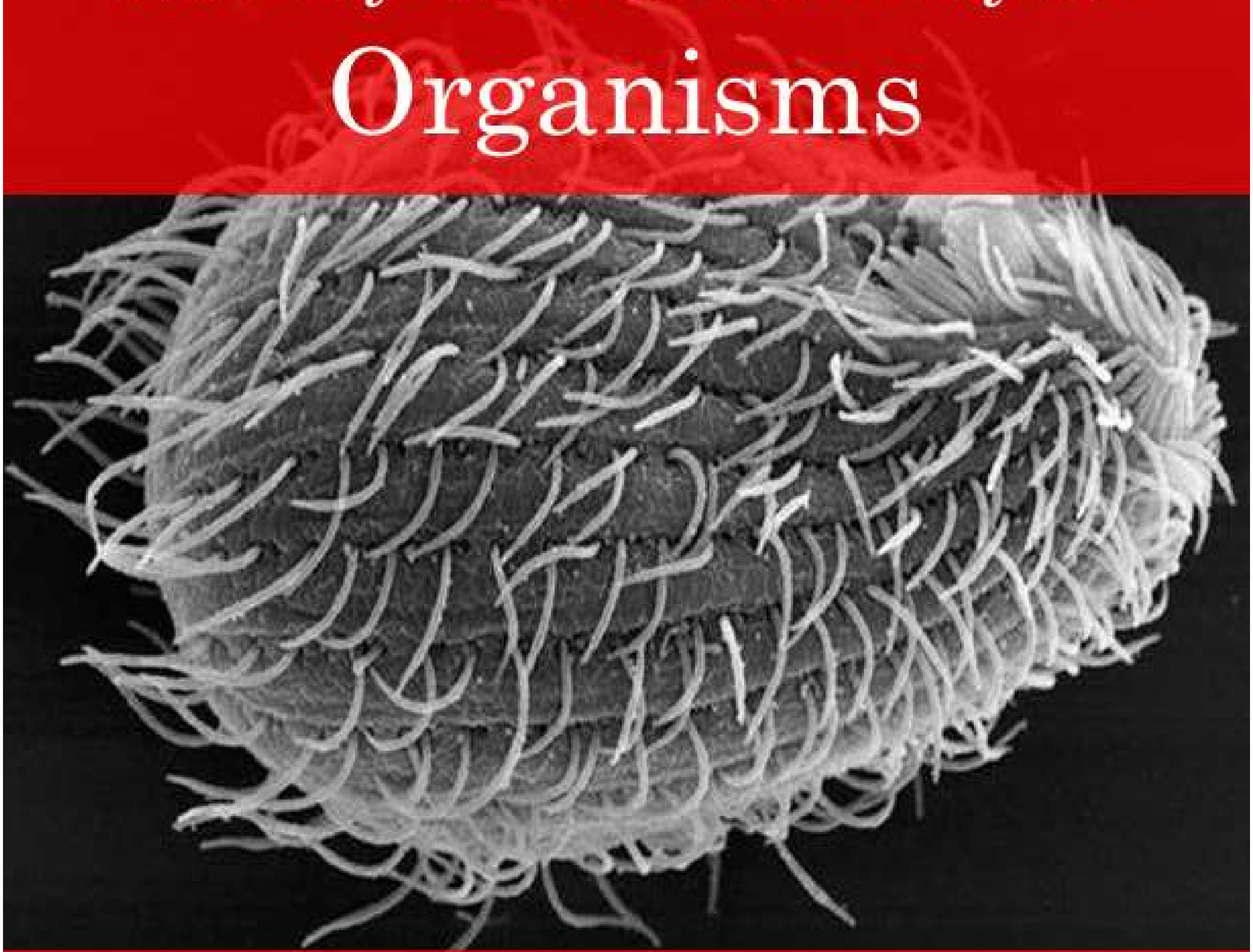
Eukaryote and Prokaryote Organisms



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Chapter 1

Eukaryote

Eukaryotes
Temporal range: Proterozoic – Recent

Ostreococcus is the smallest known free living eukaryote, with an average size of 0.8 µm.

Scientific classification

Domain:	**Eukaryota** Whittaker & Margulis,1978

Kingdoms

Animalia – Animals
Fungi
Amoebozoa
Plantae – Plants
Chromalveolata
Rhizaria
Excavata

Alternative phylogeny

- ***Unikonta***
    - **Opisthokonta**
        - Metazoa
        - Mesomycetozoa
        - Choanozoa

        - Eumycota
    - Amoebozoa
- ***Bikonta***
    - Apusozoa
    - Rhizaria
    - Excavata
    - Archaeplastida
    - Chromalveolata

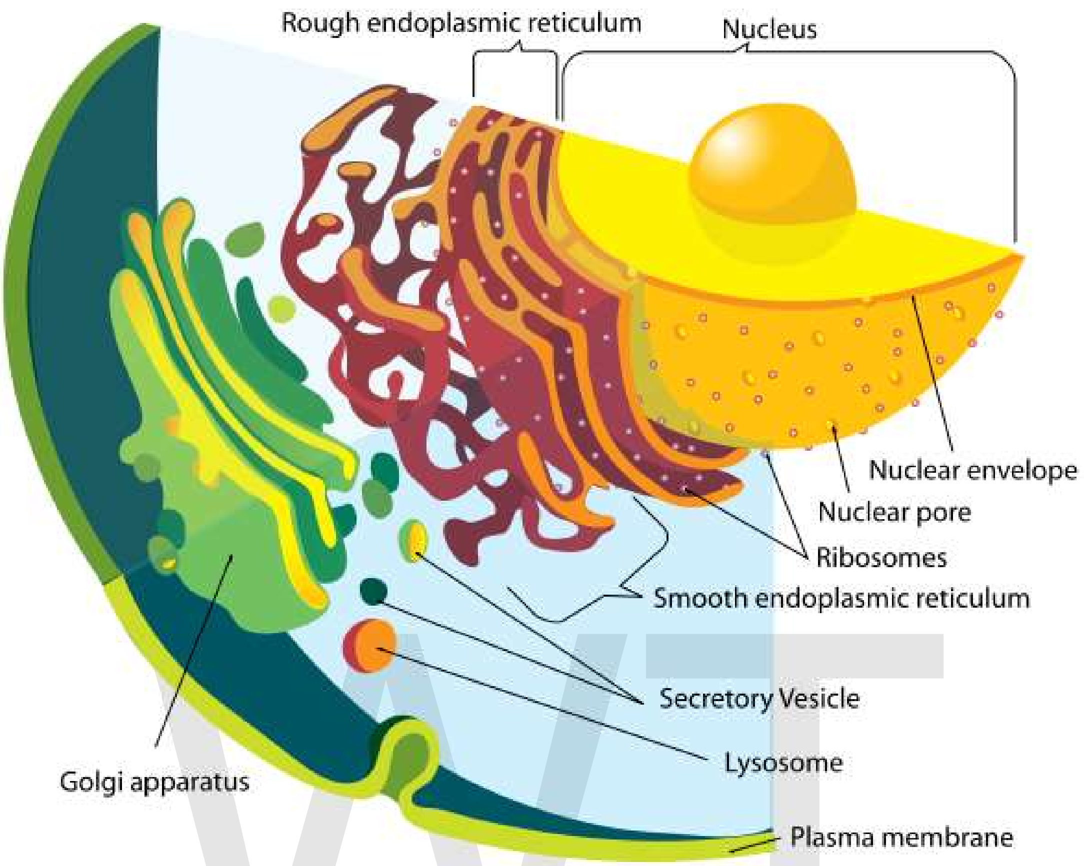
A **eukaryote** is an organism whose cells contain complex structures enclosed within membranes. The defining membrane-bound structure that sets eukaryotic cells apart from prokaryotic cells is the nucleus, or nuclear envelope, within which the genetic material is carried. The presence of a nucleus gives eukaryotes their name, which comes from the Greek ευ (*eu*, "good") and κάρυον (*karyon*, "nut" or "kernel"). Most eukaryotic cells also contain other membrane-bound organelles such as mitochondria, chloroplasts and the Golgi apparatus. All species of large complex organisms are eukaryotes, including animals, plants and fungi, although most species of eukaryotic protists are microorganisms.

Cell division in eukaryotes is different from that in organisms without a nucleus (prokaryotes). It involves separating the duplicated chromosomes, through movements directed by microtubules. There are two types of division processes. In mitosis, one cell divides to produce two genetically identical cells. In meiosis, which is required in sexual reproduction, one diploid cell (having two instances of each chromosome, one from each parent) undergoes recombination of each pair of parental chromosomes, and then two stages of cell division, resulting in four haploid cells (gametes). Each gamete has just one complement of chromosomes, each a unique mix of the corresponding pair of parental chromosomes.

Eukaryotes appear to be monophyletic, and so make up one of the three domains of life. The two other domains, Bacteria and Archaea, are prokaryotes and have none of the above features. Eukaryotes represent a tiny minority of all living things; even in a human body there are 10 times more microbes than human cells.

Cell features

Eukaryotic cells are typically much larger than those of prokaryotes. They have a variety of internal membranes and structures, called organelles, and a cytoskeleton composed of microtubules, microfilaments, and intermediate filaments, which play an important role in defining the cell's organization and shape. Eukaryotic DNA is divided into several linear bundles called chromosomes, which are separated by a microtubular spindle during nuclear division.



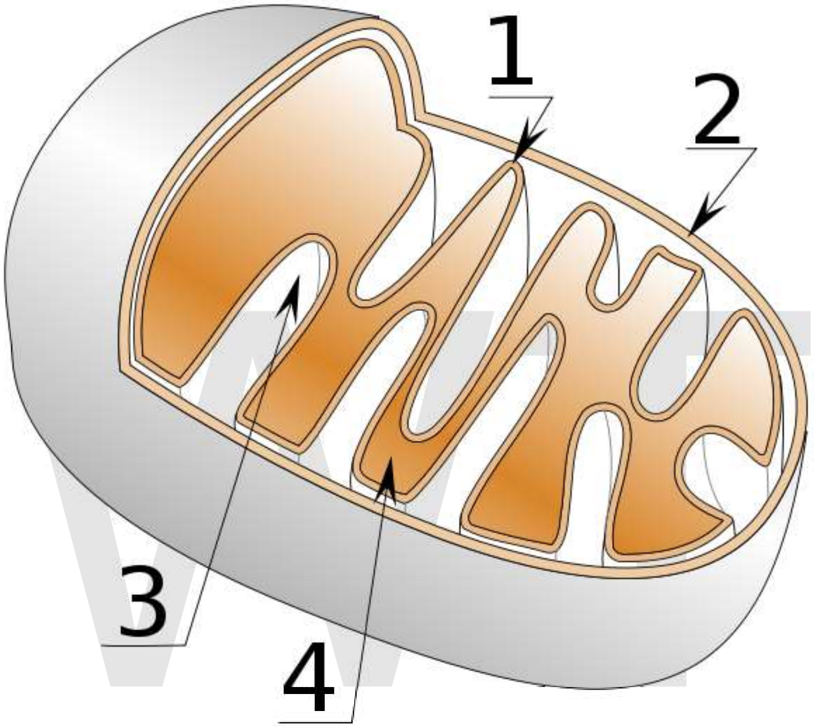
Detail of the endomembrane system and its components

Internal membrane

Eukaryotic cells include a variety of membrane-bound structures, collectively referred to as the endomembrane system. Simple compartments, called vesicles or vacuoles, can form by budding off other membranes. Many cells ingest food and other materials through a process of endocytosis, where the outer membrane invaginates and then pinches off to form a vesicle. It is probable that most other membrane-bound organelles are ultimately derived from such vesicles.

The nucleus is surrounded by a double membrane (commonly referred to as a nuclear envelope), with pores that allow material to move in and out. Various tube- and sheet-like extensions of the nuclear membrane form what is called the endoplasmic reticulum or ER, which is involved in protein transport and maturation. It includes the rough ER where ribosomes are attached to synthesize proteins, which enter the interior space or lumen. Subsequently, they generally enter vesicles, which bud off from the smooth ER. In most eukaryotes, these protein-carrying vesicles are released and further modified in stacks of flattened vesicles, called Golgi bodies or dictyosomes.

Vesicles may be specialized for various purposes. For instance, lysosomes contain enzymes that break down the contents of food vacuoles, and peroxisomes are used to break down peroxide, which is toxic otherwise. Many protozoa have contractile vacuoles, which collect and expel excess water, and extrusomes, which expel material used to deflect predators or capture prey. In multicellular organisms, hormones are often produced in vesicles. In higher plants, most of a cell's volume is taken up by a central vacuole, which primarily maintains its osmotic pressure.



Mitochondria structure:
1) Inner membrane
2) Outer membrane
3) Crista
4) Matrix

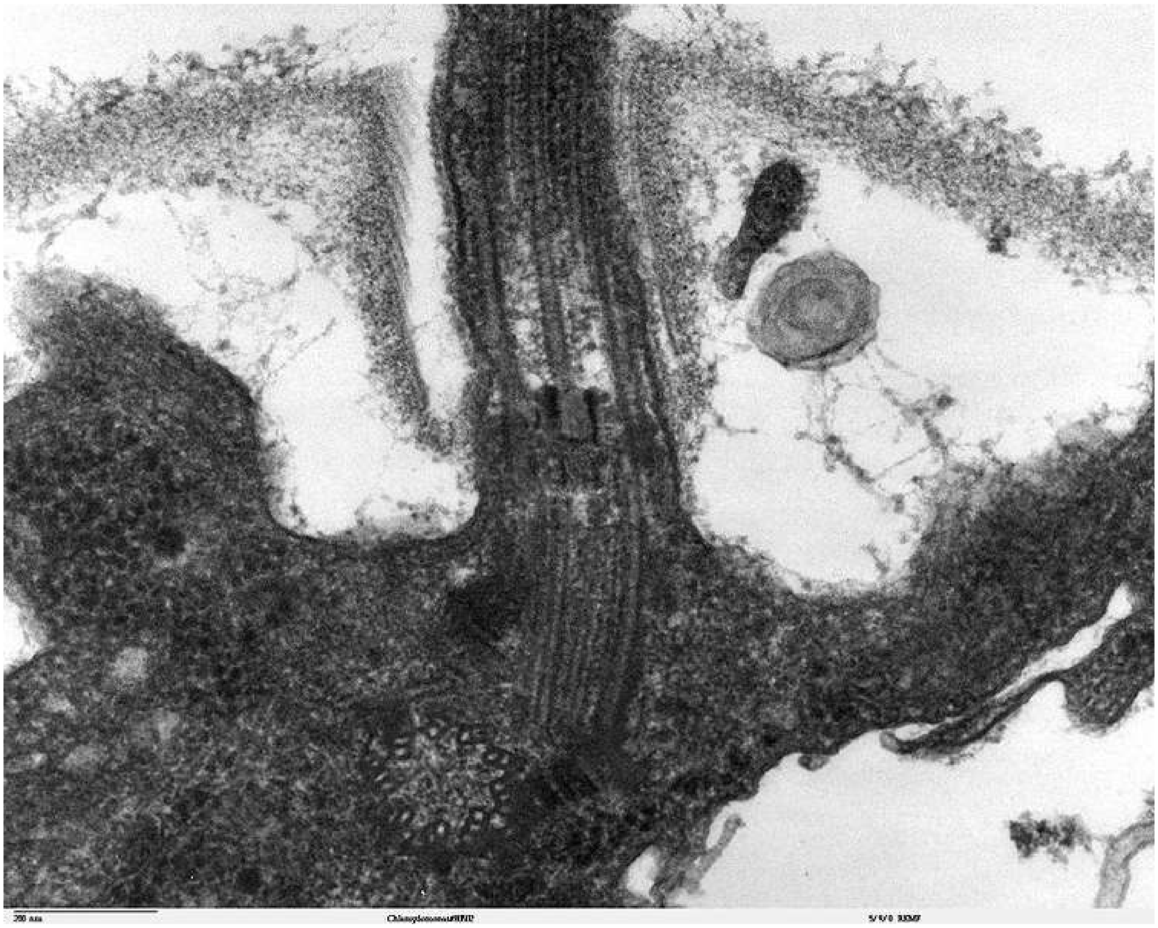
Mitochondria and plastids

Mitochondria are organelles found in nearly all eukaryotes. They are surrounded by two membranes (each a phospholipid bi-layer), the inner of which is folded into invaginations called cristae, where aerobic respiration takes place. Mitochondria contain their own DNA. They are now generally held to have developed from endosymbiotic prokaryotes, probably proteobacteria. The few protozoa that lack mitochondria have been found to contain mitochondrion-derived organelles, such as hydrogenosomes and mitosomes.

Plants and various groups of algae also have plastids. Again, these have their own DNA and developed from endosymbiotes, in this case cyanobacteria. They usually take the form of chloroplasts, which like cyanobacteria contain chlorophyll and produce organic compounds (such as glucose) through photosynthesis. Others are involved in storing food. Although plastids likely had a single origin, not all plastid-containing groups are closely related. Instead, some eukaryotes have obtained them from others through secondary endosymbiosis or ingestion.

Endosymbiotic origins have also been proposed for the nucleus, for which see below, and for eukaryotic flagella, supposed to have developed from spirochaetes. This is not generally accepted, both from a lack of cytological evidence and difficulty in reconciling this with cellular reproduction.

Cytoskeletal structures



Longitudinal section through the flagellum of *Chlamydomonas reinhardtii*

Many eukaryotes have long slender motile cytoplasmic projections, called flagella, or similar structures called cilia. Flagella and cilia are sometimes referred to as undulipodia, and are variously involved in movement, feeding, and sensation. They are composed mainly of tubulin. These are entirely distinct from prokaryotic flagella. They are supported by a bundle of microtubules arising from a basal body, also called a kinetosome or centriole, characteristically arranged as nine doublets surrounding two singlets. Flagella also may have hairs, or mastigonemes, and scales connecting membranes and internal rods. Their interior is continuous with the cell's cytoplasm.

Microfilamental structures composed by actin and actin binding proteins, e.g., α-actinin, fimbrin, filamin are present in submembraneous cortical layers and bundles, as well. Motor proteins of microtubules, e.g., dynein or kinesin and actin, e.g., myosins provide dynamic character of the network.

Centrioles are often present even in cells and groups that do not have flagella. They generally occur in groups of one or two, called kinetids, that give rise to various microtubular roots. These form a primary component of the cytoskeletal structure, and are often assembled over the course of several cell divisions, with one flagellum retained from the parent and the other derived from it. Centrioles may also be associated in the formation of a spindle during nuclear division.

Significance of cytoskeletal structures is underlined in determination of shape of the cells, as well as their being essential components of migratory responses like chemotaxis and chemokinesis. Some protists have various other microtubule-supported organelles. These include the radiolaria and heliozoa, which produce axopodia used in flotation or to capture prey, and the haptophytes, which have a peculiar flagellum-like organelle called the haptonema. An animal cell is a form of Eukaryotic cell that makes up many tissues in animals.

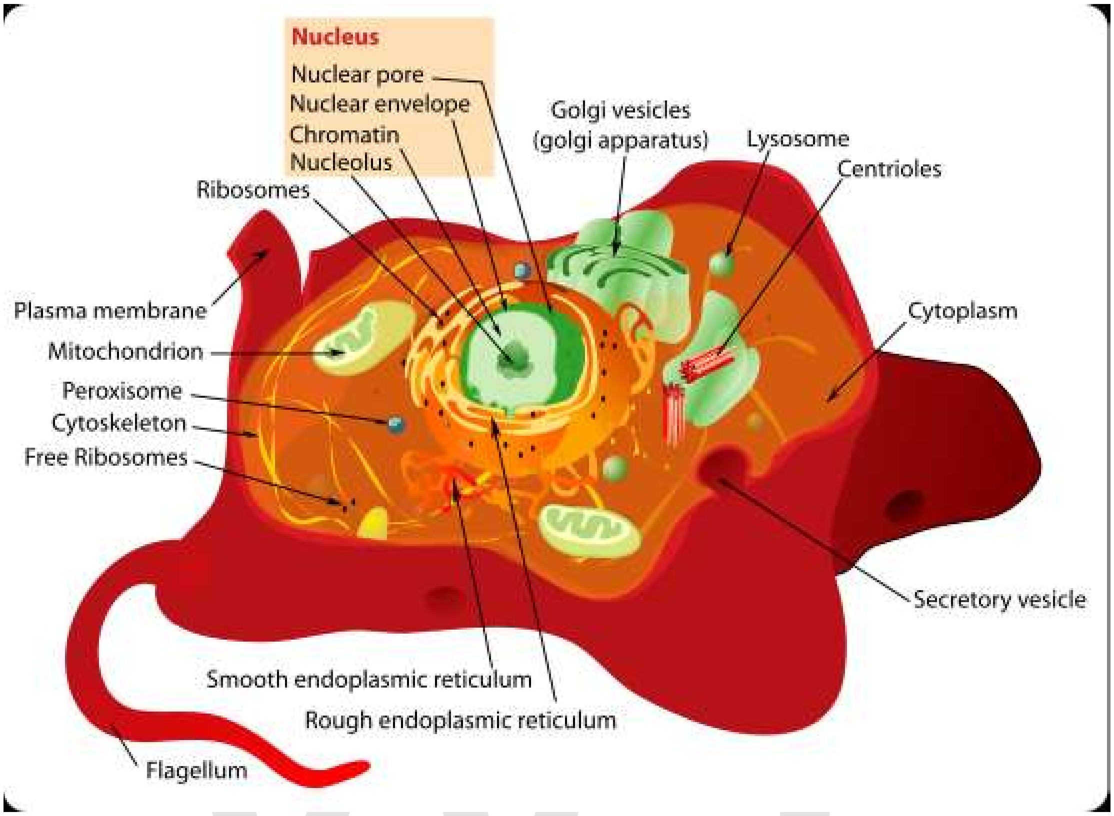
Plant cell wall

Plant cells have a cell wall, a fairly rigid layer outside the cell membrane, providing the cell with structural support, protection, and a filtering mechanism. The cell wall also prevents over-expansion when water enters the cell. The major carbohydrates making up the primary cell wall of land plants 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.

