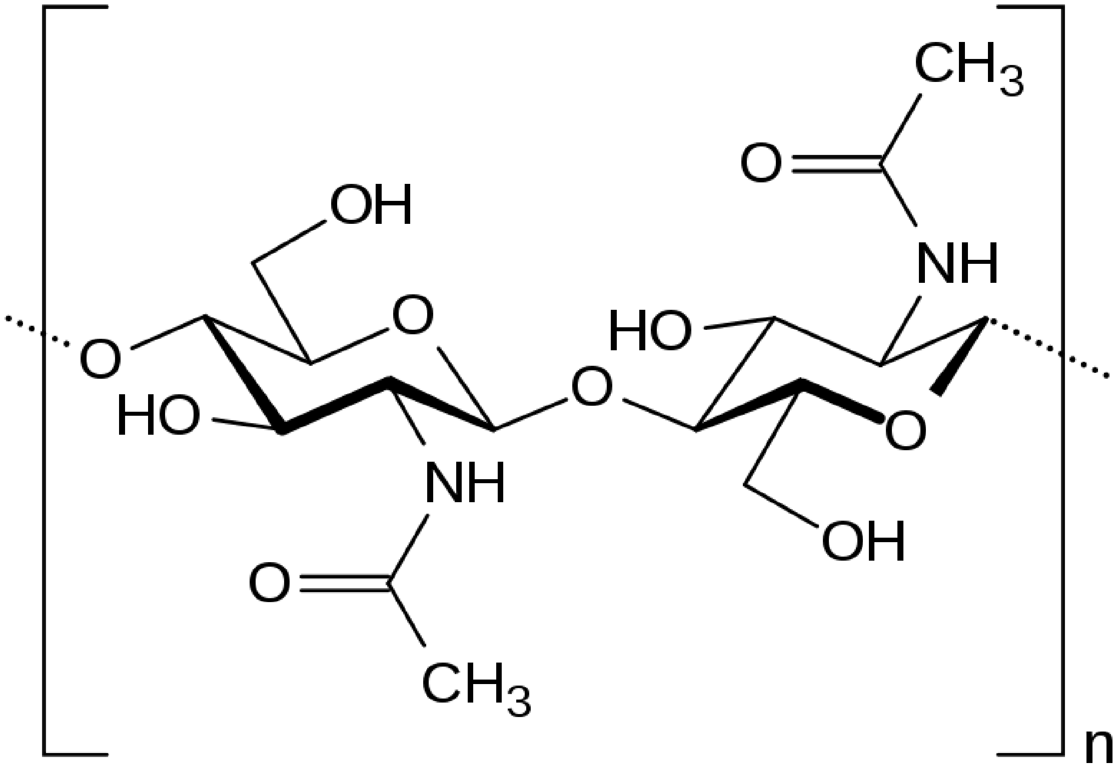
Like plants, algae have cell walls. Algal cell walls contain either polysaccharides (such as cellulose (a glucan)) or a variety of glycoproteins (Volvocales) or both. The inclusion of additional polysaccharides in algal cells walls is used as a feature for algal taxonomy.

- Mannans: They form microfibrils in the cell walls of a number of marine green algae including those from the genera, *Codium*, *Dasycladus*, and *Acetabularia* as well as in the walls of some red algae, like *Porphyra* and *Bangia*.
- Xylans:
- Alginic acid: It is a common polysaccharide in the cell walls of brown algae.
- Sulfonated polysaccharides: They occur in the cell walls of most algae; those common in red algae include agarose, carrageenan, porphyran, furcelleran and funoran.

Other compounds that may accumulate in algal cell walls include sporopollenin and calcium ions.

The group of algae known as the diatoms synthesize their cell walls (also known as frustules or valves) from silicic acid (specifically orthosilicic acid, H_4SiO_4). The acid is polymerised intra-cellularly, then the wall is extruded to protect the cell. Significantly, relative to the organic cell walls produced by other groups, silica frustules require less energy to synthesize (approximately 8%), potentially a major saving on the overall cell energy budget and possibly an explanation for higher growth rates in diatoms.

Fungal cell walls



Chemical structure of a unit from a chitin polymer chain.

There are several groups of organisms that may be called "fungi". Some of these groups have been transferred out of the Kingdom Fungi, in part because of fundamental biochemical differences in the composition of the cell wall. Most true fungi have a cell wall consisting largely of chitin and other polysaccharides. True fungi do not have cellulose in their cell walls, but some fungus-like organisms do.

True fungi

Not all species of fungi have cell walls but in those that do, the plasma membrane is followed by three layers of cell wall material. From inside out these are:

- a chitin layer (polymer consisting mainly of unbranched chains of N-acetyl-D-glucosamine)
- a layer of β-1,3-glucan (zymosan)
- a layer of mannoproteins (mannose-containing glycoproteins) which are heavily glycosylated at the outside of the cell.

Fungus-like protists

The group Oomycetes, also known as water molds, are saprotrophic plant pathogens like fungi. Until recently they were widely believed to be fungi, but structural and molecular evidence has led to their reclassification as heterokonts, related to autotrophic brown algae and diatoms. Unlike fungi, oomycetes typically possess cell walls of cellulose and glucans rather than chitin, although some genera (such as *Achlya* and *Saprolegnia*) do have chitin in their walls. The fraction of cellulose in the walls is no more than 4 to 20%, far less than the fraction comprised by glucans. Oomycete cell walls also contain the amino acid hydroxyproline, which is not found in fungal cell walls.

The dictyostelids are another group formerly classified among the fungi. They are slime molds that feed as unicellular amoebae, but aggregate into a reproductive stalk and sporangium under certain conditions. Cells of the reproductive stalk, as well as the spores formed at the apex, possess a cellulose wall. The spore wall has been shown to possess three layers, the middle of which is composed primarily of cellulose, and the innermost is sensitive to cellulase and pronase.

Prokaryotic cell walls

Bacterial cell walls

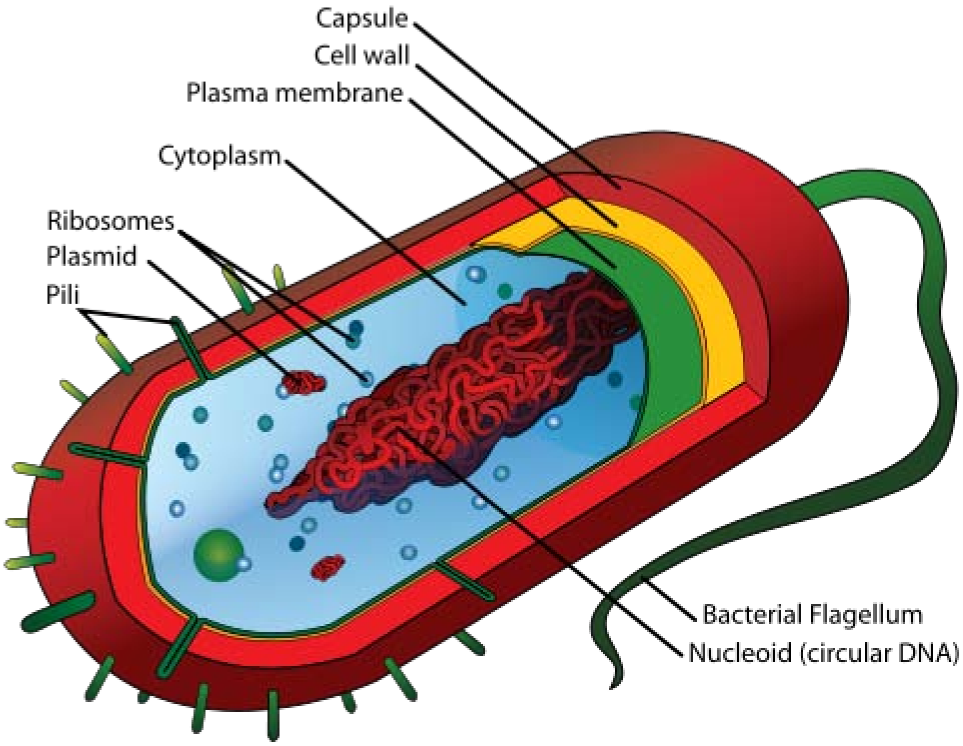
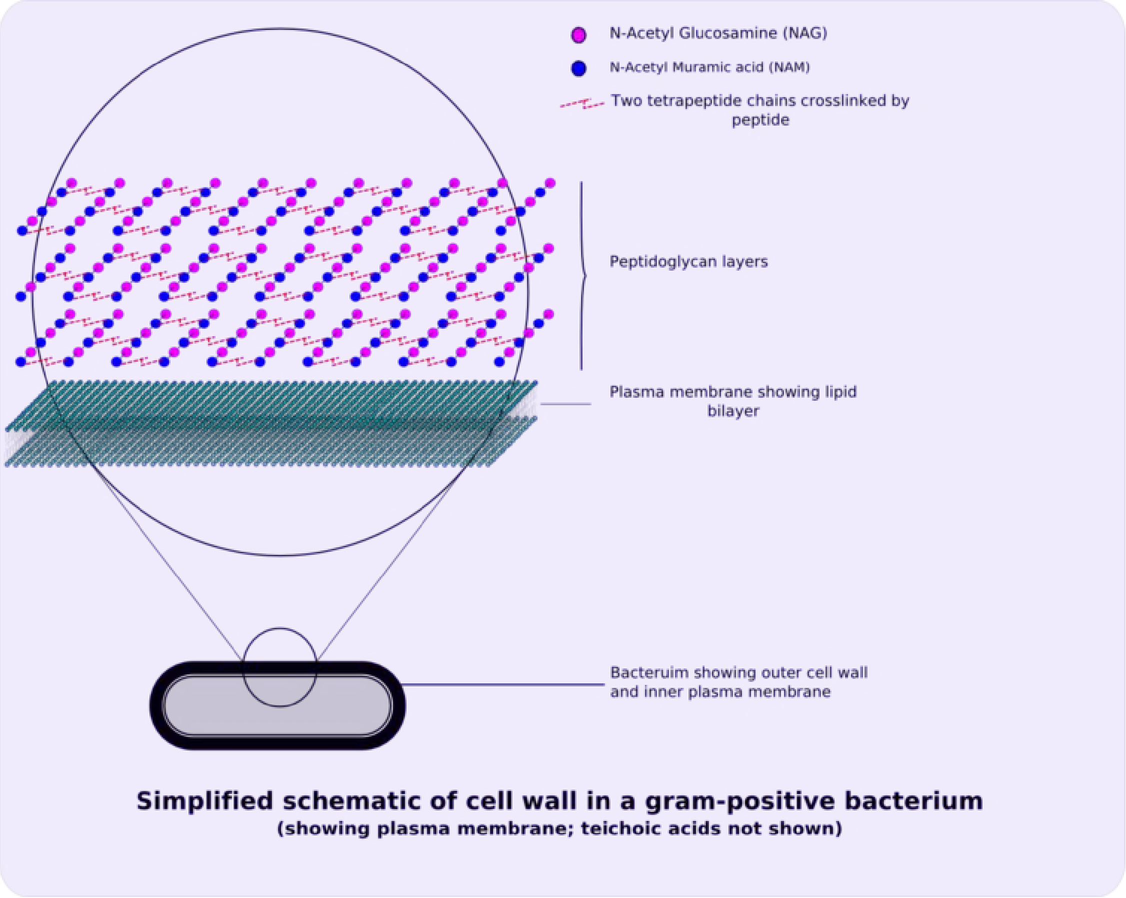


Diagram of a typical gram-negative bacterium, with the thin cell wall sandwiched between the red outer membrane and the thin green plasma membrane



Schematic of typical gram-positive cell wall showing arrangement of N-Acetylglucosamine and N-Acetlymuramic acid

Around the outside of the cell membrane is the bacterial cell wall. Bacterial cell walls are made of peptidoglycan (also called murein), which is made from polysaccharide chains cross-linked by unusual peptides containing D-amino acids. Bacterial cell walls are different from the cell walls of plants and fungi which are made of cellulose and chitin, respectively. The cell wall of bacteria is also distinct from that of Archaea, which do not contain peptidoglycan. The cell wall is essential to the survival of many bacteria, although L-form bacteria can be produced in the laboratory that lack a cell wall. The antibiotic penicillin is able to kill bacteria by preventing the cross-linking of peptidoglycan and this causes the cell wall to weaken and lyse. The lysozyme enzyme can also damage bacterial cell walls.

There are broadly speaking two different types of cell wall in bacteria, called Gram-positive and Gram-negative. The names originate from the reaction of cells to the Gram stain, a test long-employed for the classification of bacterial species.