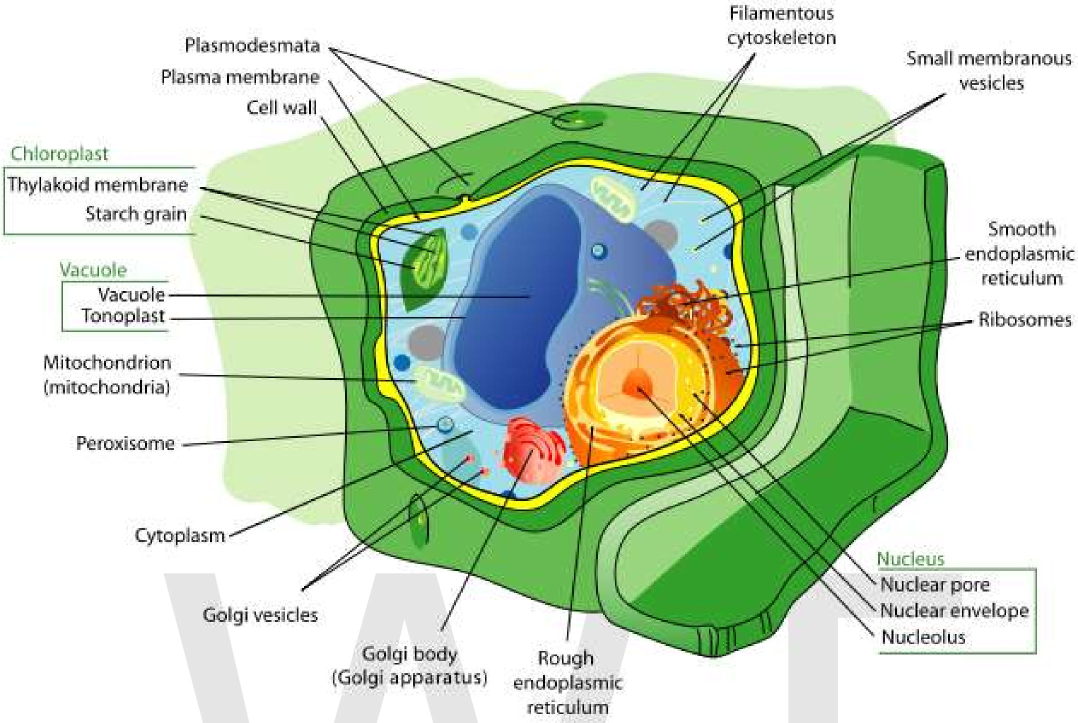
Differences among eukaryotic cells

There are many different types of eukaryotic cells, though animals and plants are the most familiar eukaryotes, and thus provide an excellent starting point for understanding eukaryotic structure. Fungi and many protists have some substantial differences, however.

Animal cell



Structure of a typical animal cell



Structure of a typical plant cell

An **animal cell** is a form of eukaryotic cell that makes up many tissues in animals. The animal cell is distinct from other eukaryotes, most notably plant cells, as they lack cell walls and chloroplasts, and they have smaller vacuoles. Due to the lack of a rigid cell wall, animal cells can adopt a variety of shapes, and a phagocytic cell can even engulf other structures.

There are many different cell types. For instance, there are approximately 210 distinct cell types in the adult human body.

Plant cell

Plant cells are quite different from the cells of the other eukaryotic organisms. Their distinctive features are:

- A large central vacuole (enclosed by a membrane, the tonoplast), which maintains the cell's turgor and controls movement of molecules between the cytosol and sap
- A primary cell wall containing cellulose, hemicellulose and pectin, deposited by the protoplast on the outside of the cell membrane; this contrasts with the cell walls of fungi, which contain chitin, and the cell envelopes of prokaryotes, in which peptidoglycans are the main structural molecules

- The plasmodesmata, linking pores in the cell wall that allow each plant cell to communicate with other adjacent cells; this is different from the functionally analogous system of gap junctions between animal cells.
- Plastids, especially chloroplasts that contain chlorophyll, the pigment that gives plants their green color and allows them to perform photosynthesis
- Higher plants, including conifers and flowering plants (Angiospermae) lack the flagellae and centrioles that are present in animal cells.

Fungal cell

Fungal cells are most similar to animal cells, with the following exceptions:

- A cell wall that contains chitin
- Less definition between cells; the hyphae of higher fungi have porous partitions called septa, which allow the passage of cytoplasm, organelles, and, sometimes, nuclei. Primitive fungi have few or no septa, so each organism is essentially a giant multinucleate supercell; these fungi are described as coenocytic.
- Only the most primitive fungi, chytrids, have flagella.

Other eukaryotic cells

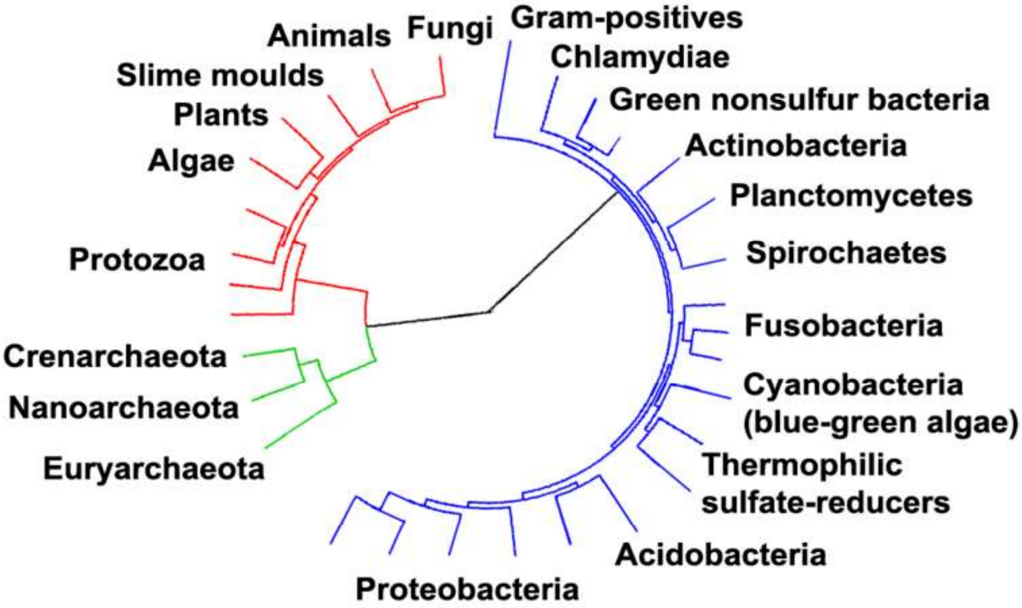
Eukaryotes are a very diverse group, and their cell structures are equally diverse. Many have cell walls; many do not. Many have chloroplasts, derived from primary, secondary, or even tertiary endosymbiosis; and many do not. Some groups have unique structures, such as the cyanelles of the glaucophytes, the haptonema of the haptophytes, or the ejectisomes of the cryptomonads. Other structures, such as pseudopods, are found in various eukaryote groups in different forms, such as the lobose amoebozoans or the reticulose foraminiferans.

Reproduction

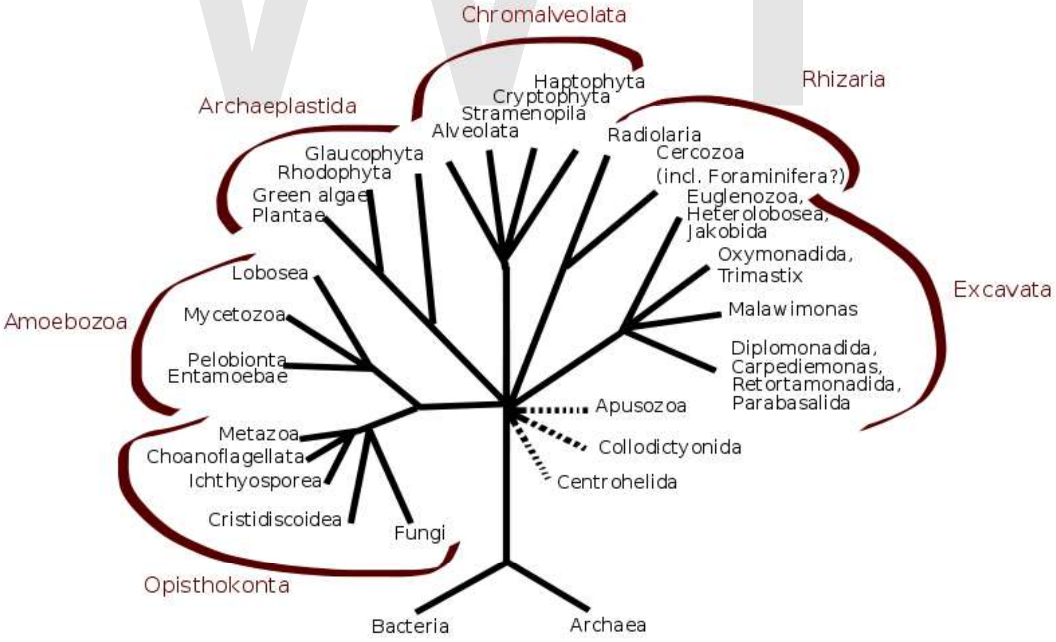
Nuclear division is often coordinated with cell division. This generally takes place by mitosis, a process that allows each daughter nucleus to receive one copy of each chromosome. In most eukaryotes, there is also a process of sexual reproduction, typically involving an alternation between haploid generations, wherein only one copy of each chromosome is present, and diploid generations, wherein two are present, occurring through nuclear fusion (syngamy) and meiosis. There is considerable variation in this pattern, however.

Eukaryotes have a smaller surface area to volume ratio than prokaryotes, and thus have lower metabolic rates and longer generation times. In some multicellular organisms, cells specialized for metabolism will have enlarged surface areas, such as intestinal vili.

Origin and evolution



Phylogenetic tree showing the relationship between the eukaryotes and other forms of life. Eukaryotes are colored red, archaea green and bacteria blue.



One hypothesis of eukaryotic relationships

The origin of the eukaryotic cell was a milestone in the evolution of life, since they include all complex cells and almost all multi-cellular organisms. The timing of this series of events is hard to determine; Knoll (2006) suggests they developed approximately 1.6–2.1 billion years ago. Some acritarchs are known from at least 1650 million years ago, and the possible alga *Grypania* has been found as far back as 2100 million years ago.

Fossils that are clearly related to modern groups start appearing around 1.2 billion years ago, in the form of a red alga, though recent work suggests the existence of fossilized filamentous algae in the Vindhya basin dating back to 1.6 to 1.7 billion years ago.

Biomarkers suggest that at least stem eukaryotes arose even earlier. The presence of steranes in Australian shales indicates that eukaryotes were present 2.7 billion years ago.

Phylogeny

rRNA trees constructed during the 1980s and 1990s left most eukaryotes in an unresolved "crown" group (not technically a true crown), which was usually divided by the form of the mitochondrial cristae. The few groups that lack mitochondria branched separately, and so the absence was believed to be primitive; but this is now considered an artifact of long-branch attraction, and they are known to have lost them secondarily.

Six supergroup/kingdom model

A classification produced in 2005 for the International Society of Protistologists, which reflected the consensus of the time, divided the eukaryotes into six supposedly monophyletic 'supergroups'. Although the published classification deliberately did not use formal taxonomic ranks, other sources have treated each of the six as a separate Kingdom.

Excavata	Various flagellate protozoa
Amoebozoa	Most lobose amoeboids and slime moulds
Opisthokonta	Animals, fungi, choanoflagellates, etc.
Rhizaria	Foraminifera, Radiolaria, and various other amoeboid protozoa
Chromalveolata	Stramenopiles (or Heterokonta), Haptophyta, Cryptophyta (or cryptomonads), and Alveolata
Archaeplastida (or Primoplantae)	Land plants, green algae, red algae, and glaucophytes

However, in the same year (2005), doubts were expressed as to whether some of these supergroups were monophyletic, particularly the Chromalveolata, and a review in 2006 noted the lack of evidence for several of the supposed six supergroups.

As of 2010, there is widespread agreement that the Rhizaria belong with the Stramenopiles and the Alveolata, in a clade dubbed the SAR supergroup, so that Rhizara is not one of the main eukaryote groups; also that the Amoeboza and Opisthokonta are each monophyletic and form a clade, often called the unikonts. Beyond this, there does not appear to be a consensus.

Relationship to Archaea

Eukaryotes are more closely related to Archaea than Bacteria, at least in terms of nuclear DNA and genetic machinery, and one controversial idea is to place them with Archaea in the clade Neomura. However, in other respects, such as membrane composition, eukaryotes are similar to Bacteria. Three main explanations for this have been proposed:

- Eukaryotes resulted from the complete fusion of two or more cells, wherein the cytoplasm formed from a eubacterium, and the nucleus from an archaeon, from a virus, or from a pre-cell.
- Eukaryotes developed from Archaea, and acquired their eubacterial characteristics from the proto-mitochondrion.
- Eukaryotes and Archaea developed separately from a modified eubacterium.

There is also the Kronocyte theory for the origin of the Eukaryotic cell. This postulates that a primitive Eukaryotic cell emerged from the pre-DNA world but retained the earlier RNA based chemistry from which all modern life emerged. This primitive cell is called the Kronocyte. According to this hypothesis an RNA based Kronocyte coexisted with the DNA based Archaea (and probably eubacteria) and became the modern eukaryotic cell after a number of major endosymbioses—the first was the incorporation of an Archaea that introduced DNA metabolism and the nucleus, then the incorporation of an alphaproteobacter that became the mitochondria (and photosynthetic bacteria found in today's plants as chloroplasts). The Kronocyte hypothesis explains the large number of genes that are today only found in Eukaryotes but not in Archaea or Bacteria.

Endomembrane system and mitochondria

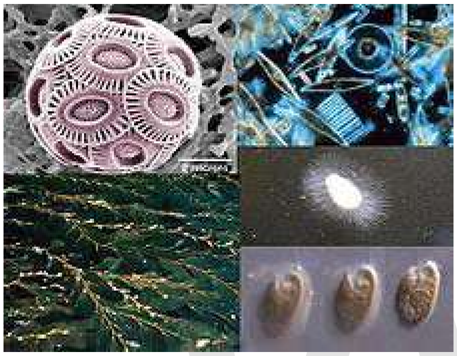
The origins of the endomembrane system and mitochondria are also unclear. The **phagotrophic hypothesis** proposes that eukaryotic-type membranes lacking a cell wall originated first, with the development of endocytosis, whereas mitochondria were acquired by ingestion as endosymbionts. The **syntrophic hypothesis** proposes that the proto-eukaryote relied on the proto-mitochondrion for food, and so ultimately grew to surround it. Here the membranes originated after the engulfment of the mitochondrion, in part thanks to mitochondrial genes (the hydrogen hypothesis is one particular version).

In a study using genomes to construct supertrees, Pisani *et al.* (2007) suggest that, along with evidence that there was never a mitochondrion-less eukaryote, eukaryotes evolved from a syntrophy between an archaea closely related to Thermoplasmatales and an α-proteobacterium, likely a symbiosis driven by sulfur or hydrogen. The mitochondrion and its genome is a remnant of the α-proteobacterial endosymbiont.

Chapter 2

Chromalveolate

Chromalveolate



Clockwise from top-left: a haptophyte, some diatoms, a water mold, a cryptomonad, and *Macrocystis*, a phaeophyte

Scientific classification

Domain:	Eukarya
(unranked)	Bikonta
(unranked):	Corticata
Kingdom:	**Chromalveolata***

Phyla

- Heterokontophyta
- Haptophyta
- Cryptophyta
- **Alveolata** (Superphylum)
    - Ciliophora
    - Apicomplexa
    - Dinoflagellata

Chromalveolata is a eukaryote supergroup first proposed by Thomas Cavalier-Smith as a refinement of his kingdom Chromista, which was first put forward in 1981. Chromalveolata was proposed to represent the result of a single secondary endosymbiosis between a line descending from a bikont and a red alga that became the progenitor of chlorophyll c containing plastids. In a major classification produced in 2005, Chromalveolata was regarded as one of the six major groups within the eukaryotes. However this has been increasingly challenged. Thus two papers published in 2008 have phylogenetic trees in which the chromalveolates are split up.

Groups and classification

Historically, many chromalveolates were considered plants, because of their cell walls, photosynthetic ability, and in some cases their morphological resemblance to the land plants (Embryophyta). However, when the five-kingdom system took prevalence over the animal-plant dichotomy, most chromalveolates were put into the kingdom Protista, with the water molds and slime nets put into the kingdom Fungi, and the brown algae staying in the plant kingdom.

In 2005, in a classification reflecting the consensus at the time, the Chromalveolata were regarded as one of the six major clades of eukaryotes. Although not given a formal taxonomic status in this classification, elsewhere the group has been treated as a Kingdom. The Chromalveolata were divided into four major subgroups:

- Cryptophyta
- Haptophyta
- Stramenopiles (or Heterokontophyta)
- Alveolata

Other groups which may be included within, or related to, chromalveolates, are:

- Telonemia

Though several groups, such as the ciliates and the water molds, have lost the ability to photosynthesize, most are autotrophic. All photosynthetic chromalveolates use chlorophylls *a* and *c*, and many use accessory pigments. Chromalveolates share similar glyceraldehyde 3-phosphate dehydrogenase proteins.

However, as early as 2005, doubts were being expressed as to whether the Chromalveolata was monophyletic, and a review in 2006 noted the lack of evidence for several of the supposed six major eukaryote groups, including the Chromalveolata. As of 2010 there seems to be an emerging consensus that the group is not monophyletic. The four original subgroups fall into two categories, one comprising the Cryptophyta and the Haptophyta, the other the Stramenopiles and the Alveolata.

Halvaria

Analyses in 2007 and 2008 agree that the Stramenopiles and the Alveolata are related, forming a reduced chromalveolate clade.

Hacrobia

The Haptophyta and Cryptophyta are related in these analyses, forming a clade which has been called 'Hacrobia'.

Position of SAR and Hacrobia

The Hacrobia appear to be more closely related to the Archaeplastida (plants in the very broad sense), being a sister group in one analysis, and actually nested inside this group in another. (Earlier, Cavalier-Smith had suggested a clade called Corticata for the grouping of *all* the chromalveolates and the Archaeplastida.) The SAR supergroup and the Archaeplastida/Hacrobia combination are grouped in the bikonts, which all appear to descend from a heterotrophic eukaryote with two flagella.

Morphology

Chromalveolates, unlike other groups with multicellular representatives, do not have very many common morphological characteristics. Each major subgroup has certain unique features, including the alveoli of the Alveolata, the haptonema of the Haptophyta, the ejectisome of the Crytophyta, and the two different flagella of the Heterokontophyta. However, none of these features are present in all of the groups.

The only common chromalveolate features are these:

- The shared origin of chloroplasts, as mentioned above
- Presence of cellulose in most cell walls

Since this is such a diverse group, it is difficult to summarize shared chromalveolate characteristics.

Ecological role

A potato plant infected with *Phytophthora infestans*.

Many chromalveolates affect our ecosystem in enormous ways. Some of these organisms can be very harmful. Dinoflagellates produce red tides which can devastate fish populations and intoxicate oyster harvests. Apicomplexans are some of the most successful specific parasites to animals. Water molds cause several plant diseases. In fact, it was a water mold, *Phytophthora infestans*, that caused the Irish potato famine.

A Californian kelp forest.

However, many chromalveolates are vital members of our ecosystem. Diatoms are one of the major photosynthetic producers, and as such produce much of the oxygen we breathe, and also take in much of the carbon dioxide from the atmosphere. Brown algae, most specifically kelps, create underwater "forest" habitats for many marine creatures, and provide a large portion of the diet of coastal communities.

Chromalveolates also provide many products that we use. The algin in brown algae is used as a food thickener, most famously in ice cream. The siliceous shells of diatoms have many uses, such as in reflective paint, in toothpaste, or as a filter, in what is known as diatomaceous earth.

Chapter 3

Archaeplastida

Archaeplastida
Temporal range: Mesoproterozoic–Recent

Had'n
Archean
Proterozoic
Pha.

Indian paintbrush and wild huckleberry

Scientific classification

Domain:	Eukaryota
(unranked):	**Archaeplastida** Adl *et al.* 2005

Subgroups

- Red algae
- Glaucophytes
- Plantae (land plants and green algae)

The **Archaeplastida** (or **Plantae** *sensu lato*) are a major group of eukaryotes, comprising the red and green algae and the land plants, together with a small group called the glaucophytes. The plastids (chloroplasts) of all of these organisms are surrounded by two membranes, suggesting they developed directly from endosymbiotic cyanobacteria. In all other groups, plastids are surrounded by three or four membranes, suggesting they were acquired secondarily from red or green algae.

Although many studies have suggested that the Archaeplastida form a monophyletic group, a 2009 paper argues that they are in fact paraphyletic. The enrichment of novel red algal genes in a recent study demonstrates a strong signal for Plantae (Archaeplastida) monophyly and an equally strong signal of gene sharing history between the red/green algae and other lineages, thus shedding lights on the complexity of eukaryote evolution.

The cells of the Archaeplastida typically lack centrioles and have mitochondria with flat cristae. There is usually a cell wall including cellulose, and food is stored in the form of starch. However, these characters are also shared with other eukaryotes. The main evidence the Archaeplastida form a monophyletic group comes from genetic studies, which indicate that their plastids probably had a single origin. This evidence is disputed.

The archaeplastidans fall into two main evolutionary lines. The red algae are pigmented with chlorophyll *a* and phycobiliproteins, like most cyanobacteria. The green algae and land plants – together known as Viridiplantae (Latin for "green plants") or Chloroplastida – are pigmented with chlorophylls *a* and *b*, but lack phycobiliproteins. The glaucophytes have typical cyanobacterial pigments, and are unusual in retaining a cell wall within their plastids (called cyanelles).

Taxonomy

The consensus in 2005, when the group consisting of the glaucophytes, red and green algae and land plants was named 'Archaeoplastida', was that it was a clade, i.e. was monophyletic. Many studies published since this date have provided evidence which is in agreement. On the other hand, other studies have suggested that the group is paraphyletic. To date, the situation appears unresolved, but a strong signal for Plantae (Archaeplastida) monophyly has been demonstrated in a recent study (with an enrichment of red algal genes). The assumption made here is that Archaeplastida is a valid clade.