Gram-positive bacteria possess a thick cell wall containing many layers of peptidoglycan and teichoic acids. In contrast, Gram-negative bacteria have a relatively thin cell wall consisting of a few layers of peptidoglycan surrounded by a second lipid membrane containing lipopolysaccharides and lipoproteins. Most bacteria have the Gram-negative cell wall and only the Firmicutes and Actinobacteria (previously known as the low G+C and high G+C Gram-positive bacteria, respectively) have the alternative Gram-positive arrangement. These differences in structure can produce differences in antibiotic susceptibility, for instance vancomycin can kill only Gram-positive bacteria and is ineffective against Gram-negative pathogens, such as *Haemophilus influenzae* or *Pseudomonas aeruginosa*.

Archaeal cell walls

Although not truly unique, the cell walls of Archaea are unusual. Whereas peptidoglycan is a standard component of all bacterial cell walls, all archaeal cell walls lack peptidoglycan, with the exception of one group of methanogens. In that group, the peptidoglycan is a modified form very different from the kind found in bacteria. There are four types of cell wall currently known among the Archaea.

One type of archaeal cell wall is that composed of pseudopeptidoglycan (also called pseudomurein). This type of wall is found in some methanogens, such as *Methanobacterium* and *Methanothermus*. While the overall structure of archaeal *pseudo*peptidoglycan superficially resembles that of bacterial peptidoglycan, there are a number of significant chemical differences. Like the peptidoglycan found in bacterial cell walls, pseudopeptidoglycan consists of polymer chains of glycan cross-linked by short peptide connections. However, unlike peptidoglycan, the sugar N-acetylmuramic acid is replaced by N-acetyltalosaminuronic acid, and the two sugars are bonded with a β,1-3 glycosidic linkage instead of β,1-4. Additionally, the cross-linking peptides are L-amino acids rather than D-amino acids as they are in bacteria.

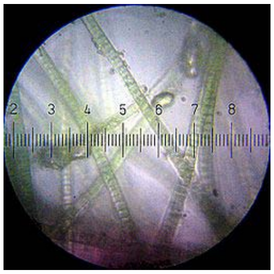
A second type of archaeal cell wall is found in *Methanosarcina* and *Halococcus*. This type of cell wall is composed entirely of a thick layer of polysaccharides, which may be sulfated in the case of *Halococcus*. Structure in this type of wall is complex and as yet is not fully investigated.

A third type of wall among the Archaea consists of glycoprotein, and occurs in the hyperthermophiles, *Halobacterium*, and some methanogens. In *Halobacterium*, the proteins in the wall have a high content of acidic amino acids, giving the wall an overall negative charge. The result is an unstable structure that is stabilized by the presence of large quantities of positive sodium ions that neutralize the charge. Consequently, *Halobacterium* thrives only under conditions with high salinity.

In other Archaea, such as *Methanomicrobium* and *Desulfurococcus*, the wall may be composed only of surface-layer proteins, known as an *S-layer*. S-layers are common in bacteria, where they serve as either the sole cell-wall component or an outer layer in conjunction with polysaccharides. Most Archaea are Gram-negative, though at least one Gram-positive member is known.

Chapter 5

Cyanobacteria

Cyanobacteria	
	
Scientific classification	
Kingdom:	Bacteria
Phylum:	**Cyanobacteria**
Orders	
The taxonomy is currently under revision.	

Cyanobacteria is a phylum of bacteria that obtain their energy through photosynthesis. The name "cyanobacteria" comes from the color of the bacteria (Greek: κυανός (kyanós) = blue).

The ability of cyanobacteria to perform oxygenic photosynthesis is thought to have converted the early reducing atmosphere into an oxidizing one, which dramatically changed the composition of life forms on Earth by stimulating biodiversity and leading to the near-extinction of oxygen-intolerant organisms. According to endosymbiotic theory, chloroplasts in plants and eukaryotic algae have evolved from cyanobacterial ancestors via endosymbiosis.

Ecology

A large bloom of cyanobacteria in Lake Atitlán

Cyanobacteria can be found in almost every conceivable environment, from oceans to fresh water to bare rock to soil. They can occur as planktonic cells or form phototrophic biofilms in fresh water and marine environments, they occur in damp soil, or even on temporarily moistened rocks in deserts. A few are endosymbionts in lichens, plants, various protists, or sponges and provide energy for the host. Some live in the fur of sloths, providing a form of camouflage.

Aquatic cyanobacteria are probably best known for the extensive and highly visible blooms that can form in both freshwater and the marine environment and can have the appearance of blue-green paint or scum. The association of toxicity with such blooms has frequently led to the closure of recreational waters when blooms are observed. Marine bacteriophages are a significant parasite of unicellular marine cyanobacteria. When they infect cells they lyse them releasing more phages into the water.

Characteristics

Cyanobacteria include unicellular and colonial species. Colonies may form filaments, sheets or even hollow balls. Some filamentous colonies show the ability to differentiate into several different cell types: vegetative cells, the normal, photosynthetic cells that are formed under favorable growing conditions; akinetes, the climate-resistant spores that may form when environmental conditions become harsh; and thick-walled heterocysts, which contain the enzyme nitrogenase, vital for nitrogen fixation. Heterocysts may also form under the appropriate environmental conditions (anoxic) when fixed nitrogen is scarce. Heterocyst-forming species are specialized for nitrogen fixation and are able to fix nitrogen gas into ammonia (NH_3), nitrites (NO^-_2) or nitrates (NO^-_3) which can be absorbed by plants and converted to protein and nucleic acids (atmospheric nitrogen cannot be used by plants directly). Rice crops utilize healthy populations of nitrogen-fixing cyanobacteria in some rice paddy fertilizers.

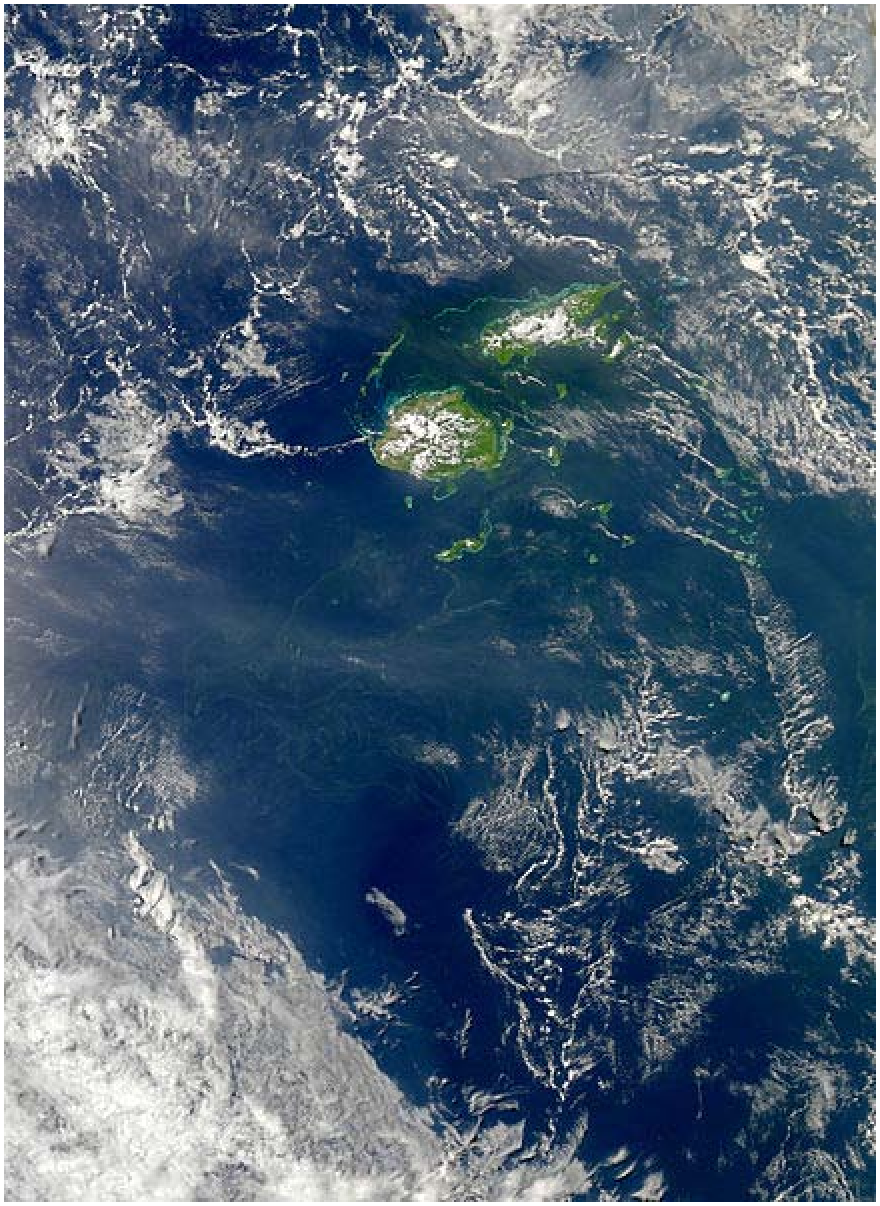
> Cyanobacteria are arguably the most successful group of microorganisms on earth. They are the most genetically diverse; they occupy a broad range of habitats across all latitudes, widespread in freshwater, marine and terrestrial ecosystems, and they are found in the most extreme niches such as hot springs, salt works, and hypersaline bays. Photoautotrophic, oxygen producing cyanobacteria created the conditions in the planet's early atmosphere that directed the evolution of aerobic metabolism and eukarotic photosynthesis. Cyanobacteria fulfil vital ecological functions in the world's oceans, being important contributors to global carbon and nitrogen budgets.
>
> – Stewart and Falconer

Many cyanobacteria also form motile filaments, called hormogonia, that travel away from the main biomass to bud and form new colonies elsewhere. The cells in a hormogonium are often thinner than in the vegetative state, and the cells on either end of the motile chain may be tapered. In order to break away from the parent colony, a hormogonium often must tear apart a weaker cell in a filament, called a necridium.

Each individual cell of a cyanobacterium typically has a thick, gelatinous cell wall. They lack flagella, but hormogonia and some species may move about by gliding along surfaces. Many of the multi-cellular filamentous forms of *Oscillatoria* are capable of a waving motion; the filament oscillates back and forth. In water columns some cyanobacteria float by forming gas vesicles, like in archaea. These vesicles are not organelles as such. They are not bounded by lipid membranes but by a protein sheath.

Some of these organisms contribute significantly to global ecology and the oxygen cycle. The tiny marine cyanobacterium *Prochlorococcus* was discovered in 1986 and accounts for more than half of the photosynthesis of the open ocean. Many cyanobacteria even display the circadian rhythms that were once thought to exist only in eukaryotic cells.

Photosynthesis



A cyanobacteria bloom near Fiji

Colonies of *Nostoc pruniforme*

Cyanobacteria account for 20–30% of Earth's photosynthetic productivity and convert solar energy into biomass-stored chemical energy at the rate of ~450 TW. Cyanobacteria utilize the energy of sunlight to drive photosynthesis, a process where the energy of light is used to split water molecules into oxygen, protons, and electrons. While most of the high-energy electrons derived from water are utilized by the cyanobacterial cells for their own needs, a fraction of these electrons are donated to the external environment via electrogenic activity. Cyanobacterial electrogenic activity is an important microbiological conduit of solar energy into the biosphere.

Cyanobacteria have an elaborate and highly organized system of internal membranes which function in photosynthesis. Cyanobacteria get their name from the bluish pigment phycocyanin, which they use to capture light for photosynthesis. Photosynthesis in cyanobacteria generally uses water as an electron donor and produces oxygen as a by-product, though some may also use hydrogen sulfide as occurs among other photosynthetic bacteria. Carbon dioxide is reduced to form carbohydrates via the Calvin cycle. In most forms the photosynthetic machinery is embedded into folds of the cell membrane, called thylakoids. The large amounts of oxygen in the atmosphere are considered to have been first created by the activities of ancient cyanobacteria. Due to their ability to fix nitrogen in aerobic conditions they are often found as symbionts with a number of other groups of organisms such as fungi (lichens), corals, pteridophytes (*Azolla*), angiosperms (*Gunnera*) etc.

Many cyanobacteria are able to reduce nitrogen and carbon dioxide under aerobic conditions, a fact that may be responsible for their evolutionary and ecological success. The water-oxidizing photosynthesis is accomplished by coupling the activity of photosystem (PS) II and I (Z-scheme). In anaerobic conditions, they are also able to use only PS I — cyclic photophosphorylation — with electron donors other than water (hydrogen sulfide, thiosulphate, or even molecular hydrogen) just like purple photosynthetic bacteria. Furthermore, they share an archaeal property, the ability to reduce elemental sulfur by anaerobic respiration in the dark. Their photosynthetic electron transport shares the same compartment as the components of respiratory electron transport. Their plasma membrane contains only components of the respiratory chain, while the thylakoid membrane hosts both respiratory and photosynthetic electron transport.

Attached to thylakoid membrane, phycobilisomes act as light harvesting antennae for the photosystems. The phycobilisome components (phycobiliproteins) are responsible for the blue-green pigmentation of most cyanobacteria. The variations on this theme are mainly due to carotenoids and phycoerythrins which give the cells the red-brownish coloration. In some cyanobacteria, the color of light influences the composition of phycobilisomes. In green light, the cells accumulate more phycoerythrin, whereas in red light they produce more phycocyanin. Thus the bacteria appear green in red light and red in green light. This process is known as complementary chromatic adaptation and is a way for the cells to maximize the use of available light for photosynthesis.

A few genera, however, lack phycobilisomes and have chlorophyll *b* instead (*Prochloron*, *Prochlorococcus*, *Prochlorothrix*). These were originally grouped together as the prochlorophytes or chloroxybacteria, but appear to have developed in several different lines of cyanobacteria. For this reason they are now considered as part of the cyanobacterial group.

Relationship to chloroplasts

Chloroplasts found in eukaryotes (algae and plants) likely evolved from an endosymbiotic relation with cyanobacteria. This endosymbiotic theory is supported by various structural and genetic similarities Primary chloroplasts are found among the "true plants" or green plants -- species ranging from sea lettuce to evergreens and flowers which contain chlorophyll *b* -- as well as among the red algae and glaucophytes, marine species which contain phycobilins. It now appears that these chloroplasts probably had a single origin, in an ancestor of the clade called Primoplantae. Other algae likely took their chloroplasts from these forms by secondary endosymbiosis or ingestion.

It was once thought that the mitochondria in eukaryotes also developed from an endosymbiotic relationship with cyanobacteria; however, it is now suspected that this evolutionary event occurred when aerobic bacteria were engulfed by anaerobic host cells. Mitochondria are believed to have originated not from cyanobacteria but from an ancestor of *Rickettsia*.

Relationship to Earth history

Stromatolites of fossilized oxygen-producing cyanobacteria have been found from 2.8 billion years ago, possibly as old as 3.5 billion years ago.

Oncolites; Guilmette Formation (Late Devonian) near Hancock Summit, Pahranagat Range, Nevada

Stromatolites; (Proterozoic) Zebra River Canyon, Namibia

The biochemical capacity to use water as the source for electrons in photosynthesis evolved once, in a common ancestor of extant cyanobacteria. The geologic record indicates that this transforming event took place early in our planet's history, at least 2450-2320 million years ago (mya), and probably much earlier. Geobiological interpretation of Archean (>2500 mya) sedimentary rocks remains a challenge; available evidence indicates that life existed 3500 mya, but the question of when oxygenic photosynthesis evolved continues to engender debate and research.

A clear paleontological window on cyanobacterial evolution opened about 2000 mya, revealing an already diverse biota of blue-greens. Cyanobacteria remained principal primary producers throughout the Proterozoic (2500-543 mya), in part because the redox structure of the oceans favored photoautotrophs capable of nitrogen fixation.

The most common cyanobacterial structures in the fossil record are the mound-producing stromatolites and related oncolites. Indeed, these fossil colonies are so common that paleobiology, micropaleontology and paleobotany cite the Pre-Cambrian and Cambrian period as an "age of stromatolites" and an "age of algae."

Green algae joined the blue-greens as major primary producers on continental shelves near the end of the Proterozoic, but only with the Mesozoic era (251-65 mya) radiations of dinoflagellates, coccolithophorids, and diatoms did primary production in marine shelf waters take modern form.

Today, the blue-green bacteria remain critical to marine ecosystems as primary producers in oceanic gyres, as agents of biological nitrogen fixation, and—in modified form—as the plastids of marine algae.

Classification

The cyanobacteria were traditionally classified by morphology into five sections, referred to by the numerals I-V. The first three - Chroococcales, Pleurocapsales, and Oscillatoriales - are not supported by phylogenetic studies. However, the latter two - Nostocales and Stigonematales - are monophyletic, and make up the heterocystous cyanobacteria. The members of Chroococales are unicellular and usually aggregate in colonies. The classic taxonomic criterion has been the cell morphology and the plane of cell division. In Pleurocapsales, the cells have the ability to form internal spores (baeocytes). The rest of the sections include filamentous species. In Oscillatoriales, the cells are uniseriately arranged and do not form specialized cells (akinetes and heterocysts). In Nostocales and Stigonematales the cells have the ability to develop heterocysts in certain conditions. Stigonematales, unlike Nostocales, includes species with truly branched trichomes. Most taxa included in the phylum or division Cyanobacteria have not yet been validly published under the Bacteriological Code. Except:

- The classes Chroobacteria, Hormogoneae and Gloeobacteria
- The orders Chroococcales, Gloeobacterales, Nostocales, Oscillatoriales, Pleurocapsales and Stigonematales
- The families Prochloraceae and Prochlorotrichaceae
- The genera Halospirulina, Planktothricoides, Prochlorococcus, Prochloron, Prochlorothrix.

Biotechnology and applications

Spirulina tablets

The unicellular cyanobacterium *Synechocystis* sp. PCC6803 was the third prokaryote and first photosynthetic organism whose genome was completely sequenced. It continues to be an important model organism. The smallest genomes have been found in *Prochlorococcus* spp. (1.7 Mb) and the largest in *Nostoc punctiforme* (9 Mb). Those of *Calothrix* spp. are estimated at 12-15 Mb, as large as yeast.

Some cyanobacteria are sold as food, notably *Aphanizomenon flos-aquae* and *Arthrospira platensis* (Spirulina).

Recent research has suggested the potential application of cyanobacteria to the generation of Clean and Green Energy via converting sunlight directly into electricity. Currently efforts are underway to commercialize algae-based fuels such as diesel, gasoline and jet fuel.

Health risks

Some cyanobacteria produce toxins, called cyanotoxins. These include anatoxin-a, anatoxin-as, aplysiatoxin, cylindrospermopsin, domoic acid, microcystin LR, nodularin R (from *Nodularia*), or saxitoxin. Cyanobacteria reproduce explosively under certain conditions. This results in algal blooms, which can become harmful to other species if the cyanobacteria involved produce toxins.

These toxins can be neurotoxins, hepatotoxins, cytotoxins, and endotoxins, and can be toxic and dangerous to humans as well as other animals and marine life in general. Several cases of human poisoning have been documented but a lack of knowledge prevents an accurate assessment of the risks. Recent studies suggest that significant exposure to high levels of some species of cyanobacteria causes amyotrophic lateral sclerosis (ALS). The Lake Mascoma ALS cluster and Gulf War veteran's cluster are two notable examples.

Chapter 6

Flagellum

A **flagellum** is a tail-like projection that protrudes from the cell body of certain prokaryotic and eukaryotic cells, and functions in locomotion. There are some notable differences between prokaryotic and eukaryotic flagella, such as protein composition, structure, and mechanism of propulsion. An example of a flagellated bacterium is the ulcer-causing *Helicobacter pylori*, which uses multiple flagella to propel itself through the mucus lining to reach the stomach epithelium. An example of a eukaryotic flagellated cell is the sperm cell, which uses its flagellum to propel itself through the female reproductive tract. Eukaryotic flagella are structurally identical to eukaryotic cilia, although distinctions are sometimes made according to function and/or length.

The word *flagellum* is the Latin word for whip.

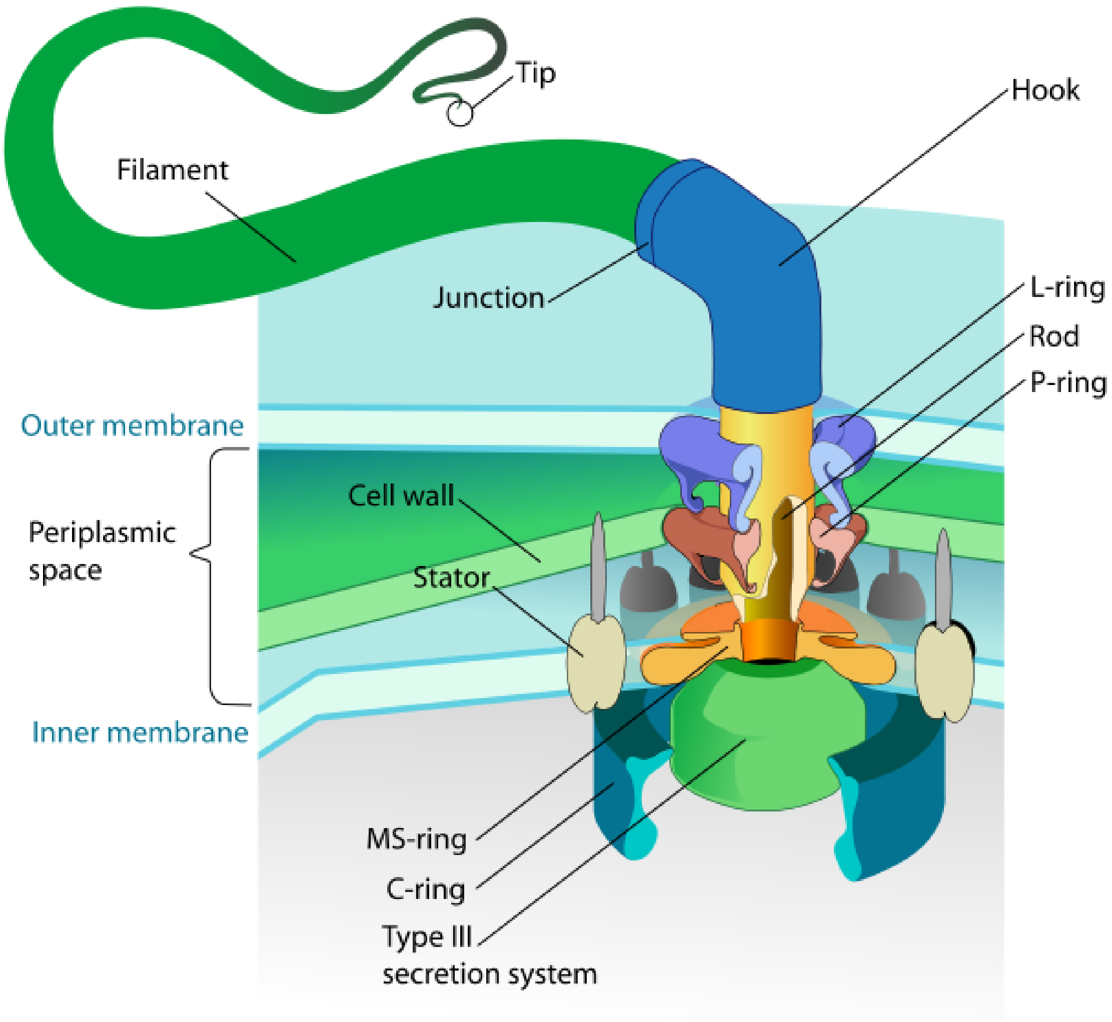
Types

Three types of flagella have so far been distinguished; bacterial, archaeal and eukaryotic.