Various names have been given to the group. Some authors have simply referred to the group as plants or Plantae. However, the name Plantae is ambiguous, since it has also been applied to less inclusive clades, such as Viridiplantae and embryophytes. To distinguish, the larger group is sometimes known as Plantae *sensu lato* ("plants in the broad sense").

To avoid ambiguity, other names have been proposed. Primoplantae, which appeared in 2004, seems to be the first new name suggested for this group.

Another name that has been applied to this node is Plastida, defined as the clade sharing "plastids of primary (direct prokaryote) origin [as] in *Magnolia virginiana* Linnaeus 1753".

The name Archaeplastida was proposed in 2005 by a large international group of authors (Adl et al.) who aimed to produce a classification for the eukaryotes which took into account morphology, biochemistry and phylogenetics, and which had "some stability in the near term." They rejected the use of formal taxonomic ranks in favour of a hierarchical arrangement where the clade names do not signify rank. Thus the phylum name 'Glaucophyta' and the class name 'Rhodophyceae' appear at the same level in their classification. The divisions proposed for the Archaeplastida are shown below in both tabular and diagrammatic form.

Archaeplastida:

- Glaucophyta Skuja 1954 (Glaucocystophyta Kies and Kremer 1986) – glaucophytes

  Glaucophytes are a small group of freshwater single-celled algae. Their chloroplasts, called *cyanelles*, have a peptidoglycan layer, making them more similar to cyanobacteria than those of the remaining Archaeplastida.

- Rhodophyceae Thuret 1855, emend. Rabenhorst 1863, emend. Adl et al. 2005 (Rhodophyta Wettstein 1901) – red algae

  Red algae form one of the largest groups of algae. Most are seaweeds, being multicellular and marine. Their red colour comes from phycobiliproteins, used as accessory pigments in light capture for photosynthesis.

- Chloroplastida Adl et al. 2005 (Viridiplantae Cavalier-Smith 1981; Chlorobionta Jeffrey 1982, emend. Bremer 1985, emend. Lewis and McCourt 2004; Chlorobiota Kendrick and Crane 1997)

  Chloroplastida is the term chosen by Adl et al. for the group made up of the green algae and land plants (embryophytes). Except where lost secondarily, all have chloroplasts without a peptidoglycan layer and lack phycobiliproteins.

    - Chlorophyta Pascher 1914, emend. Lewis and Mc Court 2004 – green algae (part)

  Adl et al. employ a narrow definition of the Chlorophyta; other sources include the Chlorodendrales and Prasinophytae, which may themselves be combined.

    - Ulvophyceae Mattox and Stewart 1984
    - Trebouxiophyceae Friedl 1995 (Pleurastrophyceae Mattox et al. 1984; Microthamniales Melkonian 1990)
    - Chlorophyceae Christensen 1994

    - Chlorodendrales Fritsch 1917 – green algae (part)
    - Prasinophytae Cavalier-Smith 1998, emend. Lewis and McCourt 2004 – green algae (part)

- *Mesostigma* Lauterborn 1894, emend. McCourt in Adl et al. 2005 (Mesostigmata Turmel, Otis, and Lemieux 2002)
- Charophyta Karol et al. 2001, emend. Lewis and McCourt 2004 (Charophyceae Smith 1938, emend. Mattox and Stewart 1984) – green algae (part) and land plants

Charophyta *sensu lato*, as used by Adl et al., is a monophyletic group which is made up of some green algae, including the stoneworts (Charophyta *sensu stricto*), as well as the land plants (embryophytes).

Morphology

All archaeplastidans have plastids (chloroplasts) that carry out photosynthesis and are believed to be derived from captured cyanobacteria. In glaucophytes, perhaps the most primitive members of the group, the chloroplast is called a *cyanelle* and shares several features with cyanobacteria, including a peptidoglycan cell wall, that are not retained in other members of the group. The resemblance of cyanelles to cyanobacteria supports the endosymbiotic theory.

The cells of most archaeplastidans have walls, commonly but not always made of cellulose.

The Archaeplastida vary widely in the degree of their cell organization, from isolated cells to filaments to colonies to multi-celled organisms. The earliest were unicellular, and many groups remain so today. Multicellularity evolved separately in several groups, including red algae, ulvophyte green algae, and in the green algae that gave rise to stoneworts and land plants.

Endosymbiosis

Because the ancestral archaeplastidan is hypothesized to have acquired its chloroplasts directly by engulfing cyanobacteria, the event is known as a *primary endosymbiosis* (as reflected in the name chosen for the group 'Archaeplastida' i.e. 'ancient plastid'). Evidence for primary endosymbosis includes the presence of a double membrane around the chloroplasts; one membrane belonged to the bacterium, and the other to the eukaryote that captured it. Over time, many genes from the chloroplast have been transferred to the nucleus of the host cell. The presence of such genes in the nuclei of eukaryotes without chloroplasts suggests this transfer happened early in the evolution of the group.

Other eukaryotes with chloroplasts appear to have gained them by engulfing a single-celled archaeplastidan with its own bacterially-derived chloroplasts. Because these events involve endosymbiosis of cells that have their own endosymbionts, the process is called *secondary endosymbiosis*. The chloroplasts of such eukaryotes are typically surrounded by more than two membranes, reflecting a history of multiple engulfment. The chloroplasts of euglenids and chlorarachniophytes appear to be captured green algae, whereas those of other photosynthetic eukaryotes, such as heterokont algae, cryptophytes, haptophytes, and dinoflagellates, appear to be captured red algae.

Fossil record

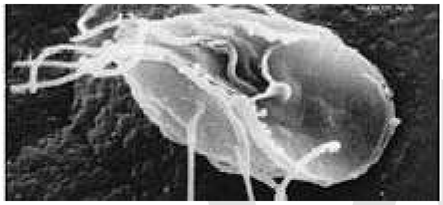
Perhaps the most ancient remains of Archaeplastida are microfossils from the Roper group in northern Australia. The structure of these single-celled fossils resembles that of modern green algae. They date to the Mesoproterozoic Era, about 1500 to 1300 Ma (million years ago) These fossils are consistent with a molecular clock study that calculated that this clade diverged about 1500 Ma. The oldest fossil that can be assigned to a specific modern group is the red alga *Bangiomorpha*, from 1200 Ma.

In the late Neoproterozoic Era, algal fossils became more numerous and diverse. Eventually, in the Paleozoic Era, plants emerged onto land, and have continued to flourish up to the present.

Chapter 4

Excavate, Opisthokont and Rhizaria

Excavate

Excavates	
	
Giardia lamblia, a parasitic diplomonad	
Scientific classification	
Domain:	Eukaryota
(unranked):	Bikonta
Kingdom:	**Excavata** (Cavalier-Smith) Simpson, 2003
Phyla	
Metamonada Loukozoa Euglenozoa Percolozoa	

The **excavates** are a major kingdom of unicellular eukaryotes, often known as **Excavata**. The phylogenetic category Excavata, proposed by Cavalier-Smith in 2002, contains a variety of free-living and symbiotic forms, and also includes some important parasites of humans.

Characteristics

Many excavates lack 'classical' mitochondria - these organisms are often referred to as 'amitochondriate', although most, perhaps all, retain a mitochondrial organelle in greatly modified form. Others have mitochondria with tubular, discoidal, or in some cases, laminar cristae. Most excavates have two, four, or more flagella and many have a conspicuous ventral feeding groove with a characteristic ultrastructure, supported by microtubules. However, various groups that lack these traits may be considered excavates based on genetic evidence (primarily phylogenetic trees of molecular sequences).

The closest that the excavates come to multicellularity are the acrasid slime moulds. Like other cellular slime moulds, they live most of their life as single cells, but will sometimes assemble into a larger cluster.

Subgroups

Excavates are classified into four major subgroups at the phylum/superphylum level. These are shown in the table below.

Superphylum	**Phylum**	**Representative genera**	**Description**
Discoba	Euglenozoa	e.g. *Euglena*, *Trypanosoma*	Many important parasites, one large group with plastids (chloroplasts)
	Percolozoa (Heterolobosea)	e.g. *Naegleria*, *Acrasis*	Most alternate between flagellate and amoeboid forms
	Jakobida	e.g. *Jakoba*, *Reclinomonas*	Free-living, sometimes loricate flagellates, with very gene-rich mitochondrial genomes
Metamonada	Preaxostyla	e.g. Oxymonads, *Trimastix*	Amitochontriate flagellates, either free-living (*Trimastix*) or living in the hindguts of insects
	Fornicata	e.g. *Giardia*, *Carpediemonas*	Amitochondriate, mostly symbiotes and parasites of animals.
	Parabasalia	e.g. *Trichomonas*	Amitochondriate flagellates, generally intestinal commensals of insects. Some human pathogens.

Heterolobosea (Percolozoa) and Euglenozoa appear to be particularly close relatives, and are united by the presence of discoid cristae within the mitochondria (Superphylum **Discicristata**). More recently a close relationship has been shown between Discicristata and Jakobida. Most jakobids have tubular cristae, like most other protists, while the metamonads are unusual in having lost classical mitochondria—instead they have 'hydrogenosomes', 'mitosomes' or uncharacterised organelles. In addition to the groups mentioned in the table above, the genus *Malawimonas* is generally considered to be a member of Excavata owing to its typical excavate morphology, and phylogenetic affinity to excavate groups in some molecular phylogenies. However, its position among excavates remains elusive.

Excavate relationships are still uncertain; it is possible that they are not a monophyletic group. The monophyly of the excavates is far from clear, although it seems like there are several clades within the excavates which are monophyletic.

Certain excavates are often considered among the most primitive eukaryotes, based partly on their placement in many evolutionary trees. This could encourage proposals that excavates are a paraphyletic grade that includes the ancestors of other living eukaryotes. However, the placement of certain excavates as 'early branches' may be an analysis artifact caused by long branch attraction, as has been seen with some other groups, for example, microsporidia.

Opisthokont

Opisthokont
Temporal range: Neoproterozoic–Recent

Had'n
Archean
Proterozoic
Pha.

Scientific classification

Domain:	Eukaryota
(unranked):	Unikonta
(unranked):	**Opisthokonta**

The **opisthokonts** (Greek: ὀπίσθιος (*opísthios*) = "rear, posterior" + κοντός (*kontós*) = "pole" i.e. "flagellum") are a broad group of eukaryotes, including both the animal and fungus kingdoms, together with the eukaryotic microorganisms that are sometimes grouped in the paraphyletic phylum Choanozoa (previously assigned to the protist "kingdom"). Both genetic and ultrastructural studies strongly support that opisthokonts form a monophyletic group.

"Opisthokonta" and "Fungi/Metazoa group" are sometimes considered synonymous.

Flagella

One common characteristic is that flagellate cells, such as most animal sperm and chytrid spores, propel themselves with a single **posterior** flagellum. This gives the groups its name.

In contrast, flagellate cells in other eukaryote groups propel themselves with one or more **anterior** flagella.

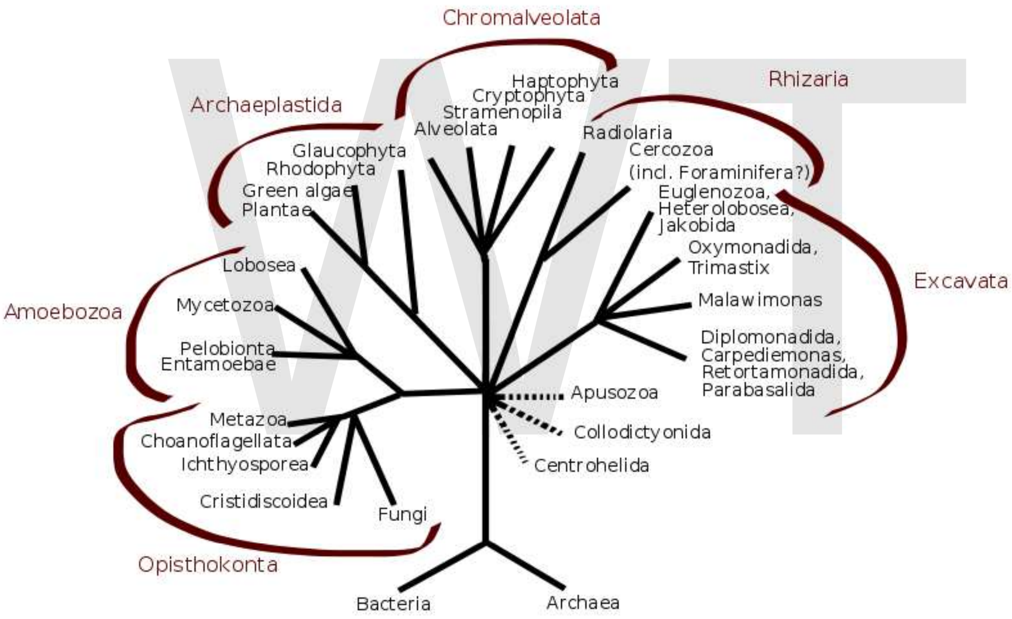
History

The close relationship between animals and fungi was suggested by Cavalier-Smith in 1987, who used the informal name opisthokonta (the formal name has been used for the chytrids), and was confirmed by later genetic studies.

Early phylogenies placed them near the plants and other groups that have mitochondria with flat cristae, but this character varies.

Cavalier-Smith and Stechmann argue that the uniciliate eukaryotes such as opisthokonts and Amoebozoa, collectively called unikonts, split off from the other biciliate eukaryotes, called bikonts, shortly after they evolved.

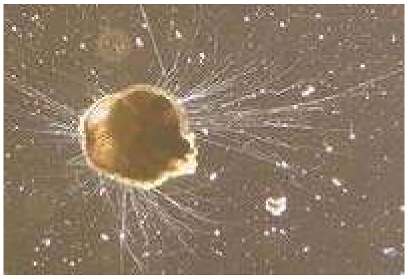
Taxonomy



One hypothesis of eukaryote relationships

Rhizaria

Rhizaria
Temporal range: Neoproterozoic - Recent



Live *Ammonia tepida* (Foraminifera)

Scientific classification

Domain:	Eukaryota
(unranked):	Bikonta
Supergroup:	**Rhizaria** Cavalier-Smith, 2002

Phyla

Cercozoa
Retaria

    Foraminifera
    Radiolaria

The **Rhizaria** are a species-rich supergroup of unicellular eukaryotes. This supergroup was proposed by Cavalier-Smith in 2002. They vary considerably in form, but for the most part they are amoeboids with filose, reticulose, or microtubule-supported pseudopods. Many produce shells or skeletons, which may be quite complex in structure, and these make up the vast majority of protozoan fossils. Nearly all have mitochondria with tubular cristae.

Groups

There are three main groups of Rhizaria:

- Cercozoa - Various amoebae and flagellates, usually with filose pseudopods and common in soil
- Foraminifera - Amoeboids with reticulose pseudopods, common as marine benthos

- Radiolaria - Amoeboids with axopods, common as marine plankton

A few other groups may be included in the Cercozoa, but on some trees appear closer to the Foraminifera. These are the Phytomyxea and Ascetosporea, parasites of plants and animals respectively, and the peculiar amoeba *Gromia*. The different groups of Rhizaria are considered close relatives based mainly on genetic similarities, and have been regarded as an extension of the Cercozoa. The name Rhizaria for the expanded group was introduced by Cavalier-Smith in 2002, who also included the centrohelids and Apusozoa.

Evolutionary relationship

Rhizaria is part of the bikont clade, which also comprises the Archaeplastida, the Chromalveolata, the Excavata, and some smaller, unresolved groups such as the Apusozoa and the Centrohelida. As bikonts, they all descend from a heterotrophic eukaryote with two flagella.

Historically, many rhizarians were considered animals, with their motility and heterotrophy as justification. However, when the five-kingdom system took prevalence over the animal-plant dichotomy, the rhizarians were put into the kingdom Protista. Then, after Woese published his three-domain system, because of the paraphyly of the kingdom Monera, taxonomists turned their attention to the eukaryote domain, and the inherent paraphyly of Protista. After much debate, which continues to this day, Rhizaria emerged as a monophyletic group.

Chapter 5

Fungus

Fungi
Temporal range: Early Devonian–Recent

Clockwise from top left: *Amanita muscaria*, a basidiomycete; *Sarcoscypha coccinea*, an ascomycete; bread covered in mold; a chytrid; a *Penicillium* conidiophore.

Scientific classification

Domain:	Eukaryota
(unranked):	Opisthokonta
Kingdom:	**Fungi** (L., 1753) R.T. Moore, 1980

Subkingdoms/Phyla/Subphyla

- Blastocladiomycota
- Chytridiomycota
- Glomeromycota
- Microsporidia
- Neocallimastigomycota

Dikarya (inc. Deuteromycota)

- Ascomycota

  - Pezizomycotina
  - Saccharomycotina
  - Taphrinomycotina
- Basidiomycota
  - Agaricomycotina
  - Pucciniomycotina
  - Ustilaginomycotina

Subphyla Incertae sedis

- Entomophthoromycotina
- Kickxellomycotina
- Mucoromycotina
- Zoopagomycotina

A **fungus** is a member of a large group of eukaryotic organisms that includes microorganisms such as yeasts and molds (British English: moulds), as well as the more familiar mushrooms. These organisms are classified as a kingdom, **Fungi**, which is separate from plants, animals, and bacteria. One major difference is that fungal cells have cell walls that contain chitin, unlike the cell walls of plants, which contain cellulose. These and other differences show that the fungi form a single group of related organisms, named the *Eumycota* (*true fungi* or *Eumycetes*), that share a common ancestor (a *monophyletic group*). This fungal group is distinct from the structurally similar myxomycetes (slime molds) and oomycetes (water molds). The discipline of biology devoted to the study of fungi is known as mycology, which is often regarded as a branch of botany, even though genetic studies have shown that fungi are more closely related to animals than to plants.

Abundant worldwide, most fungi are inconspicuous because of the small size of their structures, and their cryptic lifestyles in soil, on dead matter, and as symbionts of plants, animals, or other fungi. They may become noticeable when fruiting, either as mushrooms or molds. Fungi perform an essential role in the decomposition of organic matter and have fundamental roles in nutrient cycling and exchange. They have long been used as a direct source of food, such as mushrooms and truffles, as a leavening agent for bread, and in fermentation of various food products, such as wine, beer, and soy sauce. Since the 1940s, fungi have been used for the production of antibiotics, and, more recently, various enzymes produced by fungi are used industrially and in detergents. Fungi are also used as biological pesticides to control weeds, plant diseases and insect pests. Many species produce bioactive compounds called mycotoxins, such as alkaloids and polyketides, that are toxic to animals including humans. The fruiting structures of a few species contain psychotropic compounds and are consumed recreationally or in traditional spiritual ceremonies. Fungi can break down manufactured materials and buildings, and become significant pathogens of humans and other animals. Losses of crops due to fungal diseases (e.g. rice blast disease) or food spoilage can have a large impact on human food supplies and local economies.

The fungus kingdom encompasses an enormous diversity of taxa with varied ecologies, life cycle strategies, and morphologies ranging from single-celled aquatic chytrids to large mushrooms. However, little is known of the true biodiversity of Kingdom Fungi, which has been estimated at around 1.5 million species, with about 5% of these having been formally classified. Ever since the pioneering 18th and 19th century taxonomical works of Carl Linnaeus, Christian Hendrik Persoon, and Elias Magnus Fries, fungi have been classified according to their morphology (e.g., characteristics such as spore color or microscopic features) or physiology. Advances in molecular genetics have opened the way for DNA analysis to be incorporated into taxonomy, which has sometimes challenged the historical groupings based on morphology and other traits. Phylogenetic studies published in the last decade have helped reshape the classification of Kingdom Fungi, which is divided into one subkingdom, seven phyla, and ten subphyla.

Etymology

The English word *fungus* is directly adopted from the Latin *fungus* (mushroom), used in the writings of Horace and Pliny. This in turn is derived from the Greek word *sphongos*/σφογγος ("sponge"), which refers to the macroscopic structures and morphology of mushrooms and molds; the root is also used in other languages, such as the German *Schwamm* ("sponge"), *Schimmel* ("mold"), and the French *champignon* and the Spanish *champiñon* (which both mean "mushroom"). The use of the word *mycology*, which is derived from the Greek *mykes*/μύκης (mushroom) and *logos*/λόγος (discourse), to denote the scientific study of fungi is thought to have originated in 1836 with English naturalist Miles Joseph Berkeley's publication *The English Flora of Sir James Edward Smith, Vol. 5.*

Characteristics

Before the introduction of molecular methods for phylogenetic analysis, taxonomists considered fungi to be members of the Plant Kingdom because of similarities in lifestyle: both fungi and plants are mainly immobile, and have similarities in general morphology and growth habitat. Like plants, fungi often grow in soil, and in the case of mushrooms form conspicuous fruiting bodies, which sometimes bear resemblance to plants such as mosses. The fungi are now considered a separate kingdom, distinct from both plants and animals, from which they appear to have diverged around one billion years ago. Some morphological, biochemical, and genetic features are shared with other organisms, while others are unique to the fungi, clearly separating them from the other kingdoms:

Shared features:

- With other eukaryotes: As other eukaryotes, fungal cells contain membrane-bound nuclei with chromosomes that contain DNA with noncoding regions called introns and coding regions called exons. In addition, fungi possess membrane-bound cytoplasmic organelles such as mitochondria, sterol-containing membranes, and ribosomes of the 80S type. They have a characteristic range of soluble carbohydrates and storage compounds, including sugar alcohols (e.g., mannitol), disaccharides, (e.g., trehalose), and polysaccharides (e.g., glycogen, which is also found in animals).