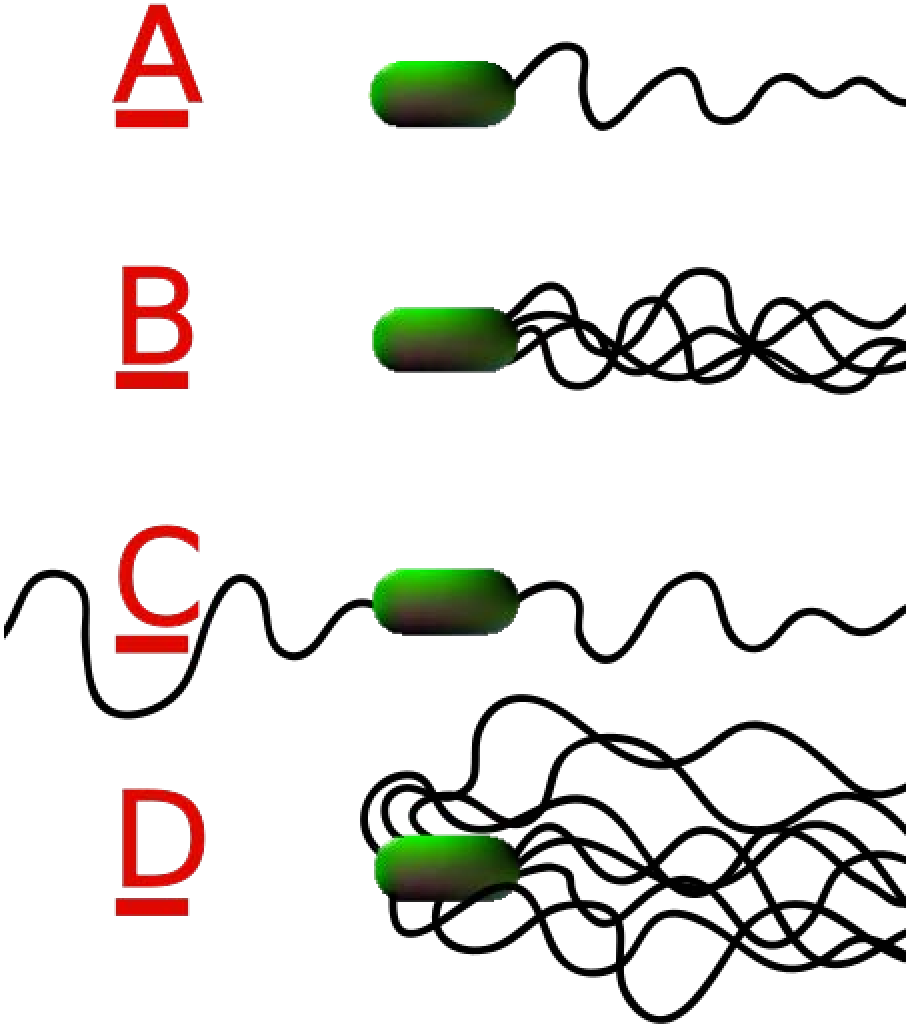
The main differences among these three types are summarized below:

- Bacterial flagella are helical filaments that rotate like screws. They provide two of several kinds of bacterial motility.
- Archaeal flagella are superficially similar to bacterial flagella, but are different in many details and considered non-homologous.
- Eukaryotic flagella - those of animal, plant, and protist cells - are complex cellular projections that lash back and forth. Eukaryotic flagella are classed along with eukaryotic *motile* cilia as *undulipodia* to emphasize their distinctive wavy appendage role in cellular function or motility. *Primary* cilia are immotile, and are not undulipodia; they have a structurally different *9+0 axoneme* rather than the *9+2 axoneme* found in both flagella and motile cilia undulopodia.

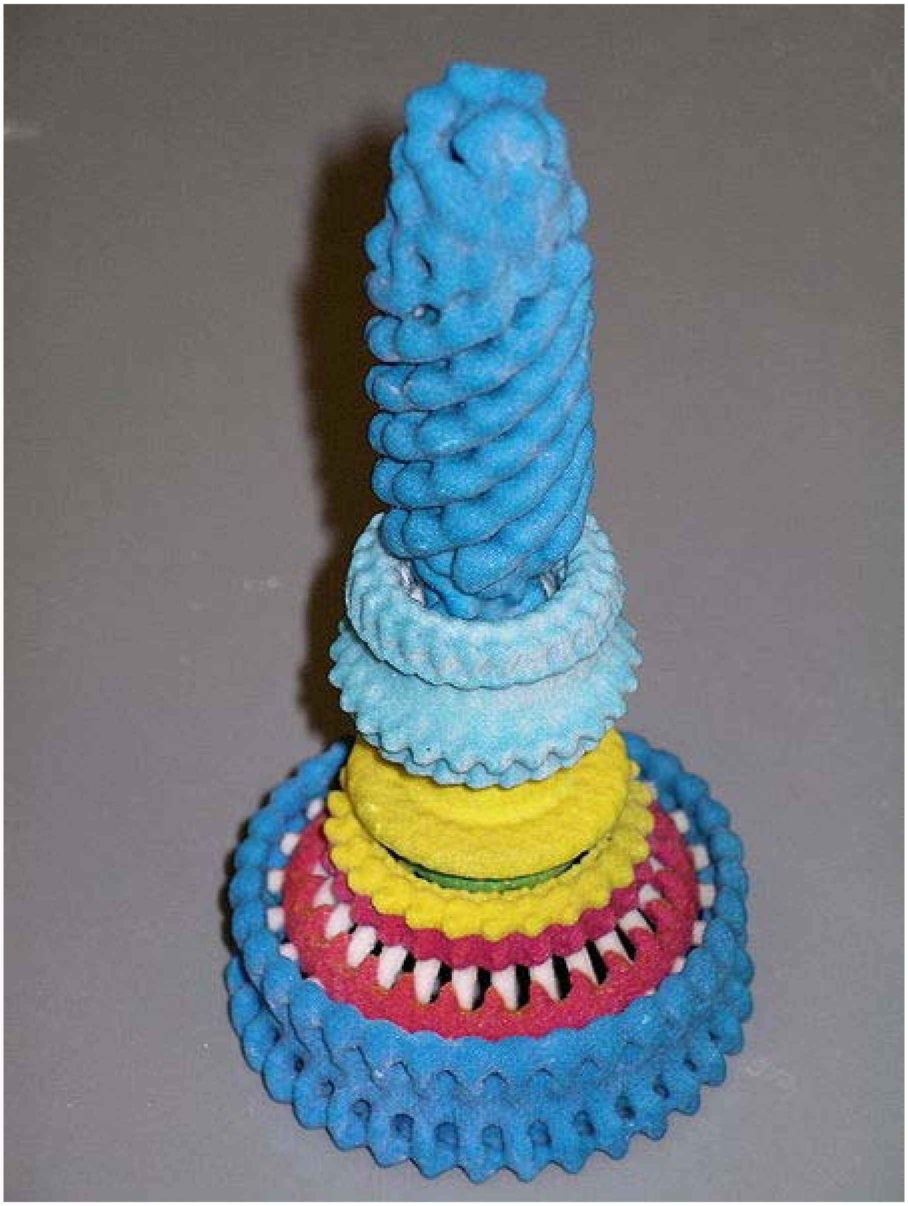
Bacterial



Flagellum of Gram-negative Bacteria



Examples of bacterial flagella arrangement schemes. A-Monotrichous; B-Lophotrichous; C-Amphitrichous; D-Peritrichous.



Physical model of a bacterial flagellum

The bacterial flagellum is made up of the protein flagellin. Its shape is a 20 nanometer-thick hollow tube. It is helical and has a sharp bend just outside the outer membrane; this "hook" allows the helix to point directly away from the cell. A shaft runs between the hook and the basal body, passing through protein rings in the cell's membrane that act as bearings. Gram-positive organisms have 2 of these basal body rings, one in the peptidoglycan layer and one in the plasma membrane. Gram-negative organisms have 4 such rings: the L ring associates with the lipopolysaccharides, the P ring associates with peptidoglycan layer, the M ring is embedded in the plasma membrane, and the S ring is directly attached to the plasma membrane. The filament ends with a capping protein.

The bacterial flagellum is driven by a rotary engine (the *Mot complex*) made up of protein, located at the flagellum's anchor point on the inner cell membrane. The engine is powered by proton motive force, i.e., by the flow of protons (hydrogen ions) across the bacterial cell membrane due to a concentration gradient set up by the cell's metabolism (in *Vibrio* species there are two kinds of flagella, lateral and polar, and some are driven by a sodium ion pump rather than a proton pump). The rotor transports protons across the membrane, and is turned in the process. The rotor alone can operate at 6,000 to 17,000 rpm, but with the flagellar filament attached usually only reaches 200 to 1000 rpm. The direction of rotation can be switched almost instantaneously, caused by a slight change in the position of a protein, FliG, in the rotor.

The cylindrical shape of flagella is suited to locomotion of microscopic organisms; these organisms operate at a low Reynolds number, where the viscosity of the surrounding water is much more important than its mass or inertia.

Flagella do not rotate at a constant speed but instead can increase or decrease their rotational speed in relation to the strength of the proton motive force. Flagellar rotation can move bacteria through liquid media at speeds of up to 60 cell lengths/second (sec). Although this is only about 0.00017 km/h (0.00011 mph), when comparing this speed with that of higher organisms in terms of number of lengths moved per second, it is extremely fast. By comparison, the cheetah, the fastest land animal, can sprint at 110 km/h (68 mph), which is approximately 25 body lengths/sec.

During flagellar assembly, components of the flagellum pass through the hollow cores of the basal body and the nascent filament. During assembly, protein components are added at the flagellar tip rather than at the base. *In vitro*, flagellar filaments assemble spontaneously in a solution containing purified flagellin as the sole protein.

The flagellar filament is the long helical screw that propels the bacterium when rotated by the motor, through the hook. In most bacteria that have been studied, including the Gram negative *Escherichia coli, Salmonella typhimurium, Caulobacter crescentus*, and *Vibrio alginolyticus*, the filament is made up of eleven protofilaments approximately parallel to the filament axis. Each protofilament is a series of tandem protein chains. However in *Campylobacter jejuni*, there are seven protofilaments.

The basal body has several traits in common with some types of secretory pores, such as the hollow rod-like "plug" in their centers extending out through the plasma membrane. Given the structural similarities between bacterial flagella and bacterial secretory systems, it is thought that bacterial flagella may have evolved from the type three secretion system; however, it is not known for certain whether these pores are derived from the bacterial flagella or the bacterial secretory system.

Through use of their flagella, *E. coli* are able to move rapidly towards attractants and away from repellents. They do this by means of a biased random walk, with 'runs' and 'tumbles' brought about by rotating the flagellum counter-clockwise and clockwise respectively.

Flagella arrangement schemes

Different species of bacteria have different numbers and arrangements of flagella. Monotrichous bacteria have a single flagellum (e.g., *Vibrio cholerae*). Lophotrichous bacteria have multiple flagella located at the same spot on the bacteria's surfaces which act in concert to drive the bacteria in a single direction. In many cases, the bases of multiple flagella are surrounded by a specialized region of the cell membrane, the so-called *polar membrane*. Amphitrichous bacteria have a single flagellum on each of two opposite ends (only one flagellum operates at a time, allowing the bacteria to reverse course rapidly by switching which flagellum is active). Peritrichous bacteria have flagella projecting in all directions (e.g., *E. coli*).

In some bacteria, such as the larger forms of *Selenomonas*, the individual flagella are organized outside the cell body, helically twining about each other to form a thick structure called a "fascicle". Other bacteria, such as Spirochetes, have a specialized type of flagellum called an "axial filament" that is located in the periplasmic space, the rotation of which causes the entire bacterium to move forward in a corkscrew-like motion.

Counterclockwise rotation of monotrichous polar flagella pushes the cell forward with the flagella trailing behind, much like a corkscrew moving inside cork. Indeed water in the microscopic scale is highly viscous, very different from our daily experience of water. The flagella are left-handed helices, and bundle and rotate together only when rotating counterclockwise. When some of the rotors reverse direction, the flagella unwind and the cell starts "tumbling". It has also been suggested that even if all flagella would rotate clockwise, they will not form a bundle, due to geometrical as well as hydrodynamical reasons. Such "tumbling" may happen occasionally, leading to the cell seemingly thrashing about in place, resulting in the reorientation of the cell. The clockwise rotation of a flagellum is suppressed by chemical compounds favorable to the cell (e.g. food), but the motor is highly adaptive to this. Therefore, when moving in a favorable direction, the concentration of the chemical attractant increases and "tumbles" are continually suppressed; however, when the cell's direction of motion is unfavorable (e.g., away from a chemical attractant), tumbles are no longer suppressed and occur much more often, with the chance that the cell will be thus reoriented in the correct direction.

In some *Vibrio* spp. (particularly *Vibrio parahemolyticus*) and related proteobacteria such as *Aeromonas*, two flagellar systems co-exist, using different sets of genes and different ion gradients for energy. The polar flagella are constitutively expressed and provide motility in bulk fluid, while the lateral flagella are expressed when the polar flagella meet too much resistance to turn. These provide swarming motility on surfaces or in viscous fluids.