- With animals: Fungi lack chloroplasts and are heterotrophic organisms, requiring preformed organic compounds as energy sources.
- With plants: Fungi possess a cell wall and vacuoles. They reproduce by both sexual and asexual means, and like basal plant groups (such as ferns and mosses) produce spores. Similar to mosses and algae, fungi typically have haploid nuclei.
- With euglenoids and bacteria: Higher fungi, euglenoids, and some bacteria produce the amino acid L-lysine in specific biosynthesis steps, called the α-aminoadipate pathway.
- The cells of most fungi grow as tubular, elongated, and thread-like (filamentous) structures and are called hyphae, which may contain multiple nuclei and extend at their tips. Each tip contains a set of aggregated vesicles—cellular structures consisting of proteins, lipids, and other organic molecules—called Spitzenkörper. Both fungi and oomycetes grow as filamentous hyphal cells. In contrast, similar-looking organisms, such as filamentous green algae, grow by repeated cell division within a chain of cells.
- In common with some plant and animal species, more than 60 fungal species display the phenomenon of bioluminescence.

Unique features:

- Some species grow as single-celled yeasts that reproduce by budding or binary fission. Dimorphic fungi can switch between a yeast phase and a hyphal phase in response to environmental conditions.
- The fungal cell wall is composed of glucans and chitin; while the former compounds are also found in plants and the latter in the exoskeleton of arthropods, fungi are the only organisms that combine these two structural molecules in their cell wall. In contrast to plants and the oomycetes, fungal cell walls do not contain cellulose.

Omphalotus nidiformis, a bioluminescent mushroom

Most fungi lack an efficient system for long-distance transport of water and nutrients, such as the xylem and phloem in many plants. To overcome these limitations, some fungi, such as *Armillaria*, form rhizomorphs, that resemble and perform functions similar to the roots of plants. Another characteristic shared with plants includes a biosynthetic pathway for producing terpenes that uses mevalonic acid and pyrophosphate as chemical building blocks. However, plants have an additional terpene pathway in their chloroplasts, a structure fungi do not possess. Fungi produce several secondary metabolites that are similar or identical in structure to those made by plants. Many of the plant and fungal enzymes that make these compounds differ from each other in sequence and other characteristics, which indicates separate origins and evolution of these enzymes in the fungi and plants.

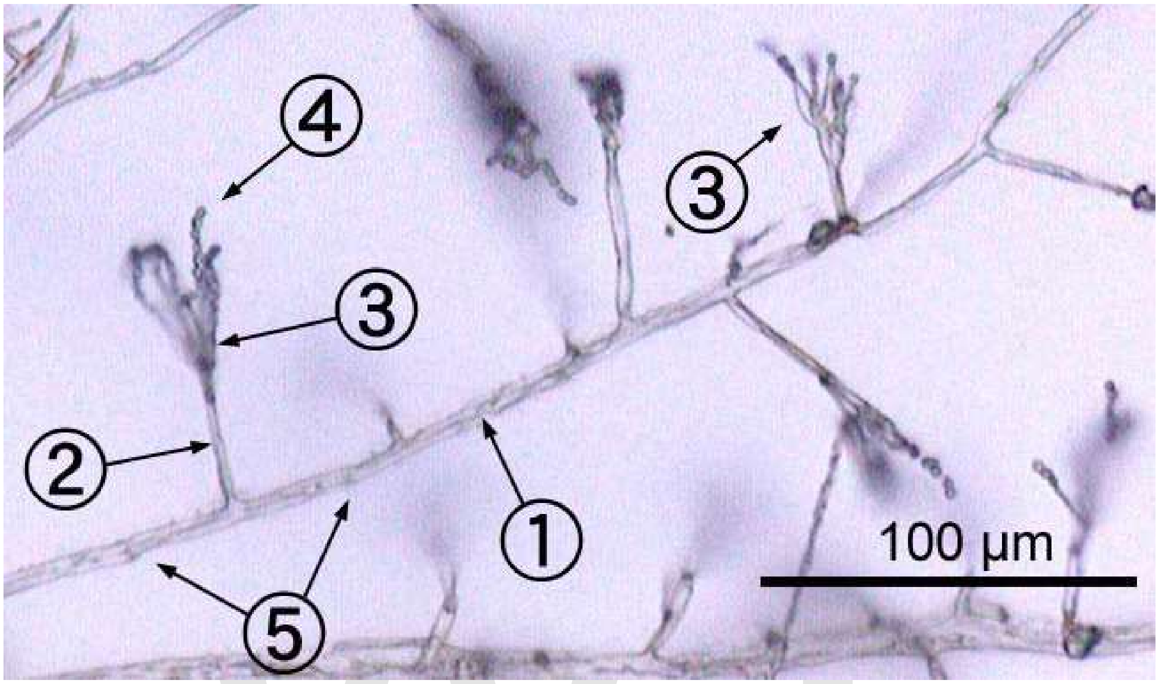
Diversity

Fungi have a worldwide distribution, and grow in a wide range of habitats, including extreme environments such as deserts or areas with high salt concentrations or ionizing radiation, as well as in deep sea sediments. Some can survive the intense UV and cosmic radiation encountered during space travel. Most grow in terrestrial environments, though several species live partly or solely in aquatic habitats, such as the chytrid fungus *Batrachochytrium dendrobatidis*, a parasite that has been responsible for a worldwide decline in amphibian populations. This organism spends part of its life cycle as a motile zoospore, enabling it to propel itself through water and enter its amphibian host. Other examples of aquatic fungi include those living in hydrothermal areas of the ocean.

Around 100,000 species of fungi have been formally described by taxonomists, but the global biodiversity of the fungus kingdom is not fully understood. On the basis of observations of the ratio of the number of fungal species to the number of plant species in selected environments, the fungal kingdom has been estimated to contain about 1.5 million species. In mycology, species have historically been distinguished by a variety of methods and concepts. Classification based on morphological characteristics, such as the size and shape of spores or fruiting structures, has traditionally dominated fungal taxonomy. Species may also be distinguished by their biochemical and physiological characteristics, such as their ability to metabolize certain biochemicals, or their reaction to chemical tests. The biological species concept discriminates species based on their ability to mate. The application of molecular tools, such as DNA sequencing and phylogenetic analysis, to study diversity has greatly enhanced the resolution and added robustness to estimates of genetic diversity within various taxonomic groups.

Morphology

Microscopic structures



An environmental isolate of *Penicillium*
1. hypha 2. conidiophore 3. phialide 4. conidia 5. septa

Most fungi grow as hyphae, which are cylindrical, thread-like structures 2–10 µm in diameter and up to several centimeters in length. Hyphae grow at their tips (apices); new hyphae are typically formed by emergence of new tips along existing hyphae by a process called *branching*, or occasionally growing hyphal tips bifurcate (fork) giving rise to two parallel-growing hyphae. The combination of apical growth and branching/forking leads to the development of a mycelium, an interconnected network of hyphae. Hyphae can be either septate or coenocytic: septate hyphae are divided into compartments separated by cross walls (internal cell walls, called septa, that are formed at right angles to the cell wall giving the hypha its shape), with each compartment containing one or more nuclei; coenocytic hyphae are not compartmentalized. Septa have pores that allow cytoplasm, organelles, and sometimes nuclei to pass through; an example is the dolipore septum in the fungi of the phylum Basidiomycota. Coenocytic hyphae are essentially multinucleate supercells.

Many species have developed specialized hyphal structures for nutrient uptake from living hosts; examples include haustoria in plant-parasitic species of most fungal phyla, and arbuscules of several mycorrhizal fungi, which penetrate into the host cells to consume nutrients.

Although fungi are opisthokonts—a grouping of evolutionarily related organisms broadly characterized by a single posterior flagellum—all phyla except for the chytrids have lost their posterior flagella. Fungi are unusual among the eukaryotes in having a cell wall that, in addition to glucans (e.g., β-1,3-glucan) and other typical components, also contains the biopolymer chitin.

Macroscopic structures

Armillaria solidipes

Fungal mycelia can become visible to the naked eye, for example, on various surfaces and substrates, such as damp walls and on spoiled food, where they are commonly called molds. Mycelia grown on solid agar media in laboratory petri dishes are usually referred to as colonies. These colonies can exhibit growth shapes and colors (due to spores or pigmentation) that can be used as diagnostic features in the identification of species or groups. Some individual fungal colonies can reach extraordinary dimensions and ages as in the case of a clonal colony of *Armillaria solidipes*, which extends over an area of more than 900 ha (3.5 square miles), with an estimated age of nearly 9,000 years.

The apothecium—a specialized structure important in sexual reproduction in the ascomycetes—is a cup-shaped fruiting body that holds the hymenium, a layer of tissue containing the spore-bearing cells. The fruiting bodies of the basidiomycetes (basidiocarps) and some ascomycetes can sometimes grow very large, and many are well-known as mushrooms.

Growth and physiology

The growth of fungi as hyphae on or in solid substrates or as single cells in aquatic environments is adapted for the efficient extraction of nutrients, because these growth forms have high surface area to volume ratios. Hyphae are specifically adapted for growth on solid surfaces, and to invade substrates and tissues. They can exert large penetrative mechanical forces; for example, the plant pathogen *Magnaporthe grisea* forms a structure called an appressorium which evolved to puncture plant tissues. The pressure generated by the appressorium, directed against the plant epidermis, can exceed 8 megapascals (1,200 psi). The filamentous fungus *Paecilomyces lilacinus* uses a similar structure to penetrate the eggs of nematodes.

Mold covering a decaying peach. The frames were taken approximately 12 hours apart over a period of six days.

The mechanical pressure exerted by the appressorium is generated from physiological processes that increase intracellular turgor by producing osmolytes such as glycerol. Morphological adaptations such as these are complemented by hydrolytic enzymes secreted into the environment to digest large organic molecules—such as polysaccharides, proteins, lipids, and other organic substrates—into smaller molecules that may then be absorbed as nutrients. The vast majority of filamentous fungi grow in a polar fashion—i.e., by extension into one direction—by elongation at the tip (apex) of the hypha. Alternative forms of fungal growth include intercalary extension (i.e., by longitudinal expansion of hyphal compartments that are below the apex) as in the case of some endophytic fungi, or growth by volume expansion during the development of mushroom stipes and other large organs. Growth of fungi as multicellular structures consisting of somatic and reproductive cells—a feature independently evolved in animals and plants—has several functions, including the development of fruiting bodies for dissemination of sexual spores and biofilms for substrate colonization and intercellular communication.

Traditionally, the fungi are considered heterotrophs, organisms that rely solely on carbon fixed by other organisms for metabolism. Fungi have evolved a high degree of metabolic versatility that allows them to use a diverse range of organic substrates for growth, including simple compounds such as nitrate, ammonia, acetate, or ethanol. For some species it has been shown that the pigment melanin may play a role in extracting energy from ionizing radiation, such as gamma radiation; however, this form of "radiotrophic" growth has only been described for a few species, the effects on growth rates are small, and the underlying biophysical and biochemical processes are not known. The authors speculate that this process might bear similarity to CO_2 fixation via visible light, but instead utilizing ionizing radiation as a source of energy.

Reproduction

Polyporus squamosus

Fungal reproduction is complex, reflecting the differences in lifestyles and genetic makeup within this kingdom of organisms. It is estimated that a third of all fungi reproduce by different modes of propagation; for example, reproduction may occur in two well-differentiated stages within the life cycle of a species, the teleomorph and the anamorph. Environmental conditions trigger genetically determined developmental states that lead to the creation of specialized structures for sexual or asexual reproduction. These structures aid reproduction by efficiently dispersing spores or spore-containing propagules.

Asexual reproduction

Asexual reproduction via vegetative spores (conidia) or through mycelial fragmentation is common; it maintains clonal populations adapted to a specific niche, and allows more rapid dispersal than sexual reproduction. The "Fungi imperfecti" (fungi lacking the perfect or sexual stage) or Deuteromycota comprise all the species which lack an observable sexual cycle.

Sexual reproduction

Sexual reproduction with meiosis exists in all fungal phyla (with the exception of the Glomeromycota). It differs in many aspects from sexual reproduction in animals or plants. Differences also exist between fungal groups and can be used to discriminate species by morphological differences in sexual structures and reproductive strategies. Mating experiments between fungal isolates may identify species on the basis of biological species concepts. The major fungal groupings have initially been delineated based on the morphology of their sexual structures and spores; for example, the spore-containing structures, asci and basidia, can be used in the identification of ascomycetes and basidiomycetes, respectively. Some species may allow mating only between individuals of opposite mating type, while others can mate and sexually reproduce with any other individual or itself. Species of the former mating system are called heterothallic, and of the latter homothallic.

Most fungi have both an haploid and diploid stage in their life cycles. In sexually reproducing fungi, compatible individuals may combine by fusing their hyphae together into an interconnected network; this process, anastomosis, is required for the initiation of the sexual cycle. Ascomycetes and basidiomycetes go through a dikaryotic stage, in which the nuclei inherited from the two parents do not combine immediately after cell fusion, but remain separate in the hyphal cells.

The 8-spored asci of *Morchella elata*, viewed with phase contrast microscopy

In ascomycetes, dikaryotic hyphae of the hymenium (the spore-bearing tissue layer) form a characteristic *hook* at the hyphal septum. During cell division, formation of the hook ensures proper distribution of the newly divided nuclei into the apical and basal hyphal compartments. An ascus (plural *asci*) is then formed, in which karyogamy (nuclear fusion) occurs. Asci are embedded in an ascocarp, or fruiting body. Karyogamy in the asci is followed immediately by meiosis and the production of ascospores. After dispersal, the ascospores may germinate and form a new haploid mycelium.

Sexual reproduction in basidiomycetes is similar to that of the ascomycetes. Compatible haploid hyphae fuse to produce a dikaryotic mycelium. However, the dikaryotic phase is more extensive in the basidiomycetes, often also present in the vegetatively growing mycelium. A specialized anatomical structure, called a clamp connection, is formed at each hyphal septum. As with the structurally similar hook in the ascomycetes, the clamp connection in the basidiomycetes is required for controlled transfer of nuclei during cell division, to maintain the dikaryotic stage with two genetically different nuclei in each hyphal compartment. A basidiocarp is formed in which club-like structures known as basidia generate haploid basidiospores after karyogamy and meiosis. The most commonly known basidiocarps are mushrooms, but they may also take other forms.

In glomeromycetes (formerly zygomycetes), haploid hyphae of two individuals fuse, forming a gametangium, a specialized cell structure that becomes a fertile gamete-producing cell. The gametangium develops into a zygospore, a thick-walled spore formed by the union of gametes. When the zygospore germinates, it undergoes meiosis, generating new haploid hyphae, which may then form asexual sporangiospores. These sporangiospores allow the fungus to rapidly disperse and germinate into new genetically identical haploid fungal mycelia.

Spore dispersal

Both asexual and sexual spores or sporangiospores are often actively dispersed by forcible ejection from their reproductive structures. This ejection ensures exit of the spores from the reproductive structures as well as travelling through the air over long distances.

The bird's nest fungus *Cyathus stercoreus*

Specialized mechanical and physiological mechanisms, as well as spore surface structures (such as hydrophobins), enable efficient spore ejection. For example, the structure of the spore-bearing cells in some ascomycete species is such that the buildup of substances affecting cell volume and fluid balance enables the explosive discharge of spores into the air. The forcible discharge of single spores termed *ballistospores* involves formation of a small drop of water (Buller's drop), which upon contact with the spore leads to its projectile release with an initial acceleration of more than 10,000 g; the net result is that the spore is ejected 0.01–0.02 cm, sufficient distance for it to fall through the gills or pores into the air below. Other fungi, like the puffballs, rely on alternative mechanisms for spore release, such as external mechanical forces. The bird's nest fungi use the force of falling water drops to liberate the spores from cup-shaped fruiting bodies. Another strategy is seen in the stinkhorns, a group of fungi with lively colors and putrid odor that attract insects to disperse their spores.

Other sexual processes

Besides regular sexual reproduction with meiosis, certain fungi, such as those in the genera *Penicillium* and *Aspergillus*, may exchange genetic material via parasexual processes, initiated by anastomosis between hyphae and plasmogamy of fungal cells. The frequency and relative importance of parasexual events is unclear and may be lower than other sexual processes. It is known to play a role in intraspecific hybridization and is likely required for hybridization between species, which has been associated with major events in fungal evolution.

Evolution

In contrast to plants and animals, the early fossil record of the fungi is meager. Factors that likely contribute to the under-representation of fungal species among fossils include the nature of fungal fruiting bodies, which are soft, fleshy, and easily degradable tissues and the microscopic dimensions of most fungal structures, which therefore are not readily evident. Fungal fossils are difficult to distinguish from those of other microbes, and are most easily identified when they resemble extant fungi. Often recovered from a permineralized plant or animal host, these samples are typically studied by making thin-section preparations that can be examined with light microscopy or transmission electron microscopy. Compression fossils are studied by dissolving the surrounding matrix with acid and then using light or scanning electron microscopy to examine surface details.

The earliest fossils possessing features typical of fungi date to the Proterozoic eon, some 1,430 million years ago (Ma); these multicellular benthic organisms had filamentous structures with septa, and were capable of anastomosis. More recent studies (2009) estimate the arrival of fungal organisms at about 760–1060 Ma on the basis of comparisons of the rate of evolution in closely related groups. For much of the Paleozoic Era (542–251 Ma), the fungi appear to have been aquatic and consisted of organisms similar to the extant Chytrids in having flagellum-bearing spores. The evolutionary adaptation from an aquatic to a terrestrial lifestyle necessitated a diversification of ecological strategies for obtaining nutrients, including parasitism, saprobism, and the development of mutualistic relationships such as mycorrhiza and lichenization. Recent (2009) studies suggest that the ancestral ecological state of the Ascomycota was saprobism, and that independent lichenization events have occurred multiple times.

The fungi probably colonized the land during the Cambrian (542–488.3 Ma), long before land plants. Fossilized hyphae and spores recovered from the Ordovician of Wisconsin (460 Ma) resemble modern-day Glomerales, and existed at a time when the land flora likely consisted of only non-vascular bryophyte-like plants. Prototaxites, which was probably a fungus or lichen, would have been the tallest organism of the late Silurian. Fungal fossils do not become common and uncontroversial until the early Devonian (416–359.2 Ma), when they are abundant in the Rhynie chert, mostly as Zygomycota and Chytridiomycota. At about this same time, approximately 400 Ma, the Ascomycota and Basidiomycota diverged, and all modern classes of fungi were present by the Late Carboniferous (Pennsylvanian, 318.1–299 Ma).

Lichen-like fossils have been found in the Doushantuo Formation in southern China dating back to 635–551 Ma. Lichens were a component of the early terrestrial ecosystems, and the estimated age of the oldest terrestrial lichen fossil is 400 Ma; this date corresponds to the age of the oldest known sporocarp fossil, a *Paleopyrenomycites* species found in the Rhynie Chert. The oldest fossil with microscopic features resembling modern-day basidiomycetes is *Palaeoancistrus*, found permineralized with a fern from the Pennsylvanian. Rare in the fossil record are the homobasidiomycetes (a taxon roughly equivalent to the mushroom-producing species of the agaricomycetes). Two amber-preserved specimens provide evidence that the earliest known mushroom-forming fungi (the extinct species *Archaeomarasmius legletti*) appeared during the mid-Cretaceous, 90 Ma.

Some time after the Permian-Triassic extinction event (251.4 Ma), a fungal spike (originally thought to be an extraordinary abundance of fungal spores in sediments) formed, suggesting that fungi were the dominant life form at this time, representing nearly 100% of the available fossil record for this period. However, the relative proportion of fungal spores relative to spores formed by algal species is difficult to assess, the spike did not appear worldwide, and in many places it did not fall on the Permian-Triassic boundary.

Taxonomy

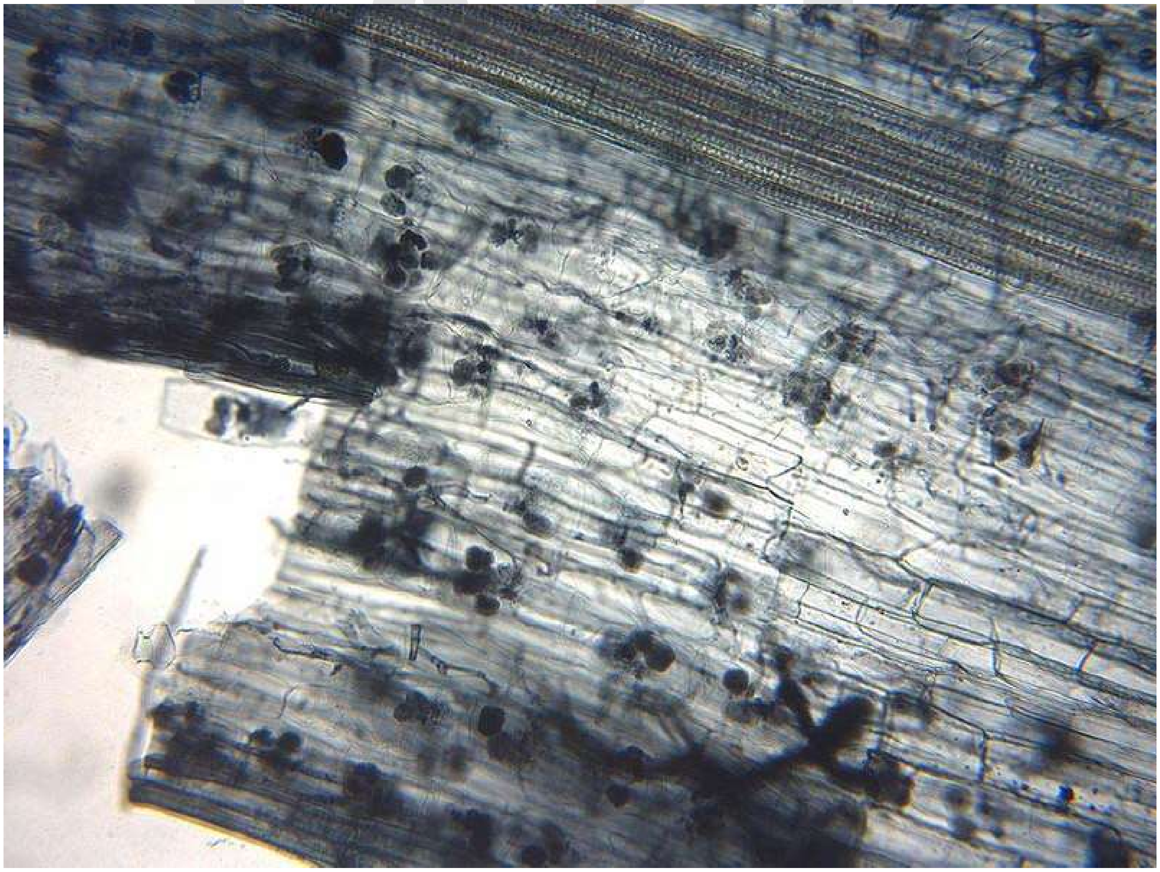
Although commonly included in botany curricula and textbooks, fungi are more closely related to animals than to plants and are placed with the animals in the monophyletic group of opisthokonts. Analyses using molecular phylogenetics support a monophyletic origin of the Fungi. The taxonomy of the Fungi is in a state of constant flux, especially due to recent research based on DNA comparisons. These current phylogenetic analyses often overturn classifications based on older and sometimes less discriminative methods based on morphological features and biological species concepts obtained from experimental matings.