Archaeal

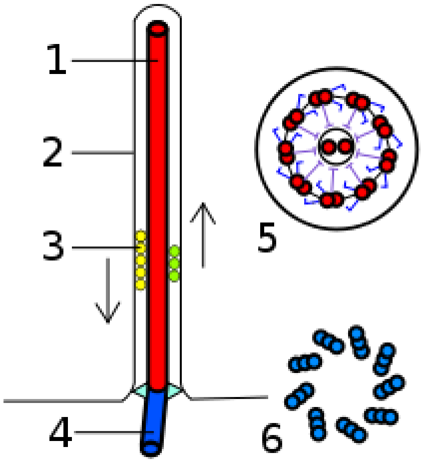
The archaeal flagellum is superficially similar to the bacterial (or eubacterial) flagellum; in the 1980s they were thought to be homologous on the basis of gross morphology and behavior. Both flagella consist of filaments extending outside the cell, and rotate to propel the cell. Archaeal flagella have a unique structure which lacks a central channel. Similar to bacterial type IV pilins, the component flagellins are made with class 3 signal peptides and they are processed by a type IV prepilin peptidase-like enzyme. The archaeal flagellins are typically modified by the addition of N-linked glycans which are necessary for proper assembly and/or function.

Discoveries in the 1990s revealed numerous detailed differences between the archaeal and bacterial flagella; these include:

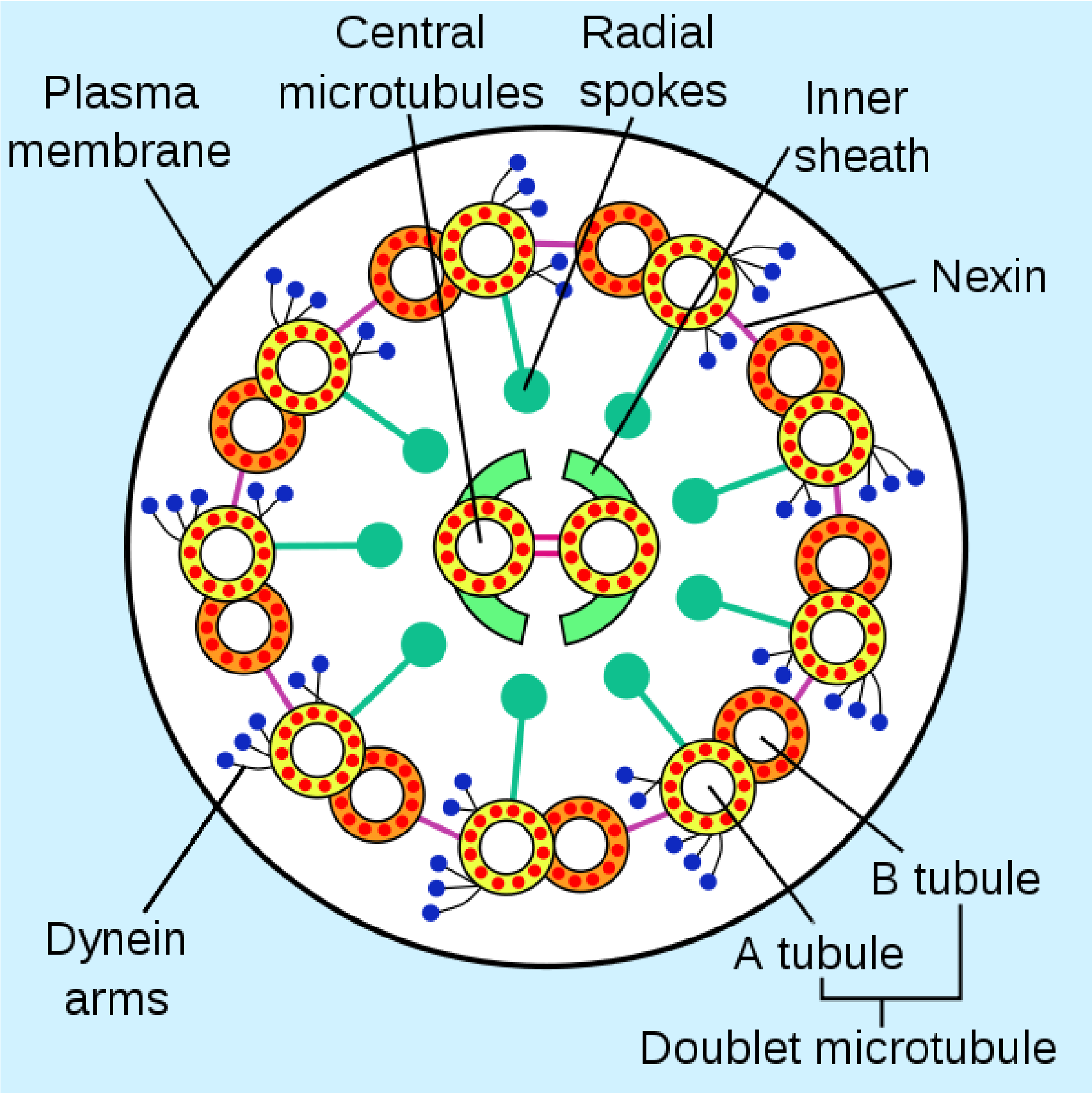
- Bacterial flagella are motorized by a flow of H^+ ions (or occasionally Na^+ ions); archaeal flagella are almost certainly powered by ATP. The torque-generating motor that powers rotation of the archaeal flagellum has not been identified.
- While bacterial cells often have many flagellar filaments, each of which rotates independently, the archaeal flagellum is composed of a bundle of many filaments that rotate as a single assembly.
- Bacterial flagella grow by the addition of flagellin subunits at the tip; archaeal flagella grow by the addition of subunits to the base.
- Bacterial flagella are thicker than archaeal flagella, and the bacterial filament has a large enough hollow "tube" inside that the flagellin subunits can flow up the inside of the filament and get added at the tip; the archaeal flagellum is too thin to allow this.
- Many components of bacterial flagella share sequence similarity to components of the type III secretion systems, but the components of bacterial and archaeal flagella share no sequence similarity. Instead, some components of archaeal flagella share sequence and morphological similarity with components of type IV pili, which are assembled through the action of type II secretion systems (the nomenclature of pili and protein secretion systems is not consistent).

These differences could mean that the bacterial and archaeal flagella could be a classic case of biological analogy, or convergent evolution, rather than homology. However, in comparison to the decades of well-publicized study of bacterial flagella (e.g. by Berg), archaeal flagella have only recently begun to get serious scientific attention. Therefore, many assume erroneously that there is only one basic kind of prokaryotic flagellum, and that archaeal flagella are homologous to it. For example, Cavalier-Smith (2002) is aware of the differences between archaeal and bacterial flagellins, but retains the misconception that the basal bodies are homologous.

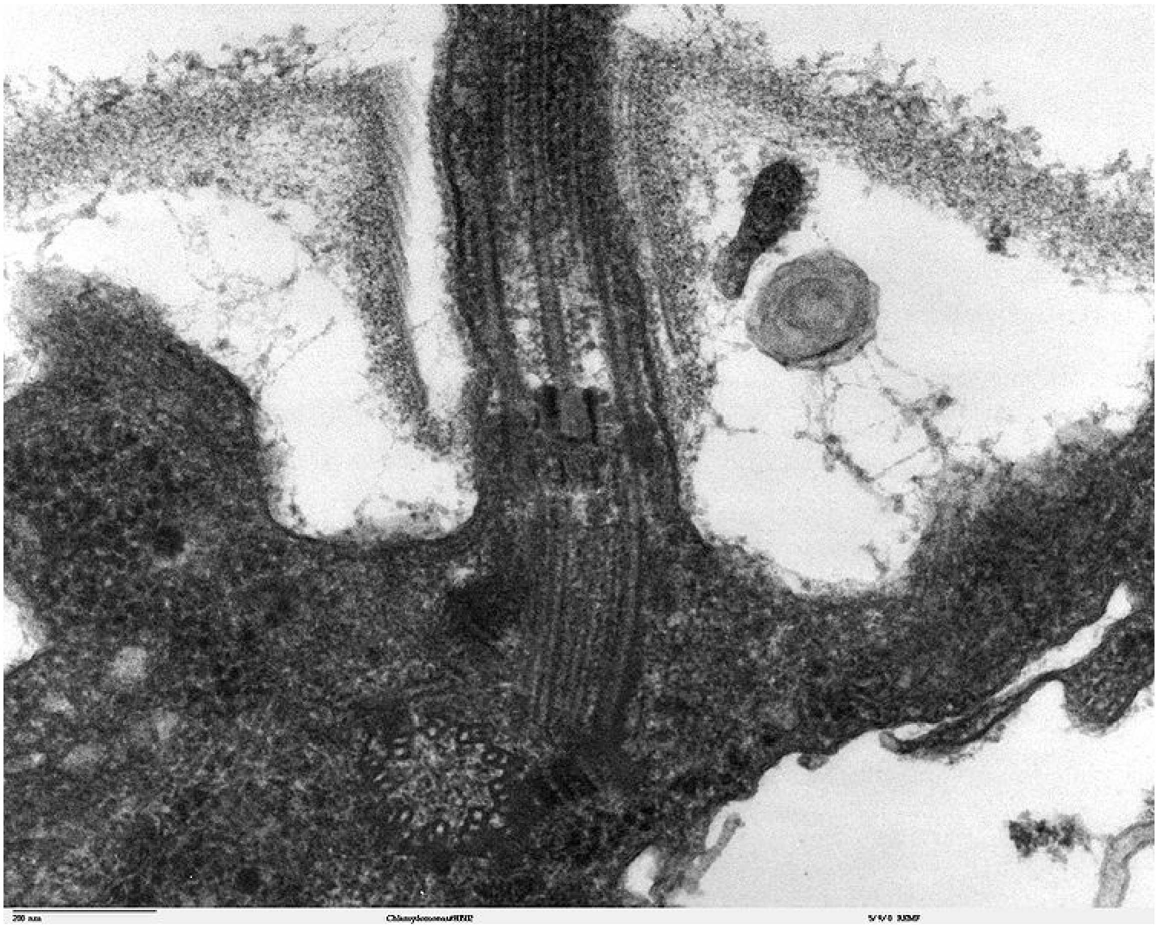
Eukaryotic



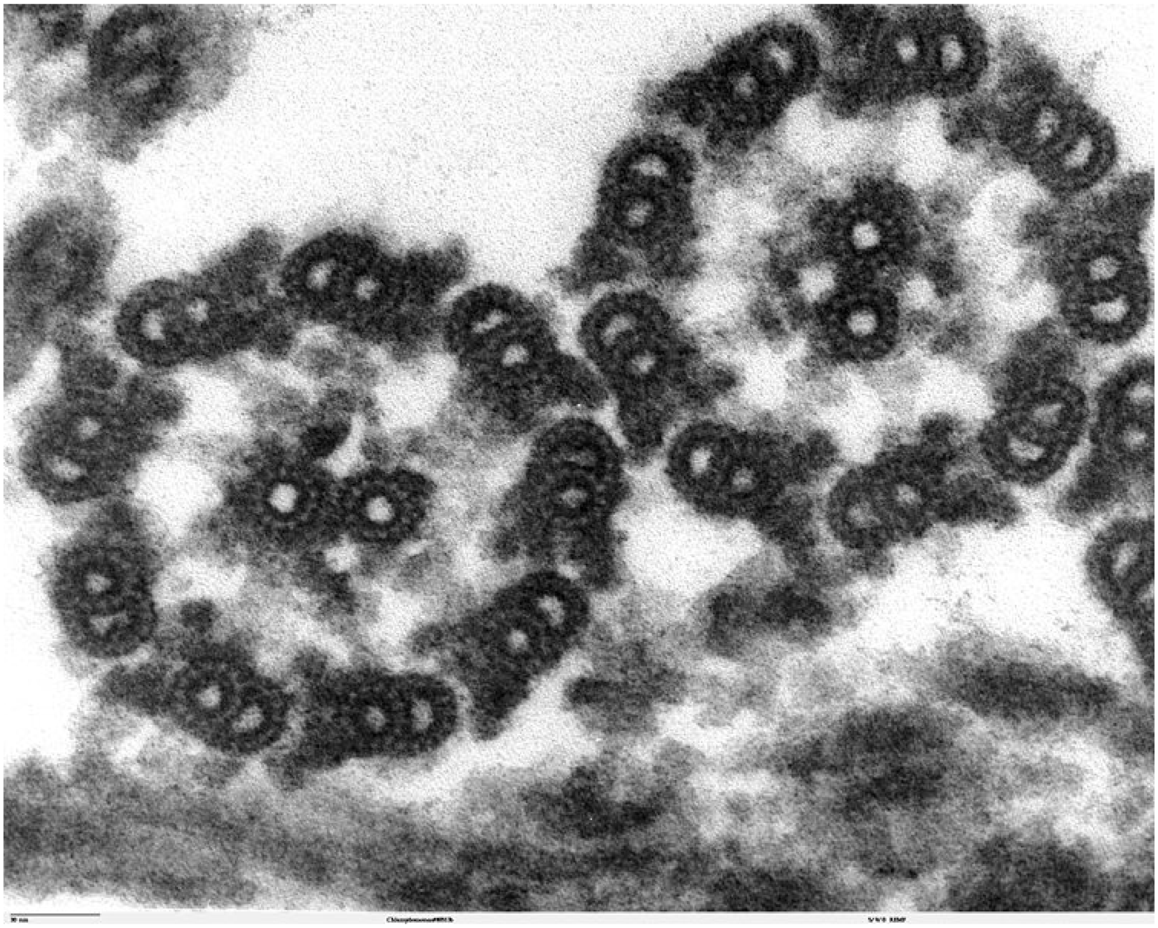
Eukaryotic flagella. 1-axoneme, 2-cell membrane, 3-IFT (IntraFlagellar Transport), 4-Basal body, 5-Cross section of flagella, 6-Triplets of microtubules of basal body



Cross section of an axoneme



Longitudinal section through the flagella area in *Chlamydomonas reinhardtii*. In the cell apex is the basal body that is the anchoring site for a flagella. Basal bodies originate from and have a substructure similar to that of centrioles, with nine peripheral microtubule triplets.