There is no unique generally accepted system at the higher taxonomic levels and there are frequent name changes at every level, from species upwards. Efforts among researchers are now underway to establish and encourage usage of a unified and more consistent nomenclature. Fungal species can also have multiple scientific names depending on their life cycle and mode (sexual or asexual) of reproduction. Web sites such as Index Fungorum and ITIS list current names of fungal species (with cross-references to older synonyms).

The 2007 classification of Kingdom Fungi is the result of a large-scale collaborative research effort involving dozens of mycologists and other scientists working on fungal taxonomy. It recognizes seven phyla, two of which—the Ascomycota and the Basidiomycota—are contained within a branch representing subkingdom Dikarya. The below cladogram depicts the major fungal taxa and their relationship to opisthokont and unikont organisms. The lengths of the branches in this tree are not proportional to evolutionary distances.

Taxonomic groups

The major phyla (sometimes called divisions) of fungi have been classified mainly on the basis of characteristics of their sexual reproductive structures. Currently, seven phyla are proposed: Microsporidia, Chytridiomycota, Blastocladiomycota, Neocallimastigomycota, Glomeromycota, Ascomycota, and Basidiomycota.



Arbuscular mycorrhiza seen under microscope. Flax root cortical cells containing paired arbuscules.

Phylogenetic analysis has demonstrated that the Microsporidia, unicellular parasites of animals and protists, are fairly recent and highly derived endobiotic fungi (living within the tissue of another species). One 2006 study concludes that the Microsporidia are a sister group to the true fungi, that is, they are each other's closest evolutionary relative. Hibbett and colleagues suggest that this analysis does not clash with their classification of the Fungi, and although the Microsporidia are elevated to phylum status, it is acknowledged that further analysis is required to clarify evolutionary relationships within this group.

The Chytridiomycota are commonly known as chytrids. These fungi are distributed worldwide. Chytrids produce zoospores that are capable of active movement through aqueous phases with a single flagellum, leading early taxonomists to classify them as protists. Molecular phylogenies, inferred from rRNA sequences in ribosomes, suggest that the Chytrids are a basal group divergent from the other fungal phyla, consisting of four major clades with suggestive evidence for paraphyly or possibly polyphyly.

The Blastocladiomycota were previously considered a taxonomic clade within the Chytridiomycota. Recent molecular data and ultrastructural characteristics, however, place the Blastocladiomycota as a sister clade to the Zygomycota, Glomeromycota, and Dikarya (Ascomycota and Basidiomycota). The blastocladiomycetes are saprotrophs, feeding on decomposing organic matter, and they are parasites of all eukaryotic groups. Unlike their close relatives, the chytrids, which mostly exhibit zygotic meiosis, the blastocladiomycetes undergo sporic meiosis.

The Neocallimastigomycota were earlier placed in the phylum Chytridomycota. Members of this small phylum are anaerobic organisms, living in the digestive system of larger herbivorous mammals and possibly in other terrestrial and aquatic environments. They lack mitochondria but contain hydrogenosomes of mitochondrial origin. As the related chrytrids, neocallimastigomycetes form zoospores that are posteriorly uniflagellate or polyflagellate.

Members of the Glomeromycota form arbuscular mycorrhizae, a form of symbiosis where fungal hyphae invade plant root cells and both species benefit from the resulting increased supply of nutrients. All known Glomeromycota species reproduce asexually. The symbiotic association between the Glomeromycota and plants is ancient, with evidence dating to 400 million years ago. Formerly part of the Zygomycota (commonly known as 'sugar' and 'pin' molds), the Glomeromycota were elevated to phylum status in 2001 and now replace the older phylum Zygomycota. Fungi that were placed in the Zygomycota are now being reassigned to the Glomeromycota, or the subphyla incertae sedis Mucoromycotina, Kickxellomycotina, the Zoopagomycotina and the Entomophthoromycotina. Some well-known examples of fungi formerly in the Zygomycota include black bread mold (*Rhizopus stolonifer*), and *Pilobolus* species, capable of ejecting spores several meters through the air. Medically relevant genera include *Mucor*, *Rhizomucor*, and *Rhizopus*.

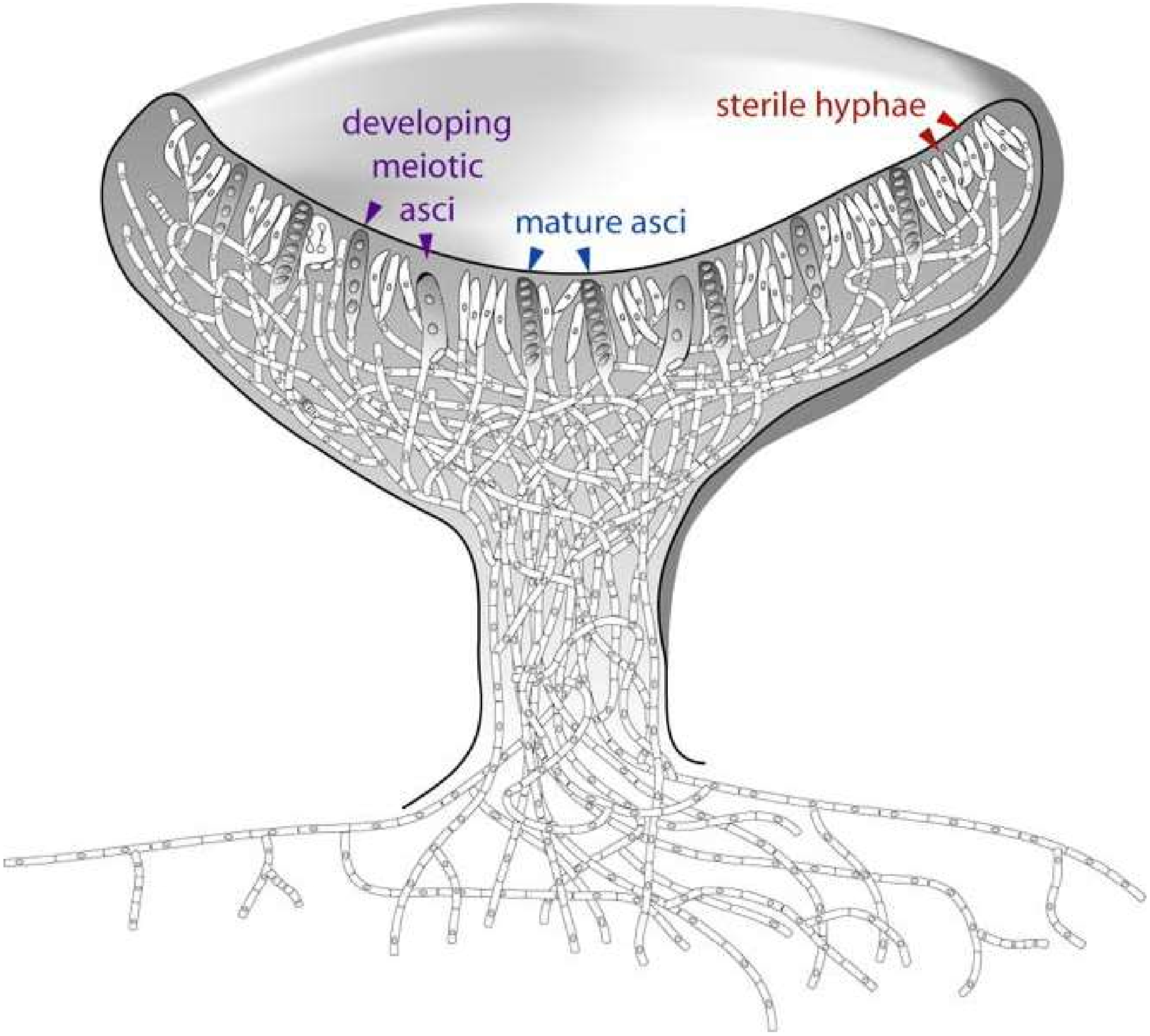


Diagram of an apothecium (the typical cup-like reproductive structure of Ascomycetes) showing sterile tissues as well as developing and mature asci.

The Ascomycota, commonly known as sac fungi or ascomycetes, constitute the largest taxonomic group within the Eumycota. These fungi form meiotic spores called ascospores, which are enclosed in a special sac-like structure called an ascus. This phylum includes morels, a few mushrooms and truffles, single-celled yeasts (e.g., of the genera *Saccharomyces*, *Kluyveromyces*, *Pichia*, and *Candida*), and many filamentous fungi living as saprotrophs, parasites, and mutualistic symbionts. Prominent and important genera of filamentous ascomycetes include *Aspergillus*, *Penicillium*, *Fusarium*, and *Claviceps*. Many ascomycete species have only been observed undergoing asexual reproduction (called anamorphic species), but analysis of molecular data has often been able to identify their closest teleomorphs in the Ascomycota. Because the products of meiosis are retained within the sac-like ascus, ascomycetes have been used for elucidating principles of genetics and heredity (e.g. *Neurospora crassa*).

Members of the Basidiomycota, commonly known as the club fungi or basidiomycetes, produce meiospores called basidiospores on club-like stalks called basidia. Most common mushrooms belong to this group, as well as rust and smut fungi, which are major pathogens of grains. Other important basidiomycetes include the maize pathogen *Ustilago maydis*, human commensal species of the genus *Malassezia*, and the opportunistic human pathogen, *Cryptococcus neoformans*.

Fungus-like organisms

Because of similarities in morphology and lifestyle, the slime molds (myxomycetes) and water molds (oomycetes) were formerly classified in the kingdom Fungi. Unlike true fungi the cell walls of these organisms contain cellulose and lack chitin. Myxomycetes are unikonts like fungi, but are grouped in the Amoebozoa. Oomycetes are diploid bikonts, grouped in the Chromalveolate kingdom. Neither water molds nor slime molds are closely related to the true fungi, and, therefore, taxonomists no longer group them in the kingdom Fungi. Nonetheless, studies of the oomycetes and myxomycetes are still often included in mycology textbooks and primary research literature.

The nucleariids, currently grouped in the Choanozoa, may be a sister group to the eumycete clade, and as such could be included in an expanded fungal kingdom.

Ecology

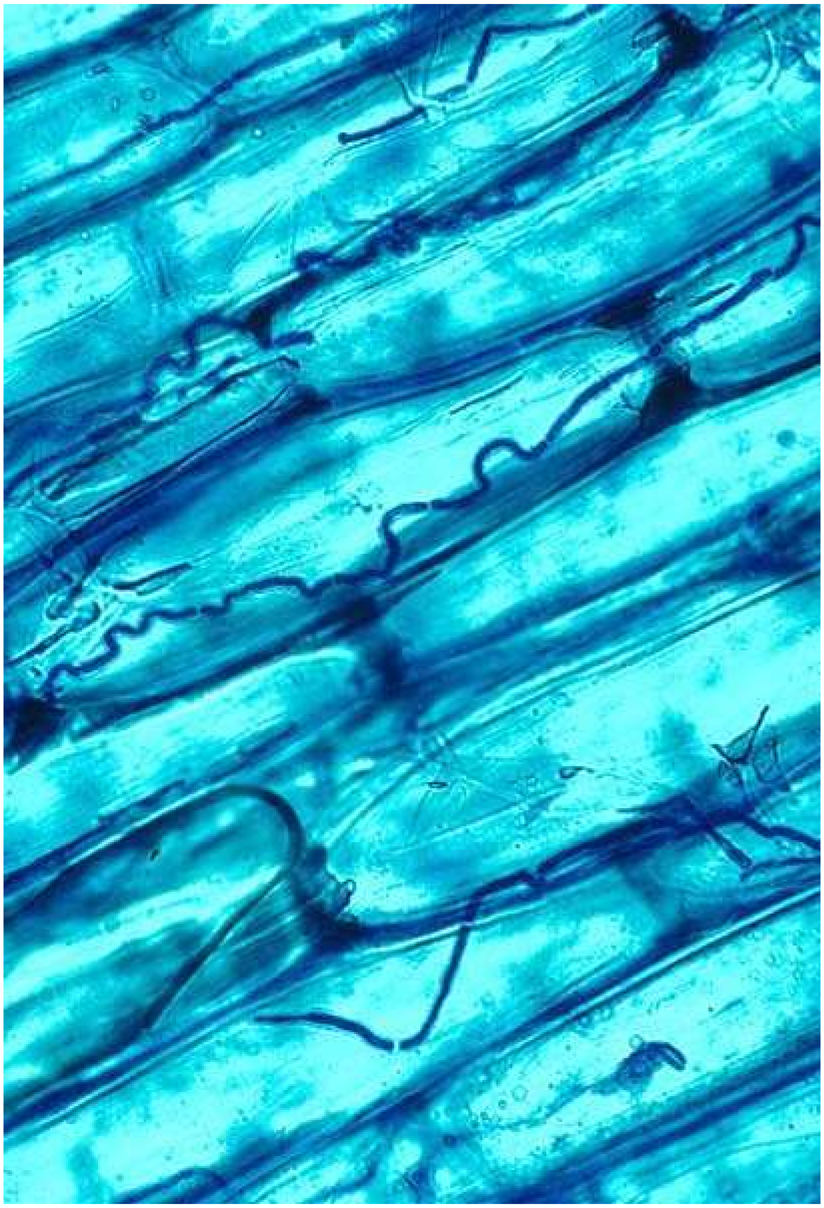
Although often inconspicuous, fungi occur in every environment on Earth and play very important roles in most ecosystems. Along with bacteria, fungi are the major decomposers in most terrestrial (and some aquatic) ecosystems, and therefore play a critical role in biogeochemical cycles and in many food webs. As decomposers, they play an essential role in nutrient cycling, especially as saprotrophs and symbionts, degrading organic matter to inorganic molecules, which can then re-enter anabolic metabolic pathways in plants or other organisms.

Symbiosis

Many fungi have important symbiotic relationships with organisms from most if not all Kingdoms. These interactions can be mutualistic or antagonistic in nature, or in the case of commensal fungi are of no apparent benefit or detriment to the host.

With plants

Mycorrhizal symbiosis between plants and fungi is one of the most well-known plant–fungus associations and is of significant importance for plant growth and persistence in many ecosystems; over 90% of all plant species engage in mycorrhizal relationships with fungi and are dependent upon this relationship for survival.



The dark filaments are hyphae of the endophytic fungus *Neotyphodium coenophialum* in the intercellular spaces of tall fescue leaf sheath tissue

The mycorrhizal symbiosis is ancient, dating to at least 400 million years ago. It often increases the plant's uptake of inorganic compounds, such as nitrate and phosphate from soils having low concentrations of these key plant nutrients. The fungal partners may also mediate plant-to-plant transfer of carbohydrates and other nutrients. Such mycorrhizal communities are called "common mycorrhizal networks". A special case of mycorrhiza is myco-heterotrophy, whereby the plant parasitizes the fungus, obtaining all of its nutrients from its fungal symbiont. Some fungal species inhabit the tissues inside roots, stems, and leaves, in which case they are called endophytes. Similar to mycorrhiza, endophytic colonization by fungi may benefit both symbionts; for example, endophytes of grasses impart to their host increased resistance to herbivores and other environmental stresses and receive food and shelter from the plant in return.

With algae and cyanobacteria

The lichen *Lobaria pulmonaria*, a symbiosis of fungal, algal, and cyanobacterial species

Lichens are formed by a symbiotic relationship between algae or cyanobacteria (referred to in lichen terminology as "photobionts") and fungi (mostly various species of ascomycetes and a few basidiomycetes), in which individual photobiont cells are embedded in a tissue formed by the fungus. Lichens occur in every ecosystem on all continents, play a key role in soil formation and the initiation of biological succession, and are the dominating life forms in extreme environments, including polar, alpine, and semiarid desert regions. They are able to grow on inhospitable surfaces, including bare soil, rocks, tree bark, wood, shells, barnacles and leaves. As in mycorrhizas, the photobiont provides sugars and other carbohydrates via photosynthesis, while the fungus provides minerals and water. The functions of both symbiotic organisms are so closely intertwined that they function almost as a single organism; in most cases the resulting organism differs greatly from the individual components. Lichenization is a common mode of nutrition; around 20% of fungi—between 17,500 and 20,000 described species—are lichenized. Characteristics common to most lichens include obtaining organic carbon by photosynthesis, slow growth, small size, long life, long-lasting (seasonal) vegetative reproductive structures, mineral nutrition obtained largely from airborne sources, and greater tolerance of desiccation than most other photosynthetic organisms in the same habitat.

With insects

Many insects also engage in mutualistic relationships with fungi. Several groups of ants cultivate fungi in the order Agaricales as their primary food source, while ambrosia beetles cultivate various species of fungi in the bark of trees that they infest. Similarly, females of several wood wasp species (genus *Sirex*) inject their eggs together with spores of the wood-rotting fungus *Amylostereum areolatum* into the sapwood of pine trees; the growth of the fungus provides ideal nutritional conditions for the development of the wasp larvae. Termites on the African savannah are also known to cultivate fungi, and yeasts of the genera *Candida* and *Lachancea* inhabit the gut of a wide range of insects, including neuropterans, beetles, and cockroaches; it is not known whether these fungi benefit their hosts.

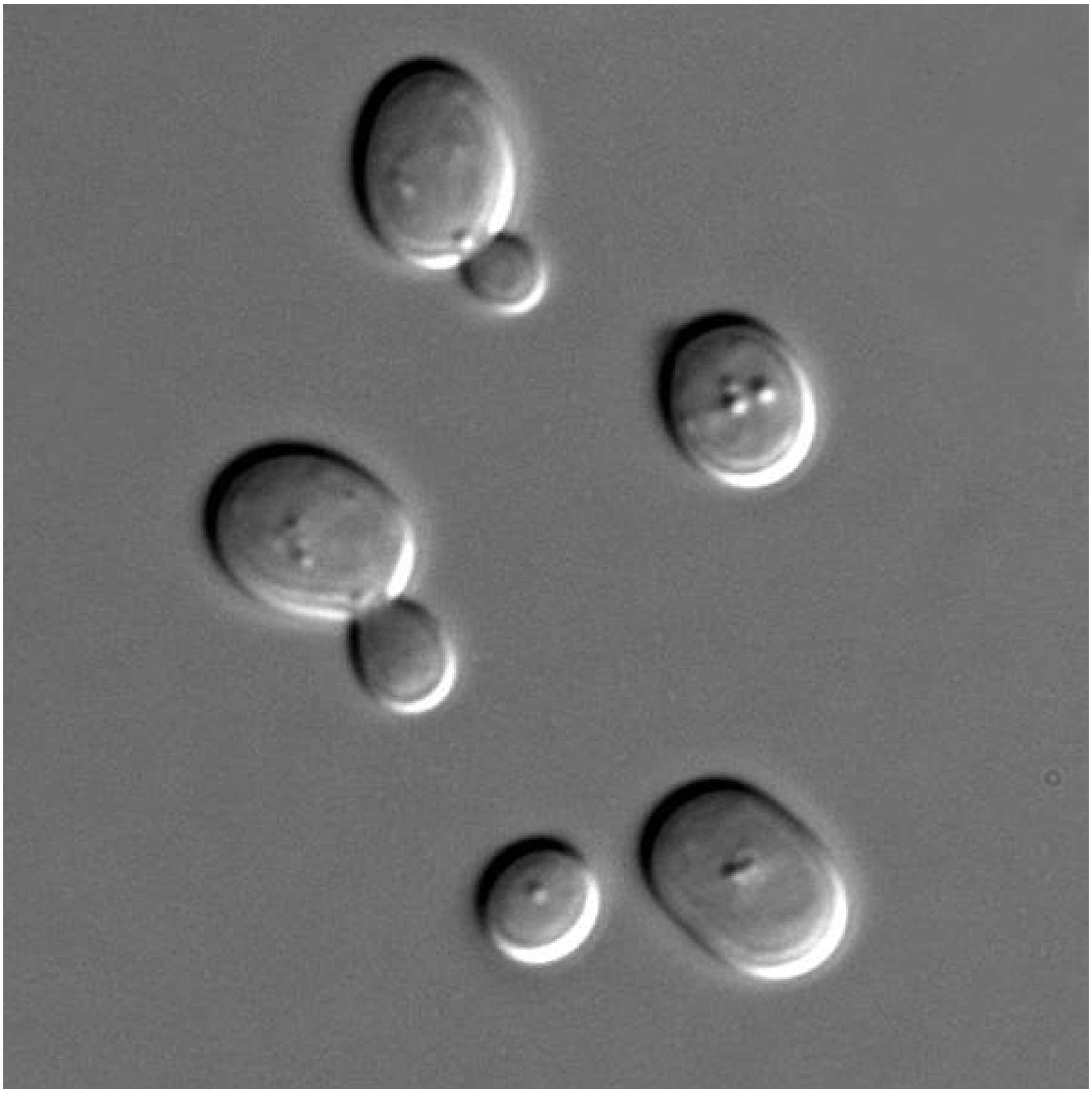
As pathogens and parasites

The plant pathogen *Aecidium magellanicum* causes calafate rust, seen here on a *Berberis* shrub in Chile.

Many fungi are parasites on plants, animals (including humans), and other fungi. Serious pathogens of many cultivated plants causing extensive damage and losses to agriculture and forestry include the rice blast fungus *Magnaporthe oryzae*, tree pathogens such as *Ophiostoma ulmi* and *Ophiostoma novo-ulmi* causing Dutch elm disease, and *Cryphonectria parasitica* responsible for chestnut blight, and plant pathogens in the genera *Fusarium*, *Ustilago*, *Alternaria*, and *Cochliobolus*. Some carnivorous fungi, like *Paecilomyces lilacinus*, are predators of nematodes, which they capture using an array of specialized structures such as constricting rings or adhesive nets.

Some fungi can cause serious diseases in humans, several of which may be fatal if untreated. These include aspergilloses, candidoses, coccidioidomycosis, cryptococcosis, histoplasmosis, mycetomas, and paracoccidioidomycosis. Furthermore, persons with immuno-deficiencies are particularly susceptible to disease by genera such as *Aspergillus*, *Candida*, *Cryptoccocus*, *Histoplasma*, and *Pneumocystis*. Other fungi can attack eyes, nails, hair, and especially skin, the so-called dermatophytic and keratinophilic fungi, and cause local infections such as ringworm and athlete's foot. Fungal spores are also a cause of allergies, and fungi from different taxonomic groups can evoke allergic reactions.

Human use



Saccharomyces cerevisiae cells shown with DIC microscopy.

The human use of fungi for food preparation or preservation and other purposes is extensive and has a long history. Mushroom farming and mushroom gathering are large industries in many countries. The study of the historical uses and sociological impact of fungi is known as ethnomycology. Because of the capacity of this group to produce an enormous range of natural products with antimicrobial or other biological activities, many species have long been used or are being developed for industrial production of antibiotics, vitamins, and anti-cancer and cholesterol-lowering drugs. More recently, methods have been developed for genetic engineering of fungi, enabling metabolic engineering of fungal species. For example, genetic modification of yeast species—which are easy to grow at fast rates in large fermentation vessels—has opened up ways of pharmaceutical production that are potentially more efficient than production by the original source organisms.

Drugs

Many species produce metabolites that are major sources of pharmacologically active drugs. Particularly important are the antibiotics, including the penicillins, a structurally related group of β-lactam antibiotics that are synthesized from small peptides. Although naturally occurring penicillins such as penicillin G (produced by *Penicillium chrysogenum*) have a relatively narrow spectrum of biological activity, a wide range of other penicillins can be produced by chemical modification of the natural penicillins. Modern penicillins are semisynthetic compounds, obtained initially from fermentation cultures, but then structurally altered for specific desirable properties. Other antibiotics produced by fungi include: ciclosporin, commonly used as an immunosuppressant during transplant surgery; and fusidic acid, used to help control infection from methicillin-resistant *Staphylococcus aureus* bacteria. Widespread use of these antibiotics for the treatment of bacterial diseases, such as tuberculosis, syphilis, leprosy, and many others began in the early 20th century and continues to play a major part in anti-bacterial chemotherapy. In nature, antibiotics of fungal or bacterial origin appear to play a dual role: at high concentrations they act as chemical defense against competition with other microorganisms in species-rich environments, such as the rhizosphere, and at low concentrations as quorum-sensing molecules for intra- or interspecies signaling.

Other drugs produced by fungi include griseofulvin isolated from *Penicillium griseofulvum*, used to treat fungal infections, and statins (HMG-CoA reductase inhibitors), used to inhibit cholesterol synthesis. Examples of statins found in fungi include mevastatin from *Penicillium citrinum* and lovastatin from *Aspergillus terreus* and the oyster mushroom.

Cultured foods

Baker's yeast or *Saccharomyces cerevisiae*, a single-celled fungus, is used to make bread and other wheat-based products, such as pizza dough and dumplings. Yeast species of the genus *Saccharomyces* are also used to produce alcoholic beverages through fermentation. Shoyu koji mold (*Aspergillus oryzae*) is an essential ingredient in brewing Shoyu (soy sauce) and sake, and the preparation of miso, while *Rhizopus* species are used for making tempeh. Several of these fungi are domesticated species that were bred or selected according to their capacity to ferment food without producing harmful mycotoxins, which are produced by very closely related *Aspergilli*. Quorn, a meat substitute, is made from *Fusarium venenatum*.

Medicinal use

The medicinal fungi *Ganoderma lucidum* (left) and *Cordyceps sinensis* (right).

Certain mushrooms enjoy usage as therapeutics in folk medicines, such as Traditional Chinese medicine. Notable medicinal mushrooms with a well-documented history of use include *Agaricus subrufescens*, *Ganoderma lucidum*, and *Cordyceps sinensis*. Research has identified compounds produced by these and other fungi that have inhibitory biological effects against viruses and cancer cells. Specific metabolites, such as polysaccharide-K, ergotamine, and β-lactam antibiotics, are routinely used in clinical medicine. The shiitake mushroom is a source of lentinan, a clinical drug approved for use in cancer treatments in several countries, including Japan. In Europe and Japan, polysaccharide-K (brand name Krestin), a chemical derived from *Trametes versicolor*, is an approved adjuvant for cancer therapy.

Edible and poisonous species

Amanita phalloides accounts for the majority of fatal mushroom poisonings worldwide.

Edible mushrooms are well-known examples of fungi. Many are commercially raised, but others must be harvested from the wild. *Agaricus bisporus*, sold as button mushrooms when small or Portobello mushrooms when larger, is a commonly eaten species, used in salads, soups, and many other dishes. Many Asian fungi are commercially grown and have increased in popularity in the West. They are often available fresh in grocery stores and markets, including straw mushrooms (*Volvariella volvacea*), oyster mushrooms (*Pleurotus ostreatus*), shiitakes (*Lentinula edodes*), and enokitake (*Flammulina* spp.).

There are many more mushroom species that are harvested from the wild for personal consumption or commercial sale. Milk mushrooms, morels, chanterelles, truffles, black trumpets, and *porcini* mushrooms (*Boletus edulis*) (also known as king boletes) demand a high price on the market. They are often used in gourmet dishes.

Certain types of cheeses require inoculation of milk curds with fungal species that impart a unique flavor and texture to the cheese. Examples include the blue color in cheeses such as Stilton or Roquefort, which are made by inoculation with *Penicillium roqueforti*. Molds used in cheese production are non-toxic and are thus safe for human consumption; however, mycotoxins (e.g., aflatoxins, roquefortine C, patulin, or others) may accumulate because of growth of other fungi during cheese ripening or storage.

Stilton cheese veined with *Penicillium roqueforti*

Many mushroom species are poisonous to humans, with toxicities ranging from slight digestive problems or allergic reactions as well as hallucinations to severe organ failures and death. Genera with mushrooms containing deadly toxins include *Conocybe*, *Galerina*, *Lepiota*, and most infamously, *Amanita*. The latter genus includes the destroying angel *(A. virosa)* and the death cap *(A. phalloides)*, the most common cause of deadly mushroom poisoning. The false morel (*Gyromitra esculenta*) is occasionally considered a delicacy when cooked, yet can be highly toxic when eaten raw. *Tricholoma equestre* was considered edible until being implicated in serious poisonings causing rhabdomyolysis. Fly agaric mushrooms (*Amanita muscaria*) also cause occasional nonfatal poisonings, mostly as a result of ingestion for use as a recreational drug for its hallucinogenic properties. Historically, fly agaric was used by different peoples in Europe and Asia and its present usage for religious or shamanic purposes is reported from some ethnic groups such as the Koryak people of north-eastern Siberia.

As it is difficult to accurately identify a safe mushroom without proper training and knowledge, it is often advised to assume that a wild mushroom is poisonous and not to consume it.

Pest control

Grasshoppers killed by *Beauveria bassiana*

In agriculture, fungi may be useful if they actively compete for nutrients and space with pathogenic microorganisms such as bacteria or other fungi via the competitive exclusion principle, or if they are parasites of these pathogens. For example, certain species may be used to eliminate or suppress the growth of harmful plant pathogens, such as insects, mites, weeds, nematodes and other fungi that cause diseases of important crop plants. This has generated strong interest in practical applications that use these fungi in the biological control of these agricultural pests. Entomopathogenic fungi can be used as biopesticides, as they actively kill insects. Examples that have been used as biological insecticides are *Beauveria bassiana*, *Metarhizium* spp, *Hirsutella* spp, *Paecilomyces* (*Isaria*) spp, and *Lecanicillium lecanii*. Endophytic fungi of grasses of the genus *Neotyphodium*, such as *N. coenophialum*, produce alkaloids that are toxic to a range of invertebrate and vertebrate herbivores. These alkaloids protect grass plants from herbivory, but several endophyte alkaloids can poison grazing animals, such as cattle and sheep. Infecting cultivars of pasture or forage grasses with *Neotyphodium* endophytes is one approach being used in grass breeding programs; the fungal strains are selected for producing only alkaloids that increase resistance to herbivores such as insects, while being non-toxic to livestock.

Bioremediation

Certain fungi, in particular "white rot" fungi, can degrade insecticides, herbicides, pentachlorophenol, creosote, coal tars, and heavy fuels and turn them into carbon dioxide, water, and basic elements. Fungi have been shown to biomineralize uranium oxides, suggesting they may have application in the bioremediation of radioactively polluted sites.

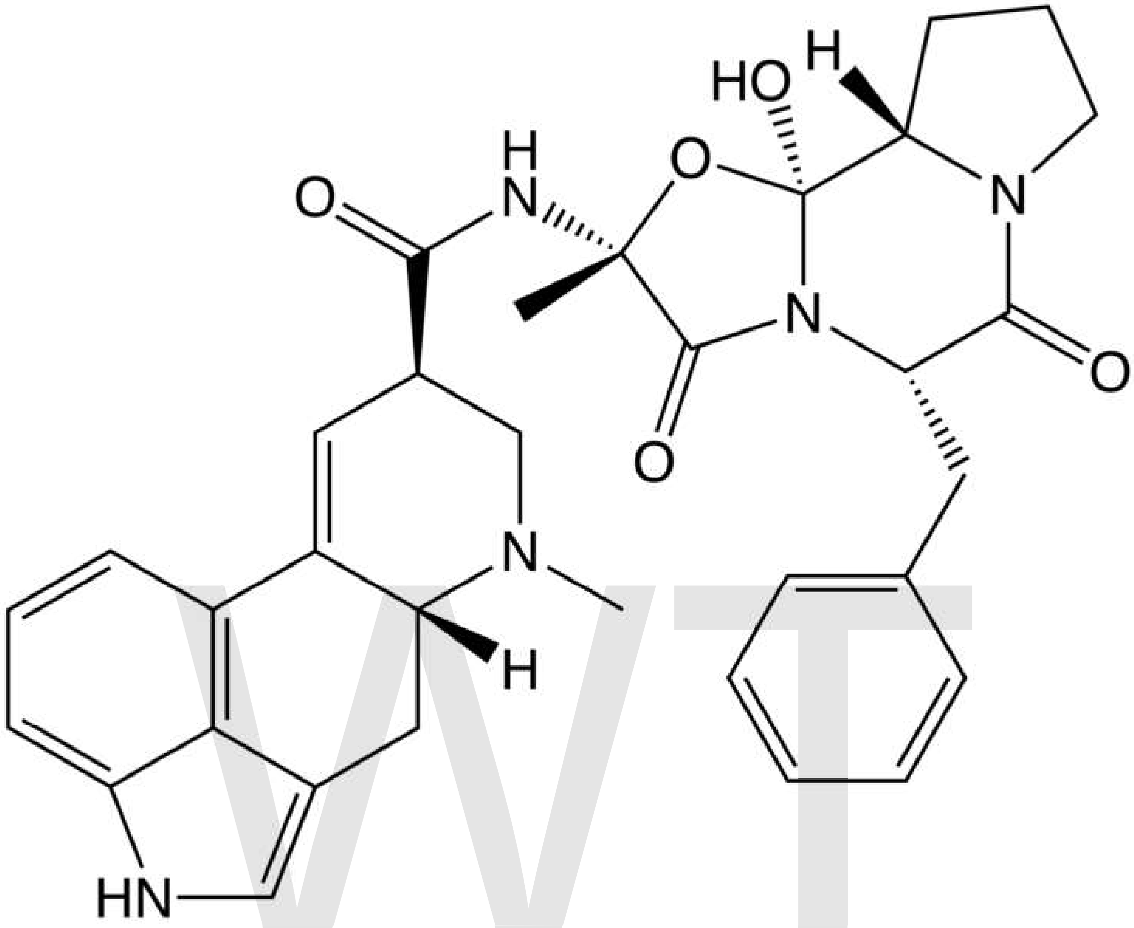
Model organisms

Several pivotal discoveries in biology were made by researchers using fungi as model organisms, that is, fungi that grow and sexually reproduce rapidly in the laboratory. For example, the one gene-one enzyme hypothesis was formulated by scientists who used the bread mold *Neurospora crassa* to test their biochemical theories. Other important model fungi are *Aspergillus nidulans* and the yeasts, *Saccaromyces cerevisiae* and *Schizosaccharomyces pombe*, each of which has a long history of use to investigate issues in eukaryotic cell biology and genetics, such as cell cycle regulation, chromatin structure, and gene regulation. Other fungal models have more recently emerged that each address specific biological questions relevant to medicine, plant pathology, and industrial uses; examples include *Candida albicans*, a dimorphic, opportunistic human pathogen, *Magnaporthe grisea*, a plant pathogen, and *Pichia pastoris*, a yeast widely used for eukaryotic protein expression.

Others

Fungi are used extensively to produce industrial chemicals like citric, gluconic, lactic, and malic acids, and industrial enzymes, such as lipases used in biological detergents, cellulases used in making cellulosic ethanol and stonewashed jeans, and amylases, invertases, proteases and xylanases. Several species, most notably *Psilocybin mushrooms* (colloquially known as *magic mushrooms*), are ingested for their psychedelic properties, both recreationally and religiously.

Mycotoxins



Ergotamine, a major mycotoxin produced by *Claviceps* species, which if ingested can cause gangrene, convulsions, and hallucinations

Many fungi produce biologically active compounds, several of which are toxic to animals or plants and are therefore called mycotoxins. Of particular relevance to humans are mycotoxins produced by molds causing food spoilage, and poisonous mushrooms. Particularly infamous are the lethal amatoxins in some *Amanita* mushrooms, and ergot alkaloids, which have a long history of causing serious epidemics of ergotism (St Anthony's Fire) in people consuming rye or related cereals contaminated with sclerotia of the ergot fungus, *Claviceps purpurea*. Other notable mycotoxins include the aflatoxins, which are insidious liver toxins and highly carcinogenic metabolites produced by certain *Aspergillus* species often growing in or on grains and nuts consumed by humans, ochratoxins, patulin, and trichothecenes (e.g., T-2 mycotoxin) and fumonisins, which have significant impact on human food supplies or animal livestock.

Mycotoxins are secondary metabolites (or natural products), and research has established the existence of biochemical pathways solely for the purpose of producing mycotoxins and other natural products in fungi. Mycotoxins may provide fitness benefits in terms of physiological adaptation, competition with other microbes and fungi, and protection from consumption (fungivory).

Mycology

Mycology is the branch of biology concerned with the systematic study of fungi, including their genetic and biochemical properties, their taxonomy, and their use to humans as a source of medicine, food, and psychotropic substances consumed for religious purposes, as well as their dangers, such as poisoning or infection. The field of phytopathology, the study of plant diseases, is closely related because many plant pathogens are fungi.

Use of fungi by humans dates back to prehistory; Ötzi the Iceman, a well-preserved mummy of a 5,300 year old Neolithic man found frozen in the Austrian Alps, carried two species of polypore mushrooms that may have been used as tinder (*Fomes fomentarius*), or for medicinal purposes (*Piptoporus betulinus*). Ancient peoples have used fungi as food sources–often unknowingly–for millennia, in the preparation of leavened bread and fermented juices. Some of the oldest written records contain references to the destruction of crops that were probably caused by pathogenic fungi.

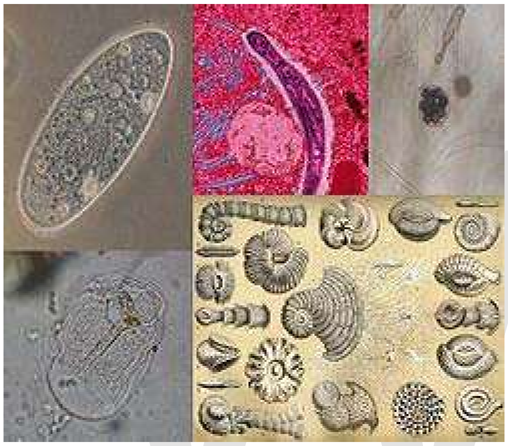
History

Mycology is a relatively new science that became systematic after the development of the microscope in the 16th century. Although fungal spores were first observed by Giambattista della Porta in 1588, the seminal work in the development of mycology is considered to be the publication of Pier Antonio Micheli's 1729 work *Nova plantarum genera*. Micheli not only observed spores, but showed that under the proper conditions, they could be induced into growing into the same species of fungi from which they originated. Extending the use of the binomial system of nomenclature introduced by Carl Linnaeus in his *Species plantarum* (1753), the Dutch Christian Hendrik Persoon (1761–1836) established the first classification of mushrooms with such skill so as to be considered a founder of modern mycology. Later, Elias Magnus Fries (1794–1878) further elaborated the classification of fungi, using spore color and various microscopic characteristics, methods still used by taxonomists today. Other notable early contributors to mycology in the 17th–19th and early 20th centuries include Miles Joseph Berkeley, August Carl Joseph Corda, Anton de Bary, the brothers Louis René and Charles Tulasne, Arthur H. R. Buller, Curtis G. Lloyd, and Pier Andrea Saccardo. The 20th century has seen a modernization of mycology that has come from advances in biochemistry, genetics, molecular biology, and biotechnology. The use of DNA sequencing technologies and phylogenetic analysis has provided new insights into fungal relationships and biodiversity, and has challenged traditional morphology-based groupings in fungal taxonomy.

Chapter 6

Protist

Protist
Temporal range: Neoproterozoic - Recent



Scientific classification

Domain:	**Eukarya**
Kingdom:	**Protista*** Haeckel, 1866

Typical phyla

- **Chromalveolata**
  - Heterokontophyta
  - Haptophyta
  - Cryptophyta (cryptomonads)
  - **Alveolata**
    - Dinoflagellata
    - Apicomplexa
    - Ciliophora (ciliates)
- **Excavata**
  - Euglenozoa
  - Percolozoa
  - Metamonada
- **Rhizaria**
  - Radiolaria
  - Foraminifera

    - Cercozoa
- **Archaeplastida (in part)**
    - Rhodophyta (red algae)
    - Glaucophyta (basal archaeplastids)
- **Unikonta (in part)**
    - Amoebozoa
    - Choanozoa

Protists are a diverse group of eukaryotic microorganisms. Historically, protists were treated as the kingdom **Protista**, which includes mostly unicellular organisms that do not fit into the other kingdoms, but this group is contested in modern taxonomy. Instead, it is "better regarded as a loose grouping of 30 or 40 disparate phyla with diverse combinations of trophic modes, mechanisms of motility, cell coverings and life cycles."

The protists do not have much in common besides a relatively simple organization—either they are unicellular, or they are multicellular without specialized tissues. This simple cellular organization distinguishes the protists from other eukaryotes, such as fungi, animals and plants.

The term *protista* was first used by Ernst Haeckel in 1866. Protists were traditionally subdivided into several groups based on similarities to the "higher" kingdoms: the one-celled animal-like protozoa, the plant-like protophyta (mostly one-celled algae), and the fungus-like slime molds and water molds. Because these groups often overlap, they have been replaced by phylogenetic-based classifications. However, they are still useful as informal names for describing the morphology and ecology of protists.

Protists live in almost any environment that contains liquid water. Many protists, such as the algae, are photosynthetic and are vital primary producers in ecosystems, particularly in the ocean as part of the plankton. Other protists, such as the Kinetoplastids and Apicomplexa, are responsible for a range of serious human diseases, such as malaria and sleeping sickness.

Classification

Historical classifications

The first division of the protists from other organisms came in the 1830s, when the German biologist Georg A. Goldfuss introduced the word *protozoa* to refer to organisms such as ciliates and corals. This group was expanded in 1845 to include all "unicellular animals", such as Foraminifera and amoebae. The formal taxonomic category *Protoctista* was first proposed in the early 1860s by John Hogg, who argued that the protists should include what he saw as primitive unicellular forms of both plants and animals. He defined the Protoctista as a "fourth kingdom of nature", in addition to the then-traditional kingdoms of plants, animals and minerals. The kingdom of minerals was later removed from taxonomy by Ernst Haeckel, leaving plants, animals, and the protists as a “kingdom of primitive forms”.

Herbert Copeland resurrected Hogg's label almost a century later, arguing that "Protoctista" literally meant "first established beings", Copeland complained that Haeckel's term *protista* included anucleated microbes such as bacteria. Copeland's use of the term *protoctista* did not. In contrast, Copeland's term included nucleated eukaryotes such as diatoms, green algae and fungi. This classification was the basis for Whittaker's later definition of Fungi, Animalia, Plantae and Protista as the four kingdoms of life. The kingdom Protista was later modified to separate prokaryotes into the separate kingdom of Monera, leaving the protists as a group of eukaryotic microorganisms. These five kingdoms remained the accepted classification until the development of molecular phylogenetics in the late 20th century, when it became apparent that neither protists nor monera were single groups of related organisms (they were not monophyletic groups).

Modern classifications

Currently, the term *protist* is used to refer to unicellular eukaryotes that either exist as independent cells, or if they occur in colonies, do not show differentiation into tissues. The term *protozoa* is used to refer to heterotrophic species of protists that do not form filaments. These terms are not used in current taxonomy, and are retained only as convenient ways to refer to these organisms.

The taxonomy of protists is still changing. Newer classifications attempt to present monophyletic groups based on ultrastructure, biochemistry, and genetics. Because the protists as a whole are paraphyletic, such systems often split up or abandon the kingdom, instead treating the protist groups as separate lines of eukaryotes. The recent scheme by Adl *et al.* (2005) is an example that does not bother with formal ranks (phylum, class, etc.) and instead lists organisms in hierarchical lists. This is intended to make the classification more stable in the long term and easier to update. Some of the main groups of protists, which may be treated as phyla, are listed in the taxobox at right. Many are thought to be monophyletic, though there is still uncertainty. For instance, the excavates are probably not monophyletic and the chromalveolates are probably only monophyletic if the haptophytes and cryptomonads are excluded.