The "9+2" structure is visible in this cross-section micrograph of axoneme

Along with cilia, flagella make up a group of organelles known as undulipodia.

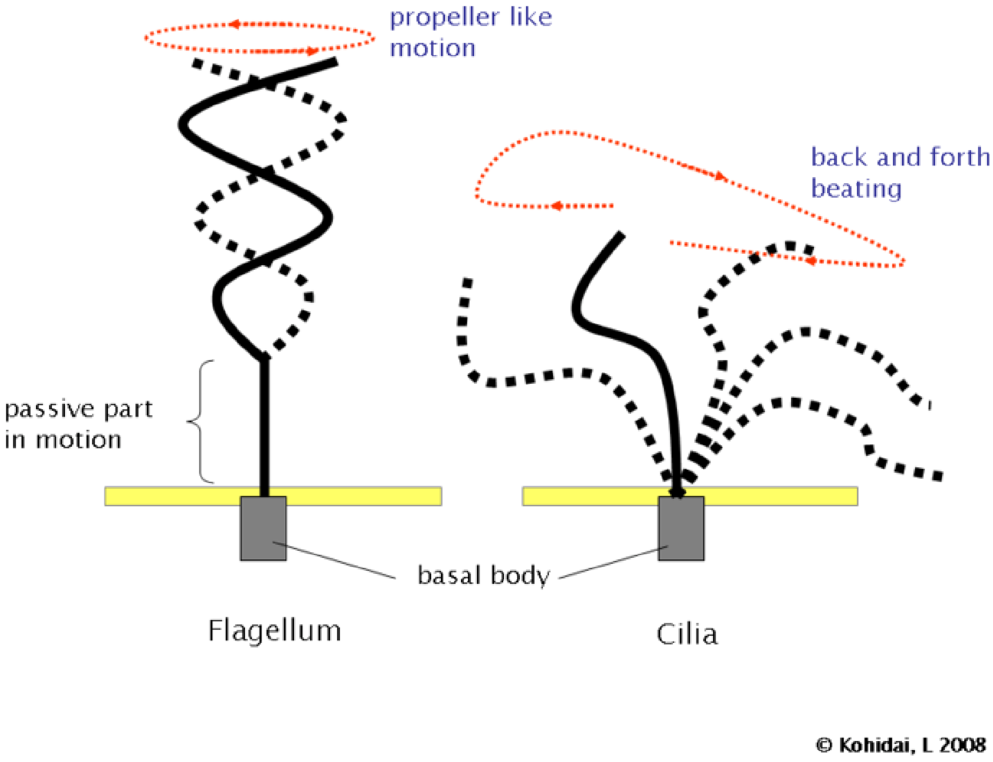
Structure

A eukaryotic flagellum is a bundle of nine fused pairs of microtubule *doublets* surrounding two central single microtubules. The so-called *"9+2"* structure is characteristic of the core of the eukaryotic flagellum called an *axoneme*. At the base of a eukaryotic flagellum is a basal body, "blepharoplast" or kinetosome, which is the microtubule organizing center (MTOC) for flagellar microtubules and is about 500 nanometers long. Basal bodies are structurally identical to centrioles. The flagellum is encased within the cell's plasma membrane, so that the interior of the flagellum is accessible to the cell's cytoplasm.

Mechanism

Each of the outer 9 doublet microtubules extends a pair of dynein arms (an "inner" and an "outer" arm) to the adjacent microtubule; these dynein arms are responsible for flagellar beating, as the force produced by the arms causes the microtubule doublets to slide against each other and the flagellum as a whole to bend. These dynein arms produce force through ATP hydrolysis. The flagellar axoneme also contains radial spokes, polypeptide complexes extending from each of the outer 9 microtubule doublets towards the central pair, with the "head" of the spoke facing inwards. The radial spoke is thought to be involved in the regulation of flagellar motion, although its exact function and method of action are not yet understood.

Flagella vs Cilia



Difference of beating pattern of flagellum and cilia

Though eukaryotic flagella and motile cilia are ultrastructurally identical, the beating pattern of the two organelles can be different. In the case of flagella (e.g. the tail of a sperm) the motion is propeller-like. In contrast, beating of motile cilia consists of coordinated back-and-forth cycling of many cilia on the cell surface. Thus, flagella serve for the propulsion of single cells (e.g. swimming of protozoa and spermatozoa), and motile cilia for the transport of fluids (e.g. transport of mucus by stationary ciliated cells in the trachea). However, cilia are also used for locomotion (through liquids) in organisms such as *Paramecium*.

Intraflagellar Transport

Intraflagellar transport (IFT), the process by which axonemal subunits, transmembrane receptors, and other proteins are moved up and down the length of the flagellum, is essential for proper functioning of the flagellum, in both motility and signal transduction.

Evolution of flagella and debate

Based on similarity in structure and partial similarity in amino acid sequence, it is generally accepted among scientists that the eukaryotic flagellum and cilium have evolved from the cytoskeleton, while the eubacterial flagellum has evolved either from the type III secretion system or from a more ancient secretion system from which the type III secretion system has evolved as well. The archaeal flagellum has probably evolved from the type IV pili. More details appear under Evolution of flagella.

In his 1996 book *Darwin's Black Box*, intelligent design proponent Michael Behe, under funding from the Templeton Foundation, cited the bacterial flagellum as an example of an irreducibly complex structure that could not have evolved through naturalistic means. Behe argued that the flagellum becomes useless if any one of its constituent parts is removed, and thus could not have arisen through numerous, successive, slight modifications; therefore, it is hopelessly improbable that the proteins making up the flagellar motor could have come together all at once, by chance. Mark Perakh explained that while Behe popularized the idea, biologist Hermann J. Müller had already explored it (under the slightly different name of “interlocking complexity”) and more than a decade before Behe’s book the same idea was explored by A. Graham Cairns-Smith, but neither claimed that “irreducible complexity” was a “marker” of a supernatural design.

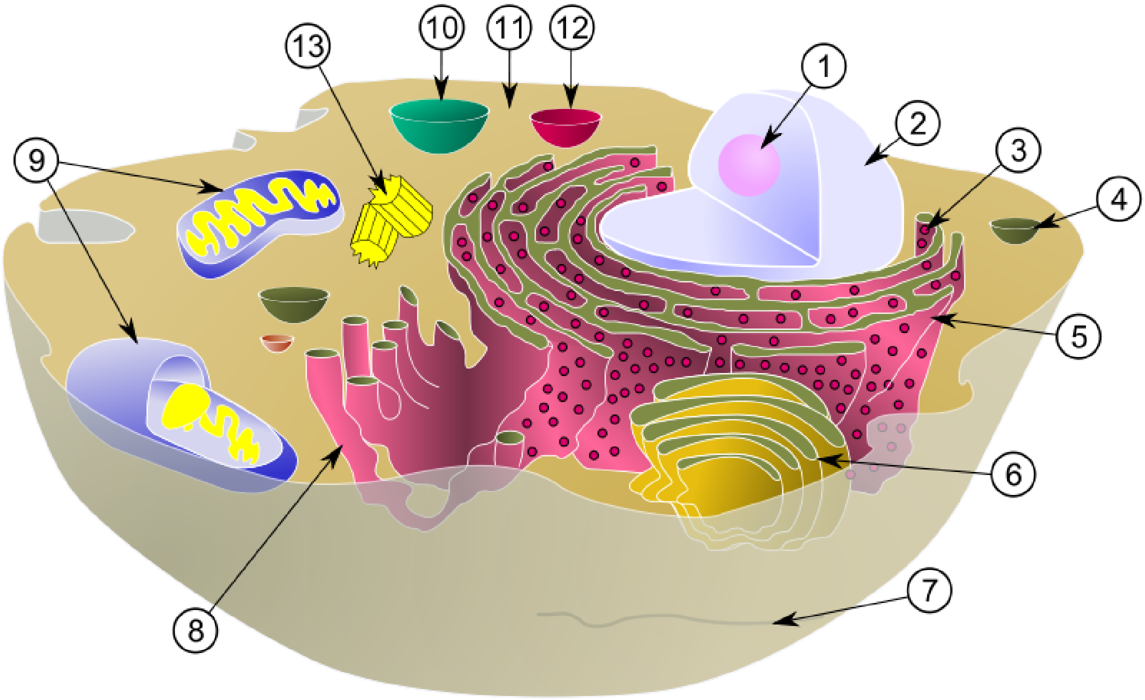
While Behe discussed the immune system and the blood clotting cascade in greater detail, the bacterial flagellum has become a "poster child" for intelligent design proponents and other creationists, as during the Kitzmiller v. Dover Area School District trial of 2005. It is one of two identified rotary structures found in nature (the other being ATP synthase) and it is billions of years older than Behe's other two examples, which exist in many homologous forms, simplifying the explanation of their origin.

Evolutionary pathways supported by the Theory of Natural Selection and Evolution (see: "The Flagellum Unspun and PBS/Nova Science's television production of Intelligent Design on Trial) have since been identified for the bacterial flagellum; thus, undermining Behe's argument. In addition, the Type three secretion system, a molecular syringe which bacteria use to inject toxins into other cells, appears to be a simplified sub-set of the bacterial flagellum's components, meaning that it is much less likely to be irreducibly complex in the way that the bacterial flagellum could have in fact evolved from the type three secretion system.

Chapter 7

Cytoplasm and Nucleoid

Cytoplasm



Schematic showing the cytoplasm, with major components of a typical animal cell (organelles):
(1) nucleolus
(2) nucleus
(3) ribosomes (indicated by purple dots)
(4) vesicle
(5) rough endoplasmic reticulum (ER)
(6) Golgi apparatus
(7) cytoskeleton
(8) smooth ER

(9) mitochondria
(10) vacuole
(11) cytosol
(12) lysosome
(13) centrioles within centrosome

The **cytoplasm** is a thick liquid residing between the cell membrane holding organelles, except for the nucleus. All the contents of the cells of prokaryote organisms (which lack a cell nucleus) are contained within the cytoplasm. Within the cells of eukaryote organisms the contents of the cell nucleus are separated from the cytoplasm, and are then called the nucleoplasm.

In eukaryotic cells also, the cytoplasm contains organelles, such as mitochondria, which are filled with liquid that is kept separate from the rest of the cytoplasm by biological membranes. It is within the cytoplasm that most cellular activities occur, such as many metabolic pathways including glycolysis, and processes such as cell division. The inner, granular mass is called the endoplasm and the outer, clear and glassy layer is called the cell cortex or the ectoplasm.

The part of the cytoplasm that is not held within organelles is called the cytosol. The cytosol is a complex mixture of cytoskeleton filaments, dissolved molecules, and water that fills much of the volume of a cell. The cytosol is a gel, with a network of fibers dispersed through water. Due to this network of pores and high concentrations of dissolved macromolecules, such as proteins, an effect called macromolecular crowding occurs and the cytosol does not act as an ideal solution. This crowding effect alters how the components of the cytosol interact with each other.