Metabolism

Nutrition in some different types of protists is variable. In flagellates, for example, filter feeding may sometimes occur where the flagella find the prey. Other protists can engulf bacteria and digest them internally, by extending their cell membrane around the food material to form a food vacuole. This is then taken into the cell via endocytosis (usually phagocytosis; sometimes pinocytosis).

Nutritional types in protist metabolism

Nutritional type	Source of energy	Source of carbon	Examples
Phototrophs	Sunlight	Organic compounds or carbon fixation	Algae, Dinoflagellates or Euglena
Organotrophs	Organic compounds	Organic compounds	Apicomplexa, Trypanosomes or Amoebae

Reproduction

Some protists reproduce sexually (conjugation), while others reproduce asexually (binary fission).

Some species, for example *Plasmodium falciparum*, have extremely complex life cycles that involve multiple forms of the organism, some of which reproduce sexually and others asexually. However, it is unclear how frequently sexual reproduction causes genetic exchange between different strains of *Plasmodium* in nature and most populations of parasitic protists may be clonal lines that rarely exchange genes with other members of their species.

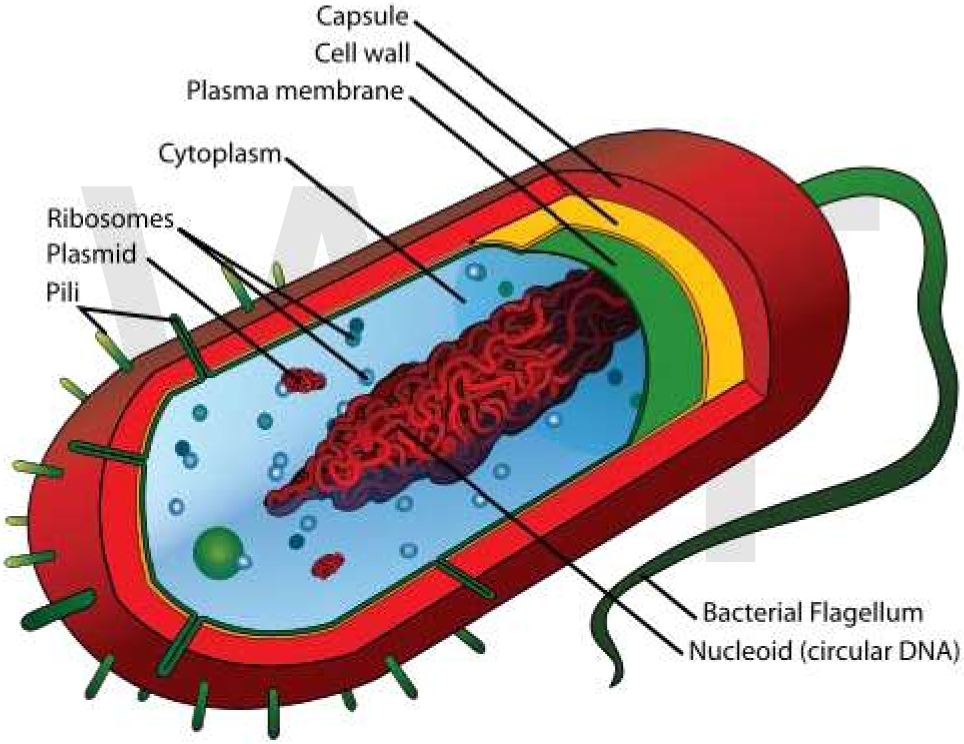
Role as pathogens

Some protists are significant pathogens of both animals and plants; for example *Plasmodium falciparum*, which causes malaria in humans, and *Phytophthora infestans*, which causes potato blight. A more thorough understanding of protist biology may allow these diseases to be treated more efficiently.

Researchers from the Agricultural Research Service are taking advantage of protists as pathogens in an effort to control red imported fire ant (*Solenopsis invicta*) populations in Argentina. With the help of spore-producing protists such as *Kneallhazia solenopsae* the red fire ant populations can be reduced by 53-100%. Researchers have also found a way to infect phorid flies with the protist without harming the flies. This is important because the flies act as a vector to infect the red fire ant population with the pathogenic protist.

Chapter 7

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.

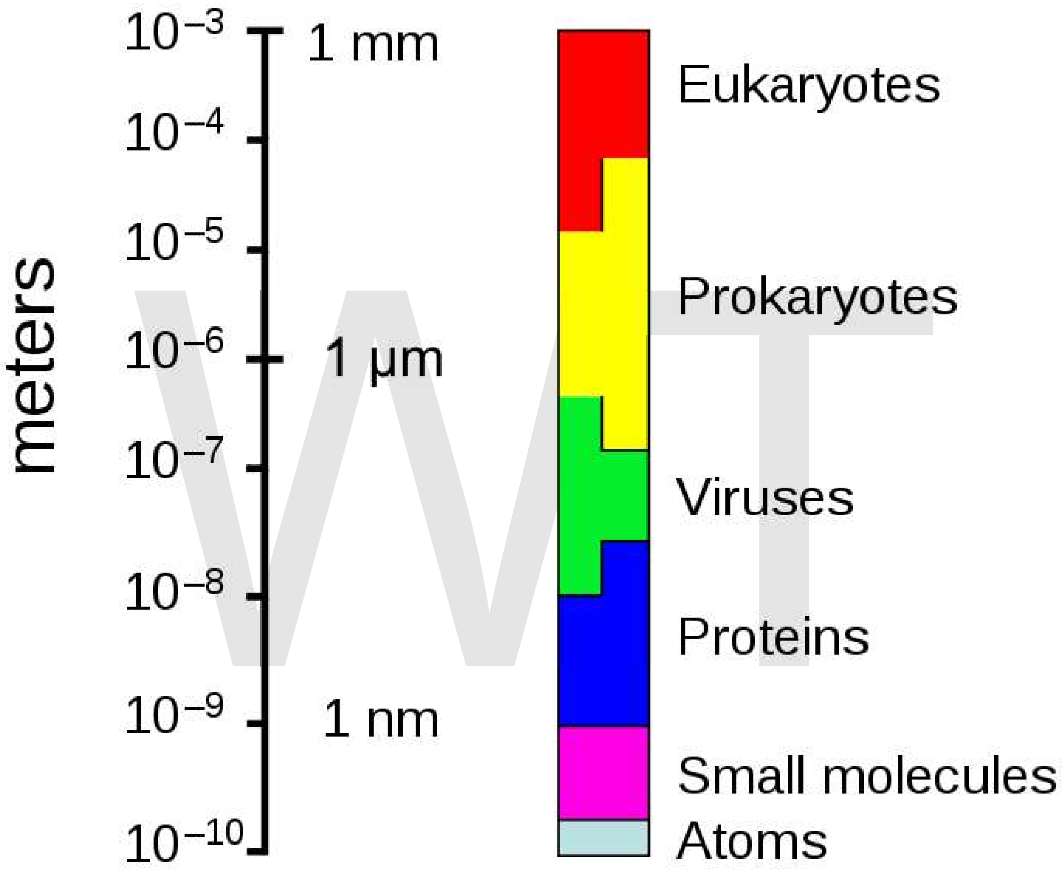
Biofilms may be highly heterogeneous and structurally complex and may attach to solid surfaces, or exist at liquid-air interfaces, or potentially even liquid-liquid interfaces. Bacterial biofilms are often made up of microcolonies (approximately dome-shaped masses of bacteria and matrix) separated by “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

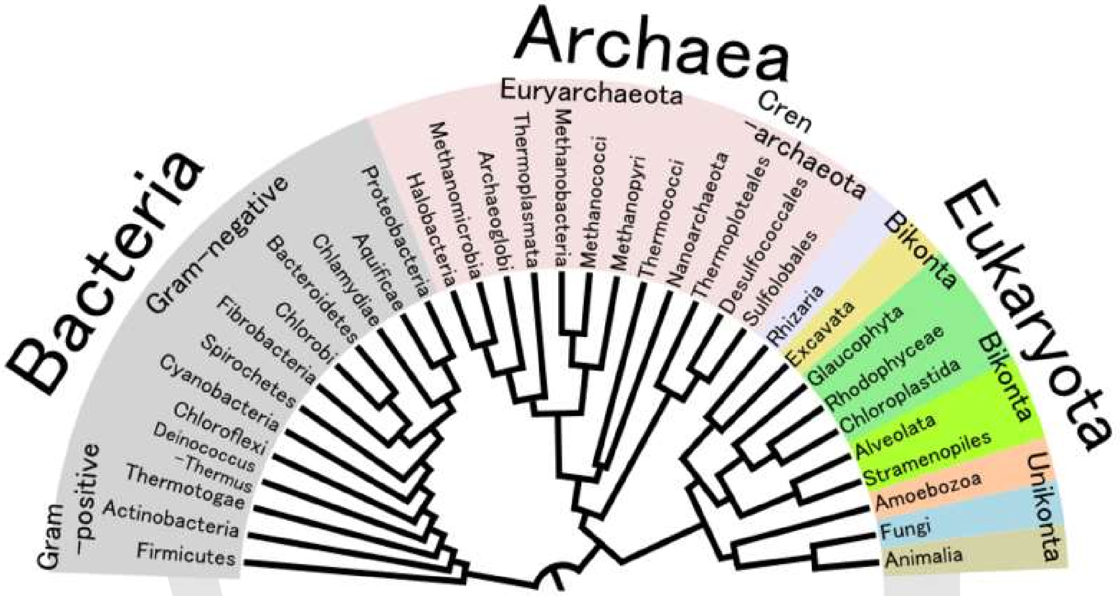
Prokaryotic cells have various shapes; the four basic shapes are:

- 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.

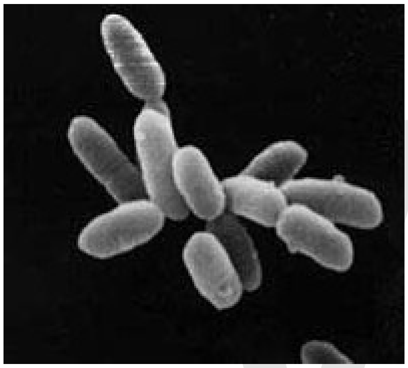
While Earth is the only place in the universe where life is known to exist, some have suggested that there is evidence on Mars of fossil or living prokaryotes; but this possibility remains the subject of considerable debate and skepticism.

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 8

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

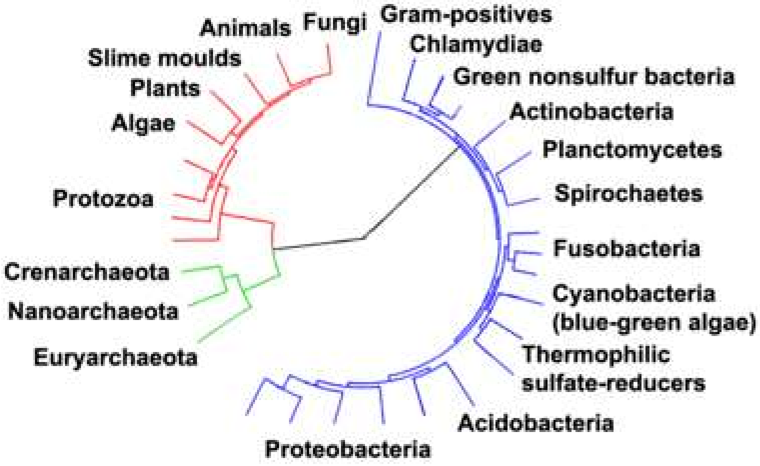
The classification of archaea into species is also controversial. Biology defines a species as a group of related organisms. The familiar exclusive breeding criterion (organisms that can breed with each other but not with others), is of no help because archaea reproduce asexually.

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.*

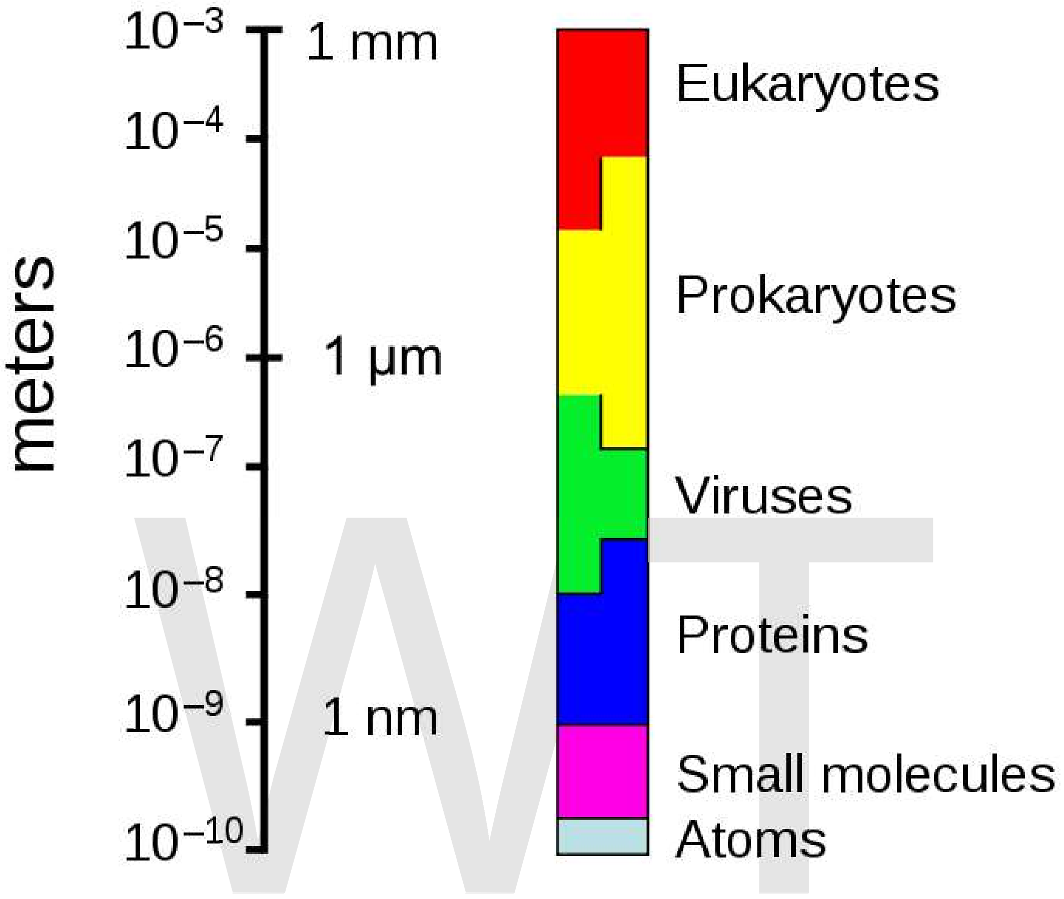
Woese argued that the bacteria, archaea, and eukaryotes represent separate lines of descent that diverged early on from an ancestral colony of organisms. However, a few biologists argue that the Archaea and Eukaryota arose from a group of bacteria. In any case, it is thought that viruses and archaea 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)

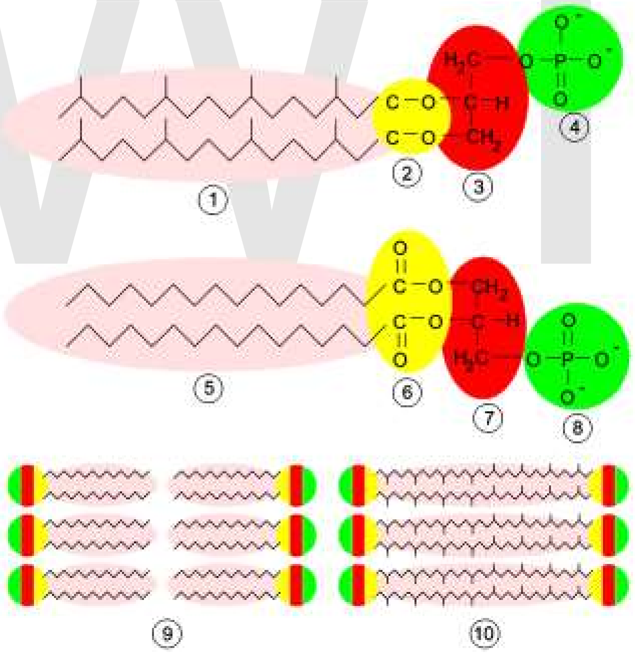
Individual archaea range from 0.1 micrometers (μm) to over 15 μm in diameter, and occur in various shapes, commonly as spheres, rods, spirals or plates. Other morphologies in the Crenarchaeota include irregularly shaped lobed cells in *Sulfolobus*, needle-like filaments that are less than half a micrometer 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

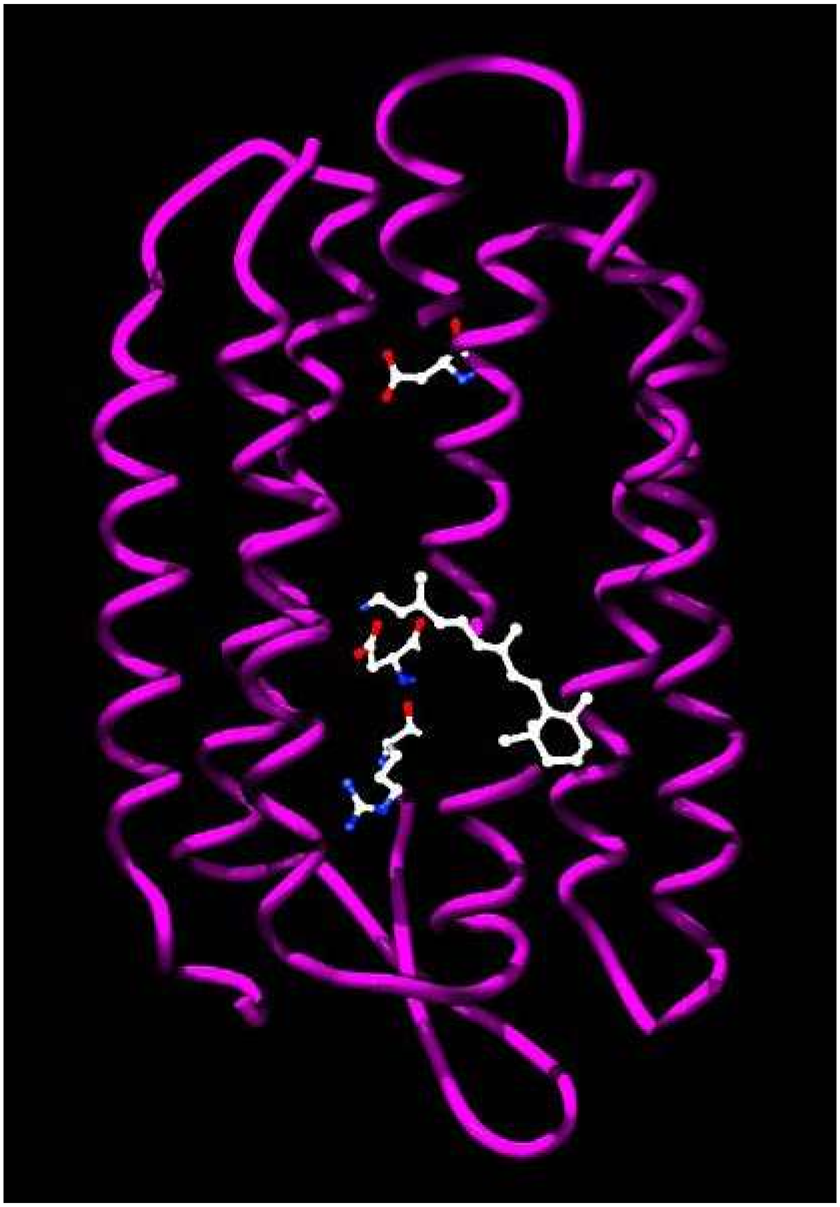
Archaea exhibit a great variety of chemical reactions in their metabolism and use many sources of energy. These reactions are classified into nutritional groups, depending on energy and carbon sources. Some archaea obtain energy from inorganic compounds such as sulfur or ammonia (they are lithotrophs). 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.