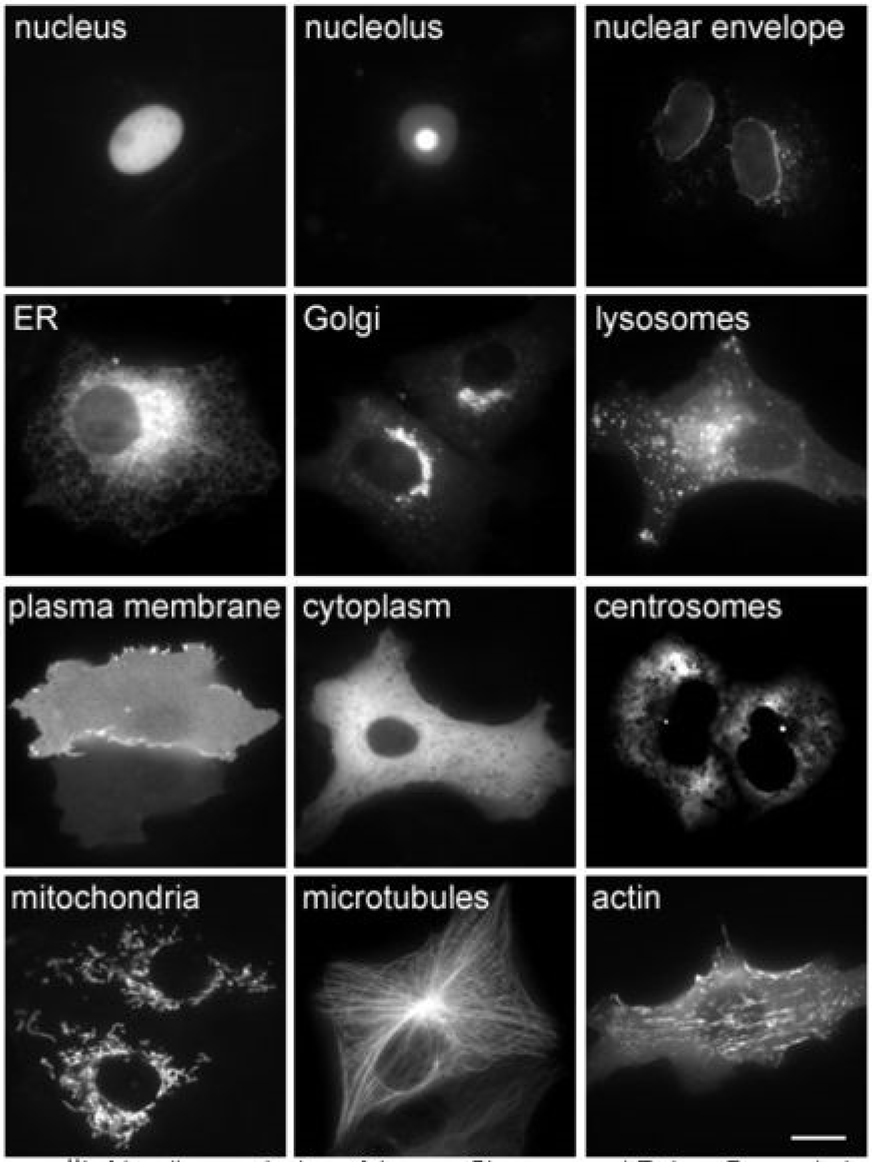
Movement of calcium ions in and out of the cytoplasm is thought to be a signaling activity for metabolic processes.

Constituents

The cytoplasm has three major elements; the cytosol, organelles and inclusions.

Cytosol

The cytosol is the portion not within membrane-bound organelles. The cytosol is a translucent fluid in which the plasmic elements are suspended. Cytosol makes up about 70% of the cell volume and is composed of water, salts and organic molecules. The cytoplasm also contains the protein filaments that make up the cytoskeleton, as well as soluble proteins and small structures such as ribosomes, proteasomes, and the mysterious vault complexes. The inner, granular and more fluid portion of the cytoplasm is referred to as endoplasm.



with friendly permission of Jeremy Simpson and Rainer Pepperkok

Proteins in different cellular compartments and structures tagged with green fluorescent protein.

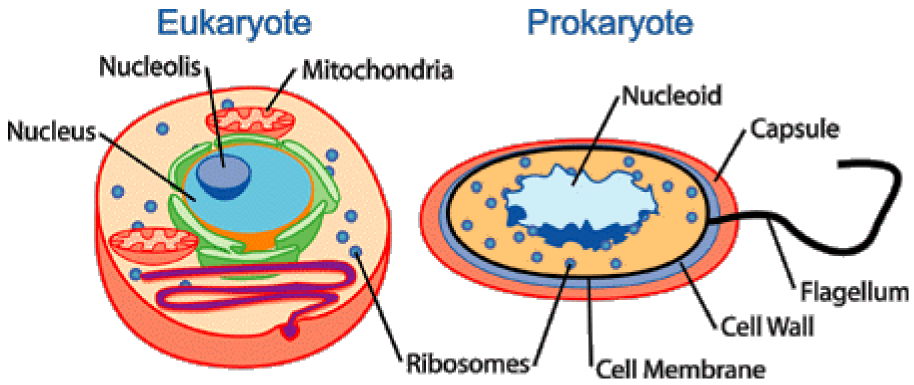
Organelles

Organelles are membrane-bound "organs" inside the cell that have specific functions. Some major organelles that are suspended in the cytosol are the mitochondria, the endoplasmic reticulum, the Golgi apparatus, vacuoles, lysosomes, and in plant cells chloroplasts.

Cytoplasmic inclusions

The inclusions are small particles of insoluble substances suspended in the cytosol. A huge range of inclusions exist in different cell types, and range from crystals of calcium oxalate or silicon dioxide in plants, to granules of energy-storage materials such as starch, glycogen, or polyhydroxybutyrate. A particularly widespread example are lipid droplets, which are spherical droplets composed of lipids and proteins that are used in both prokaryotes and eukaryotes as a way of storing lipids such as fatty acids and sterols. Lipid droplets make up much of the volume of adipocytes, which are specialized lipid-storage cells, but they are also found in a range of other cell types.

Nucleoid



Prokaryote cell showing the nucleoid.

The **nucleoid** (meaning *nucleus-like*) is an irregularly-shaped region within the cell of prokaryotes which has nuclear material without a nuclear membrane and where the genetic material is localized. The genome of prokaryotic organisms generally is a circular, double-stranded piece of DNA, of which multiple copies may exist at any time. The length of a genome widely varies, but generally is at least a few million base pairs. Storage of the genome within a nucleoid can be contrasted against that within eukaryotes, where the genome is packed into chromatin and sequestered within a membrane-enclosed organelle called the nucleus.

A *genophore* is the DNA of a prokaryote. This is commonly referred to as a prokaryotic chromosome. The term chromosome is misleading for a genophore because the genophore lacks chromatin . The genophore is compacted through a mechanism known as supercoiling, whereas a chromosome is compacted via chromatin. The genophore is circular in most prokaryotes, and linear in very few. The circular nature of the genophore allows replication to occur without telomeres. Genophores are generally of a much smaller size than Eukaryotic chromosomes. A genophore of a true organism can be as small as 580,073 base pairs (Mycoplasma genitalium). Many eukaryotes (such as plants and animals) carry genophores in organelles such as mitochondria and chloroplasts. These organelles are very similar to true prokaryotes.

Visualization

The nucleoid can be clearly visualized on an electron micrograph at high magnification, where, although its appearance may differ, it is clearly visible against the cytosol. Sometimes even strands of what is thought to be DNA are visible. By staining with the Feulgen stain, which specifically stains DNA, the nucleoid can also be seen under a light microscope. The DNA-intercalating stains DAPI and ethidium bromide are widely used for fluorescence microscopy of nucleoids.

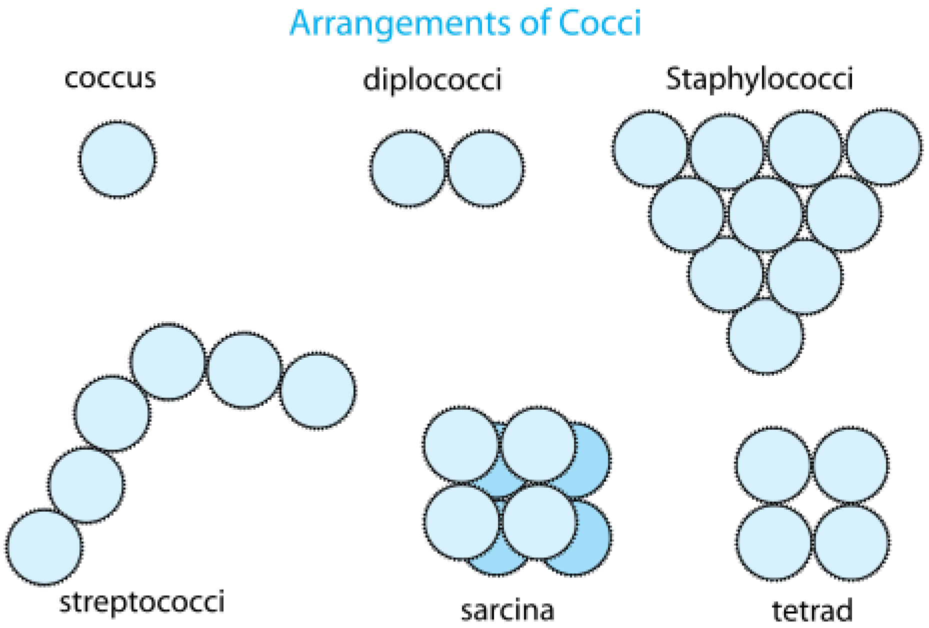
Composition

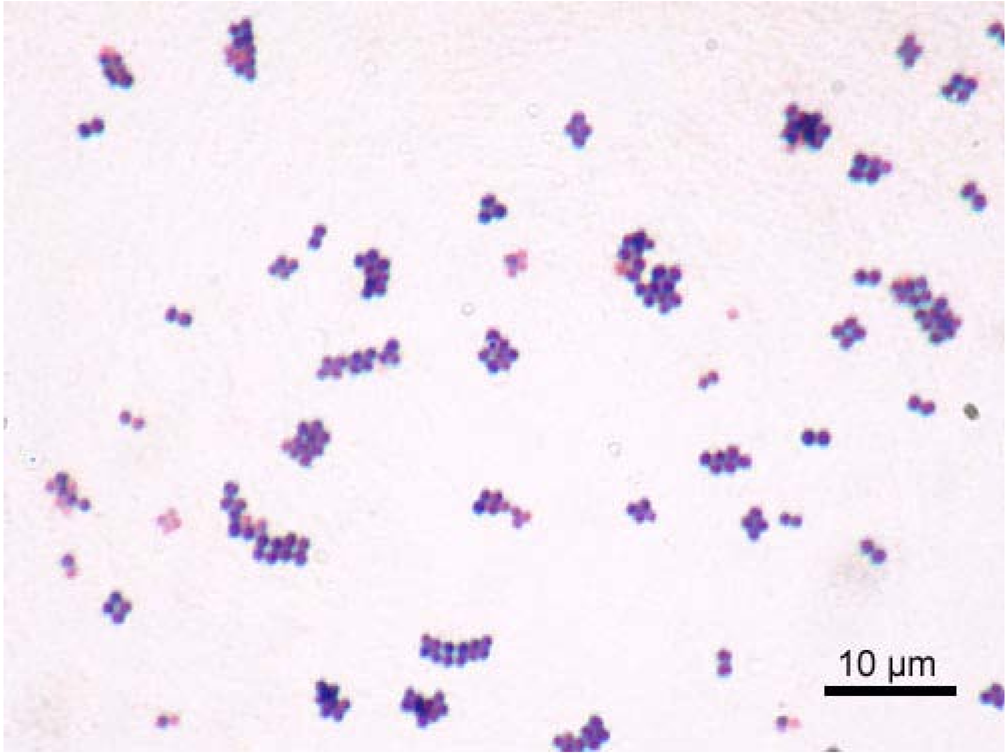
Experimental evidence suggests that the nucleoid is largely composed of DNA, about 60%, with a small amount of RNA and protein. The latter two constituents are likely to be mainly messenger RNA and the transcription factor proteins found regulating the bacterial genome. Proteins helping to maintain the supercoiled structure of the nucleic acid are known as *nucleoid proteins* or nucleoid-associated proteins and are distinct from histones of eukaryotic nuclei. In contrast to histones, the DNA-binding proteins of the nucleoid do not form nucleosomes, in which DNA is wrapped around a protein core. Instead, these proteins often use other mechanisms to promote compaction such as DNA bending.

Chapter 8

Morphology of Prokaryotic Cells

Coccus





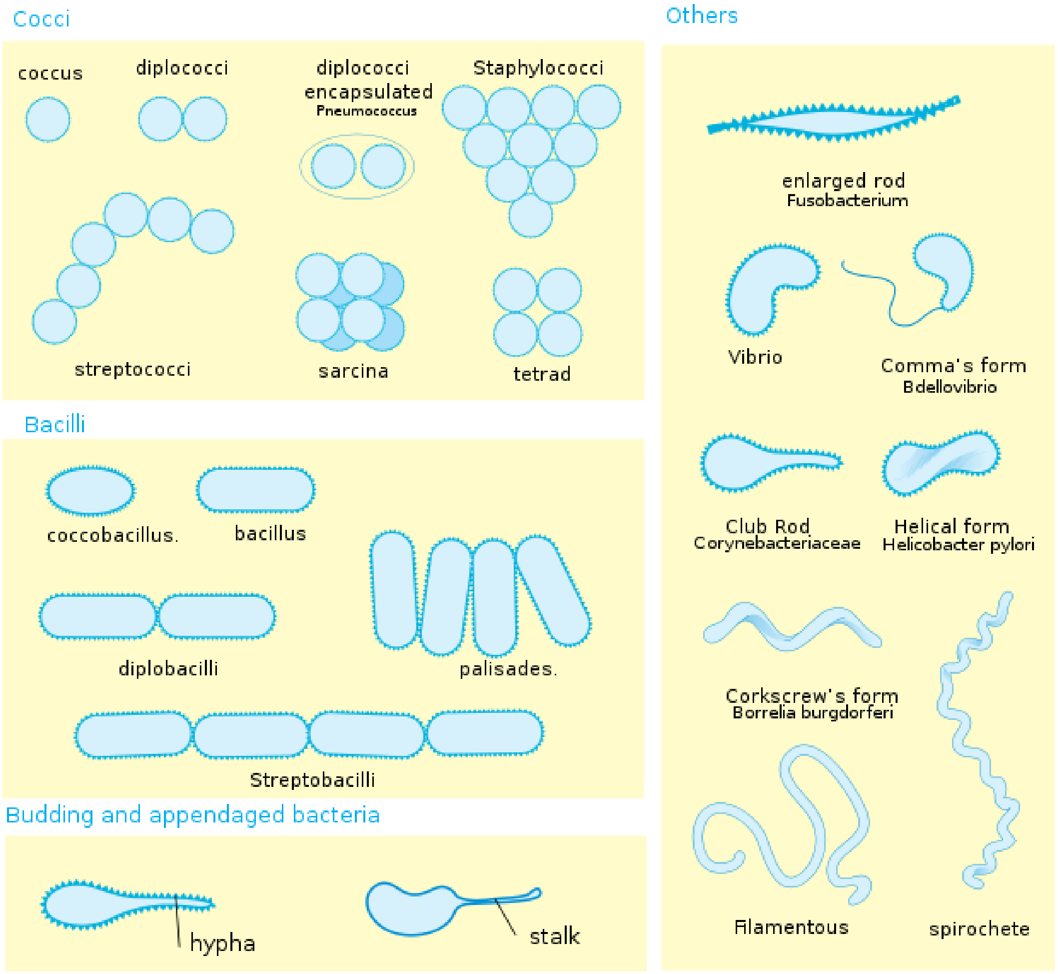
Staphylococcus bacteria

Coccus (plural **cocci**) can be used to describe any bacterium that has a spherical shape. It is one of the three distinct types of bacteria shapes, the other two being bacillus (rod-shaped) and spirillum (spiral-shaped) cells.

Arrangement

Like all bacteria, each single coccus bacterium is an entire living organism. However, some species exist in groups of cells. If they do group together, the patterns they arrange themselves in are given certain names based on the shape. Diplococci bacteria are arranged in two-cell pairs, while bacteria in the *Streptococci* genus are arranged in chains. Bacteria in the *Sarcina* genus have a cuboidal cell arrangement, while tetrad bacteria are arranged in a square formation. *Staphylococcus* is a genus of bacteria that contains cells arranged in large groups. While cells together may form these shapes, the individual bacterial cells themselves remain spherical.

Bacillus (shape)



Bacteria display a large diversity of cell morphologies and arrangements.

The word ***bacillus*** (plural ***bacilli***) may be used to describe any rod-shaped bacterium, and such bacilli are found in many different taxonomic groups of bacteria. However, the name *Bacillus*, capitalized and italicized, refers to a specific genus of bacteria. The name Bacilli, capitalized but not italicized, can also refer to a more specific taxonomic class of bacteria that includes two orders, one of which contains the genus *Bacillus*.

Bacilli are usually solitary, but can combine to form diplobacilli, streptobacilli, and palisades.

There is no connection between the shape of a bacterium and its colors in the Gram staining. MacConkey agar can be used to distinguish among Gram negative bacilli such as E. coli and salmonella .

Examples of Gram positive Bacilli

Clostridium species

Corynebacteriumspecies

Examples of Gram negative Bacilli

Salmonella

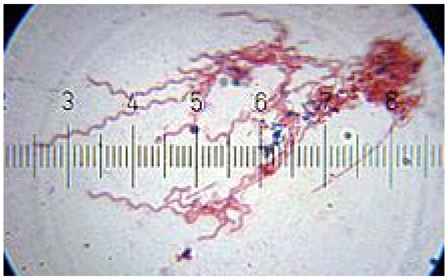
Escherichia coli

pseudomonas species

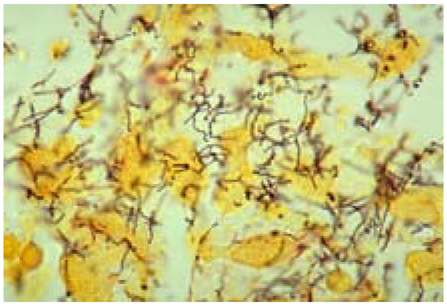
bacteriodes species

Spirochaete

Spirochaete



Spirochaetes. Numbered ticks are 10 µm apart. Gram-stained.



Treponema pallidum spirochetes.

Scientific classification

Domain:	Bacteria
Phylum:	**Spirochaetes**

Order: **Spirochaetales**
Buchanan 1917

Families and genera

Brachyspiraceae
Brachyspira
Leptospiraceae
Leptonema
Leptospira
Turneria
Spirochaetaceae
Borrelia
Brevinema
Cristispira
Spirochaeta
Spironema
Treponema

Spirochaetes (also spelled Spirochetes) belong to a phylum of distinctive Gram-negative bacteria, which have long, helically coiled (spiral-shaped) cells. Spirochetes are chemoheterotrophic in nature, with lengths between 5 and 250 µm and diameters around 0.1-0.6 µm.

Spirochaetes are distinguished from other bacterial phyla by the location of their flagella, sometimes called *axial filaments*, which run lengthwise between the cell wall and outer membrane. These cause a twisting motion which allows the spirochaete to move about. When reproducing, a spirochaete will undergo asexual transverse binary fission.

Most spirochaetes are free-living and anaerobic, but there are numerous exceptions.

Classification

The spirochetes are divided into three families (Brachyspiraceae, Leptospiraceae, and Spirochaetaceae), all placed within a single order (Spirochaetales). Disease-causing members of this phylum include the following:

- *Leptospira* species, which causes leptospirosis
- *Borrelia burgdorferi*, which causes Lyme disease
- *Borrelia recurrentis*, which causes relapsing fever
- *Treponema pallidum*, which causes syphilis
- *Treponema pertenue*, which causes yaws

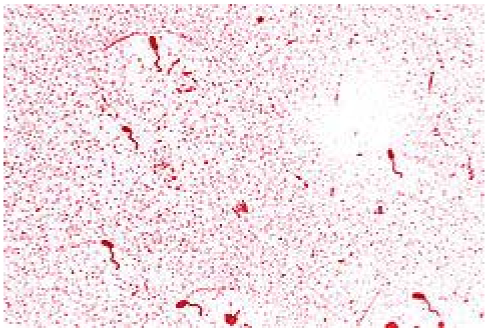
Cavalier-Smith has postulated that the Spirochaetes belong in a larger clade called Gracilicutes.

Historical

Salvarsan, the first partially organic antimicrobial drug in medical history, was effective against spirochaetes only and was primarily used to cure syphilis.

It has been suggested by biologist Lynn Margulis that eukaryotic flagella were derived from symbiotic spirochaetes, but few biologists accept this, as there is no close structural similarity between the two.

Vibrio

Vibrio	
	
Flagellar stain of *V. cholerae*	
Scientific classification	
Kingdom:	Bacteria
Phylum:	Proteobacteria
Class:	Gamma Proteobacteria
Order:	Vibrionales
Family:	Vibrionaceae
Genus:	***Vibrio*** Pacini 1854
Type species	
Vibrio cholerae	
Species	
V. adaptatus *V. aerogenes* *V. aestuarianus* *V. agarivorans* *V. albensis* *V. alginolyticus*	

V. anguillarum
V. brasiliensis
V. bubulus
V. calviensis
V. campbellii
V. chagasii
V. cholerae
V. cincinnatiensis
V. coralliilyticus
V. crassostreae
V. cyclitrophicus
V. diabolicus
V. diazotrophicus
V. ezurae
V. fischeri
V. fluvialis
V. fortis
V. furnissii
V. gallicus
V. gazogenes
V. gigantis
V. halioticoli
V. harveyi
V. hepatarius
V. hispanicus
V. hollisae
V. ichthyoenteri
V. indicus
V. kanaloae
V. lentus
V. litoralis
V. logei
V. mediterranei
V. metschnikovii
V. mimicus
V. mytili
V. natriegens
V. navarrensis
V. neonatus
V. neptunius
V. nereis
V. nigripulchritudo
V. ordalii
V. orientalis
V. pacinii
V. parahaemolyticus

V. pectenicida
V. penaeicida
V. pomeroyi
V. ponticus
V. proteolyticus
V. rotiferianus
V. ruber
V. rumoiensis
V. salmonicida
V. scophthalmi
V. splendidus
V. superstes
V. tapetis
V. tasmaniensis
V. tubiashii
V. vulnificus
V. wodanis
V. xuii

Vibrio is a genus of Gram-negative bacteria possessing a curved rod shape, several species of which can cause foodborne infection, usually associated with eating undercooked seafood. Typically found in saltwater, *Vibrio* are facultative anaerobes that test positive for oxidase and do not form spores. All members of the genus are motile and have polar flagella with sheaths. Recent phylogenies have been constructed based on a suite of genes (multi-locus sequence analysis).

The name *Vibrio* derives from Filippo Pacini who isolated microorganisms he called "vibrions" from cholera patients in 1854.

Pathogenic strains

Several species of *Vibrio* are pathogens. Most disease causing strains are associated with gastroenteritis but can also infect open wounds and cause septicemia. It can be carried by numerous sea-living animals, such as crabs or prawns, and has been known to cause fatal infections in humans during exposure. Pathogenic *Vibrio* include *V. cholerae* (the causative agent of cholera), *V. parahaemolyticus*, and *V. vulnificus. Vibrio cholerae* is generally transmitted via contaminated water. Pathogenic *Vibrio* can cause foodborne infection, usually associated with eating undercooked seafood.

Vibrio vulnificus outbreaks commonly occur in warm climates and small, generally lethal, outbreaks occur regularly. An outbreak occurred in New Orleans after Hurricane Katrina and several lethal cases occur most years in Florida.

V. parahaemolyticus is also associated with the *Kanagawa phenomenon*, in which strains isolated from human hosts (clinical isolates) are hemolytic on blood agar plates, while those isolated from non-human sources are non-hemolytic.

Many *Vibrio* are also zoonotic. They cause disease in fish and shellfish, and are common causes of mortality among domestic marine life.

Other strains

Vibrio fischeri, *Photobacterium phosphoreum*, and *V. harveyi* are notable for their ability to communicate. Both *V. fischeri* and *Ph. phosphoreum* are symbiotes of other marine organisms (typically jellyfish, fish, or squid), and produce light via bioluminescence through the mechanism of quorum sensing. *Vibrio harveyi* is a pathogen of several aquatic animals and notable as a cause of luminous vibriosis in shrimps (prawns)

Flagella

The "typical", early-discovered *Vibrio* such as *V. cholerae* have a single polar flagellum (monotrichous) with sheath. Some species such as *V. parahaemolyticus* and *V. alginolyticus* have both a single polar flagellum with sheath and thin flagella projecting in all directions (peritrichous), and the other species such as *V. fischeri* have tufts of polar flagella with sheath (lophotrichous).