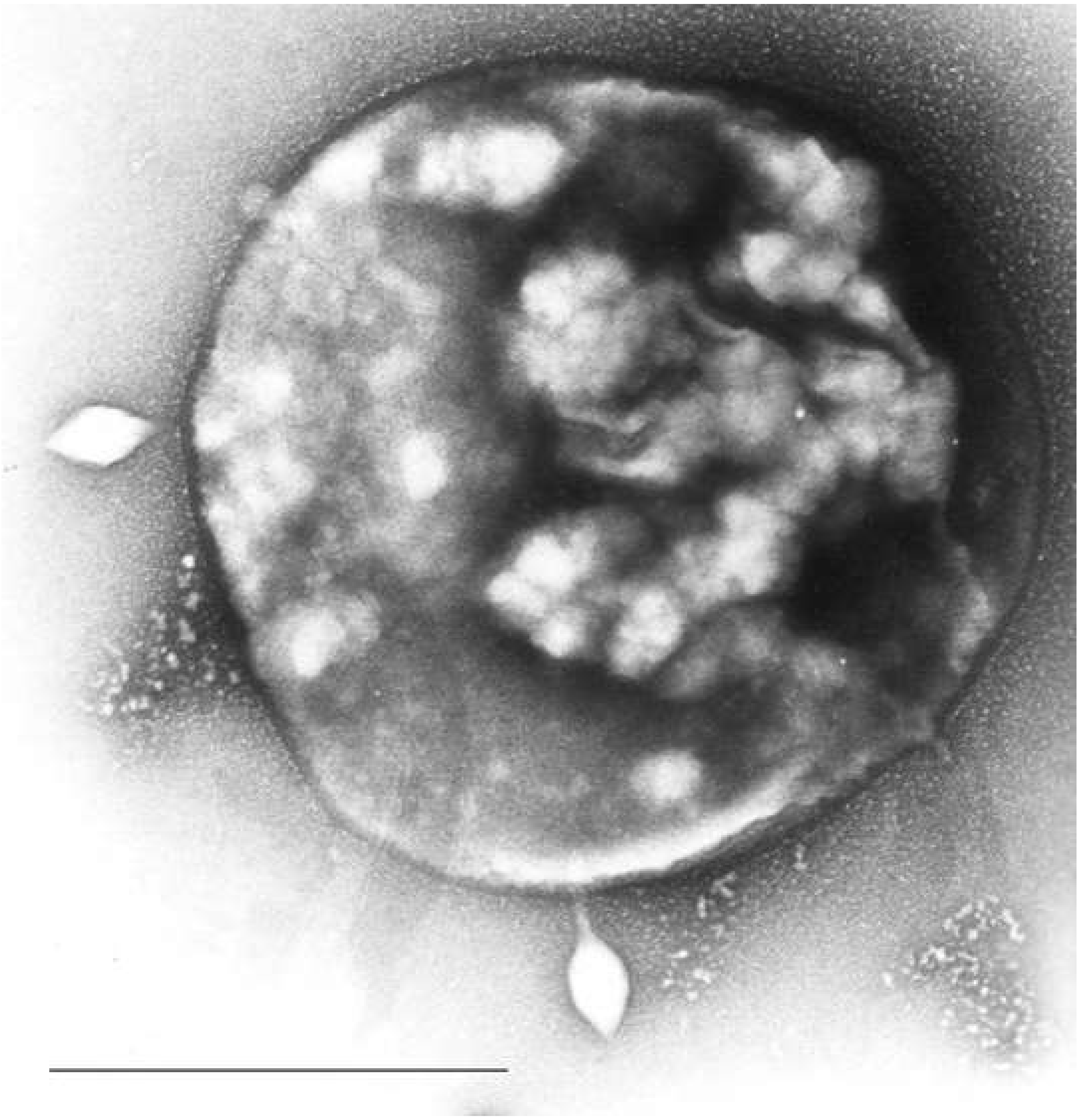
Bacteriorhodopsin from *Halobacterium salinarum*. The retinol cofactor and residues involved in proton transfer are shown as ball-and-stick models.

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.

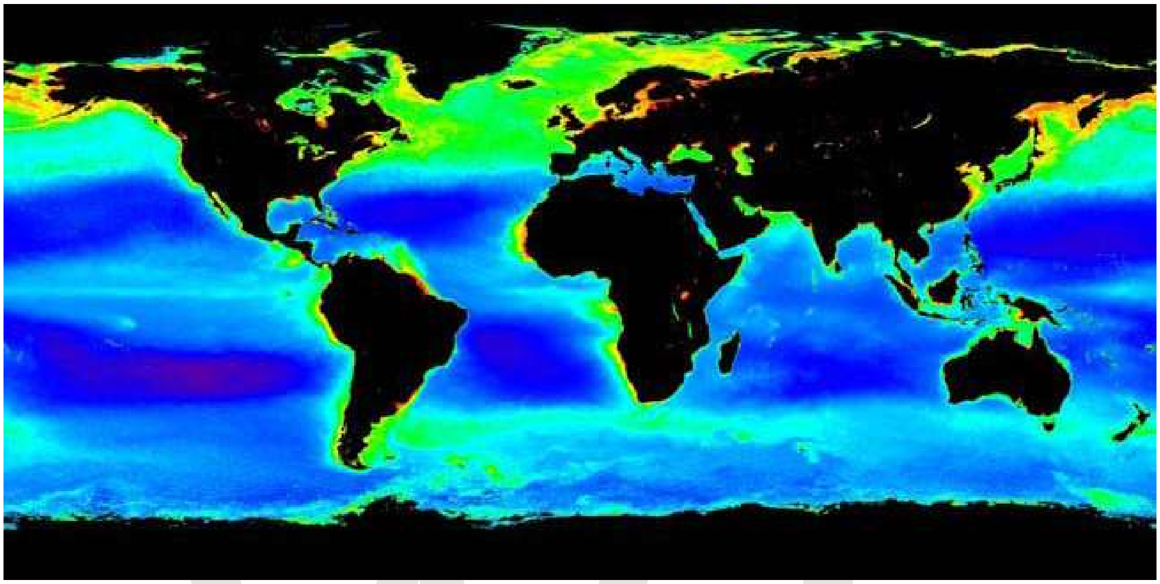


Image of plankton (light green) in the oceans; archaea form a major part of oceanic life.

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.

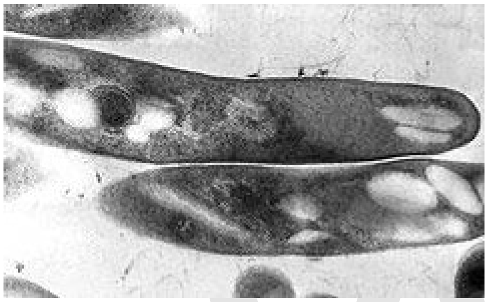
In contrast to the range of applications of archaean enzymes, the use of the organisms themselves in biotechnology is less developed. Methanogenic archaea are a vital part of sewage treatment, since they are part of the community of microorganisms that carry out anaerobic digestion and produce biogas. 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 9

Mycobacterium

Mycobacterium



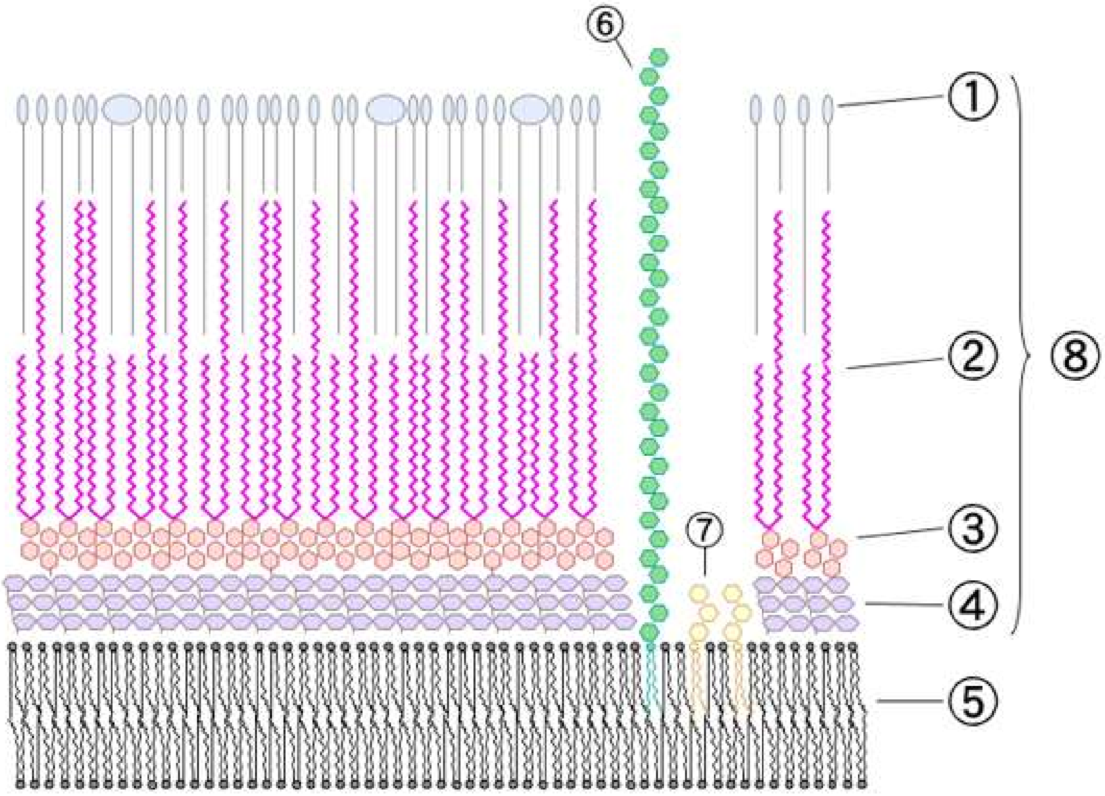
TEM micrograph of *M. tuberculosis*.

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

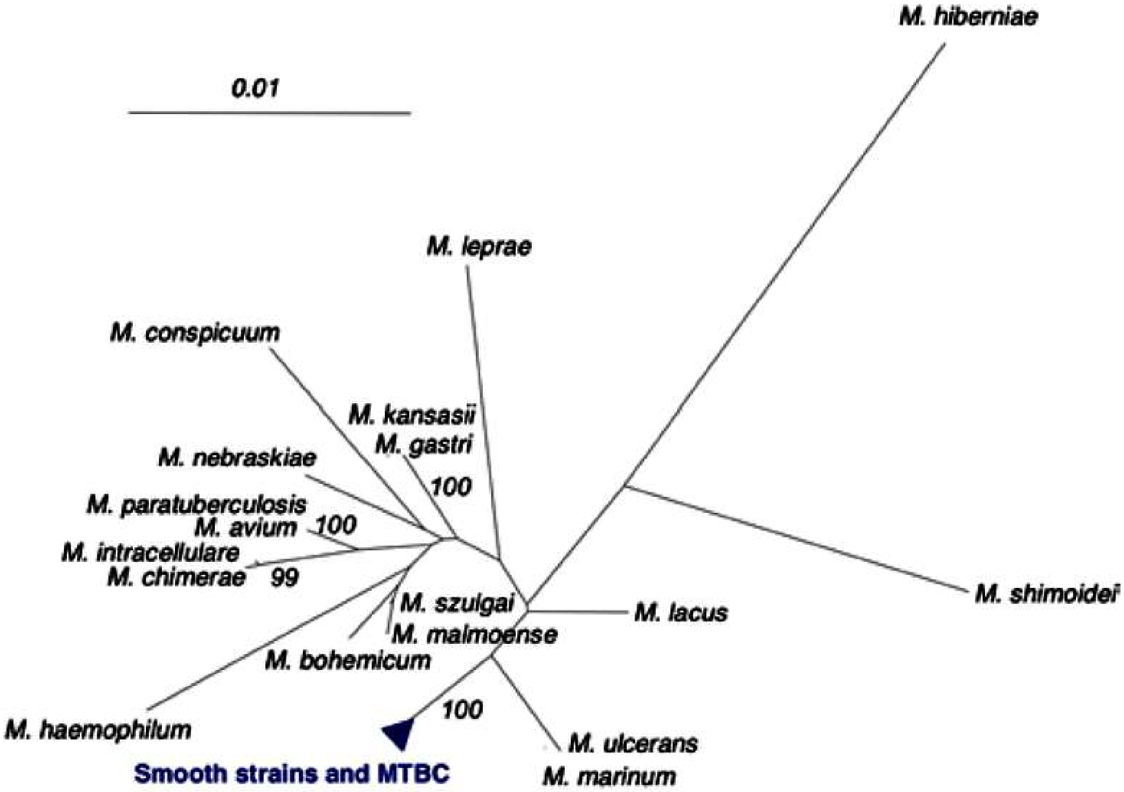
Various phenotypic tests can be used to identify and distinguish different Mycobacteria species and strains.

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 10

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

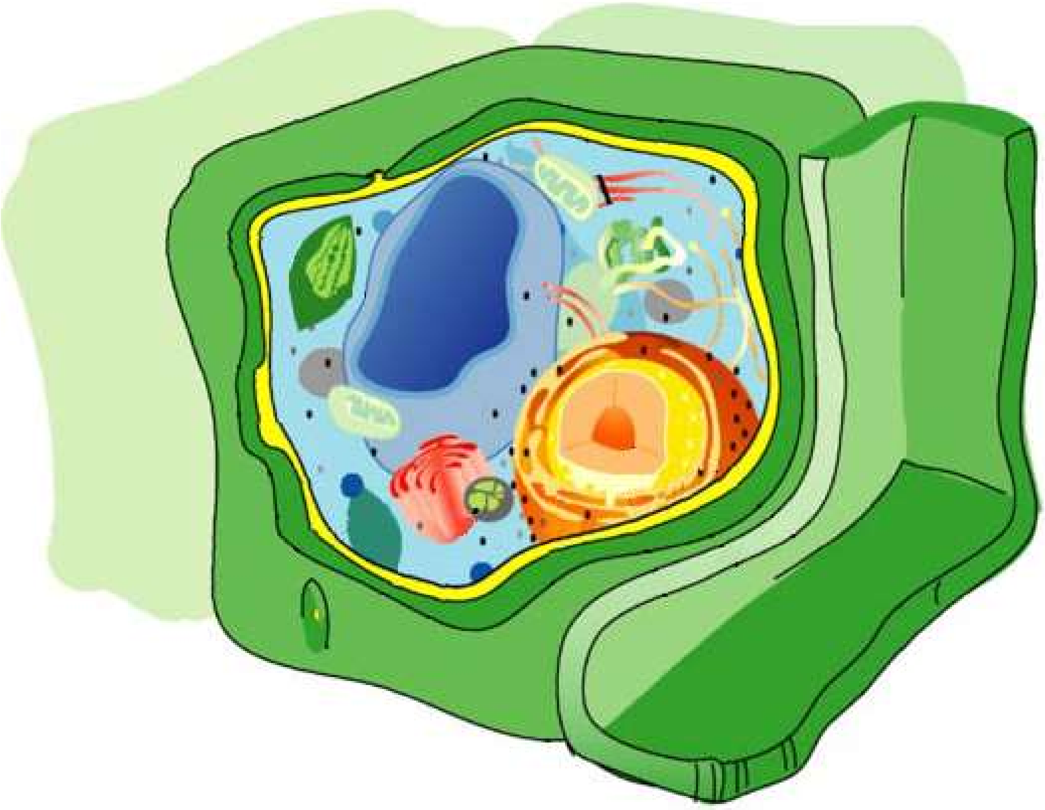


Diagram of the plant cell, with the cell wall in green.

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.

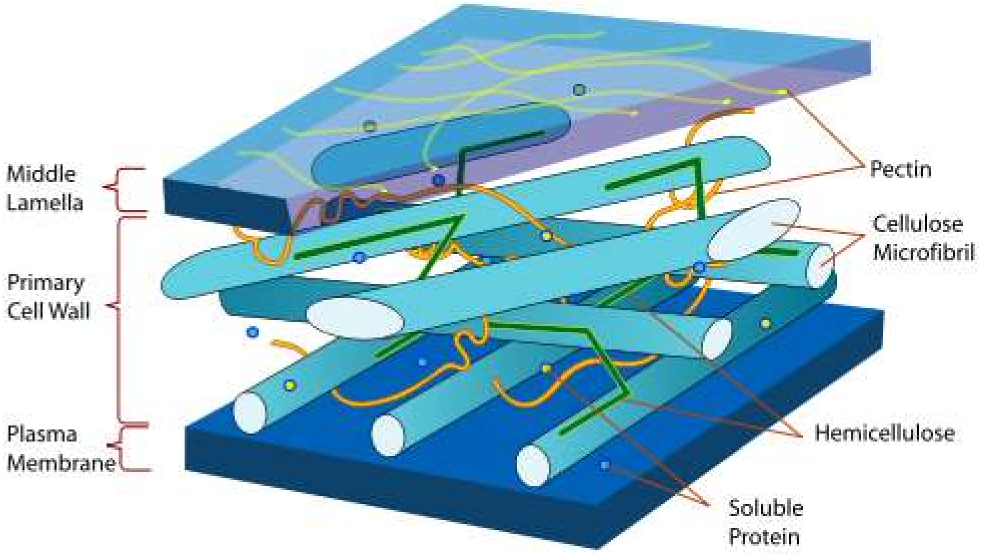
Permeability

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.

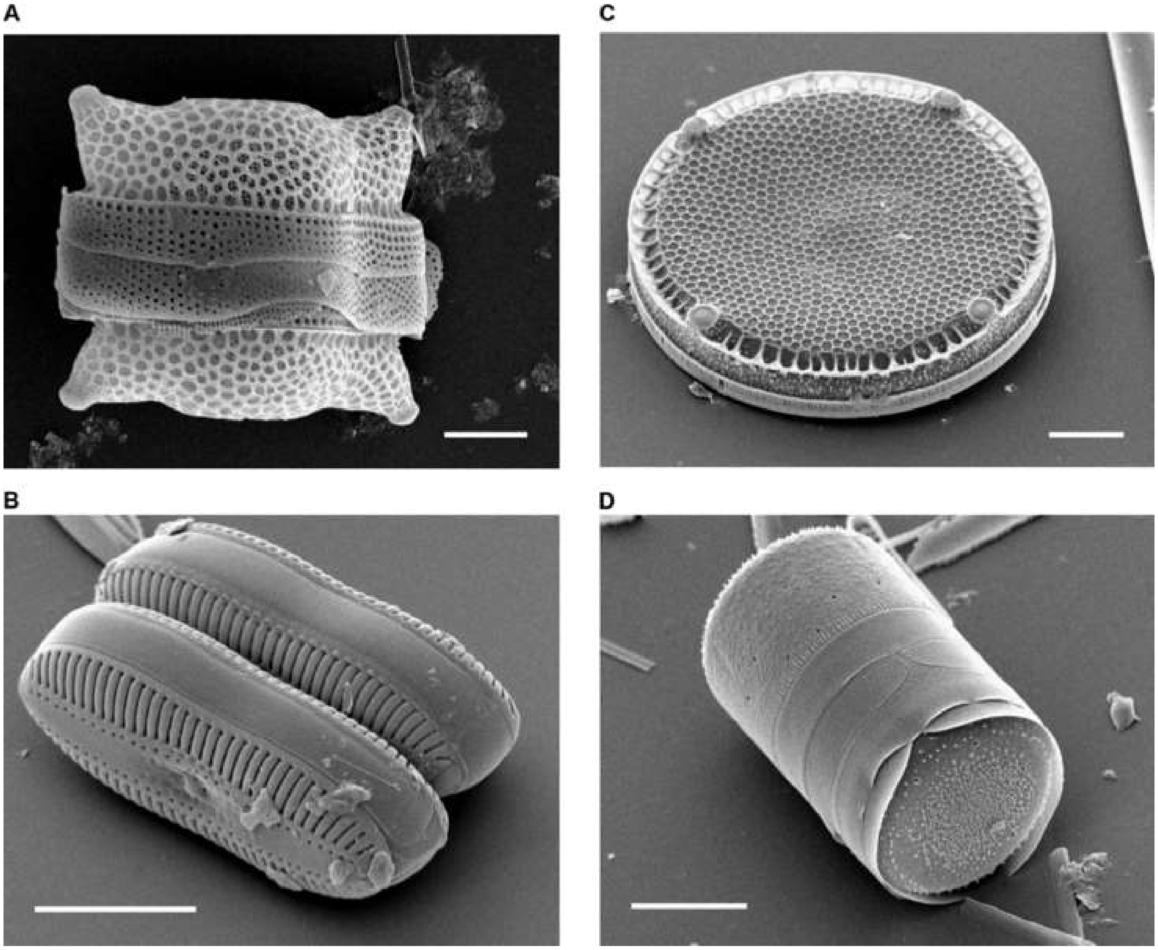
Cell walls in some plant tissues also function as storage depots for carbohydrates that can be broken down and resorbed to supply the metabolic and growth needs of the plant. For example, endosperm cell walls in the seeds of cereal grasses, nasturtium, and other species, are rich in glucans and other 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

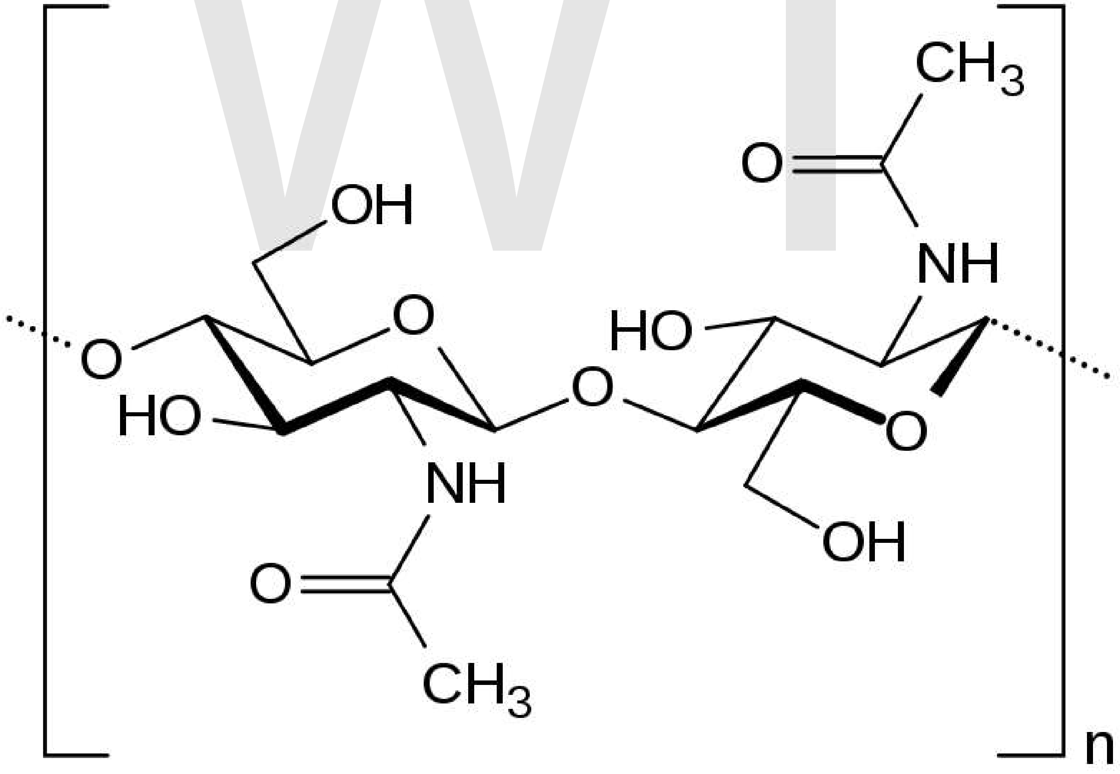
Like plants, algae have cell walls. Algal cell walls contain either polysaccharides (such as cellulose (a glucan)) or a variety of glycoproteins (Volvocales) or both. The inclusion of additional polysaccharides in algal cells walls is used as a feature for algal taxonomy.

- 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

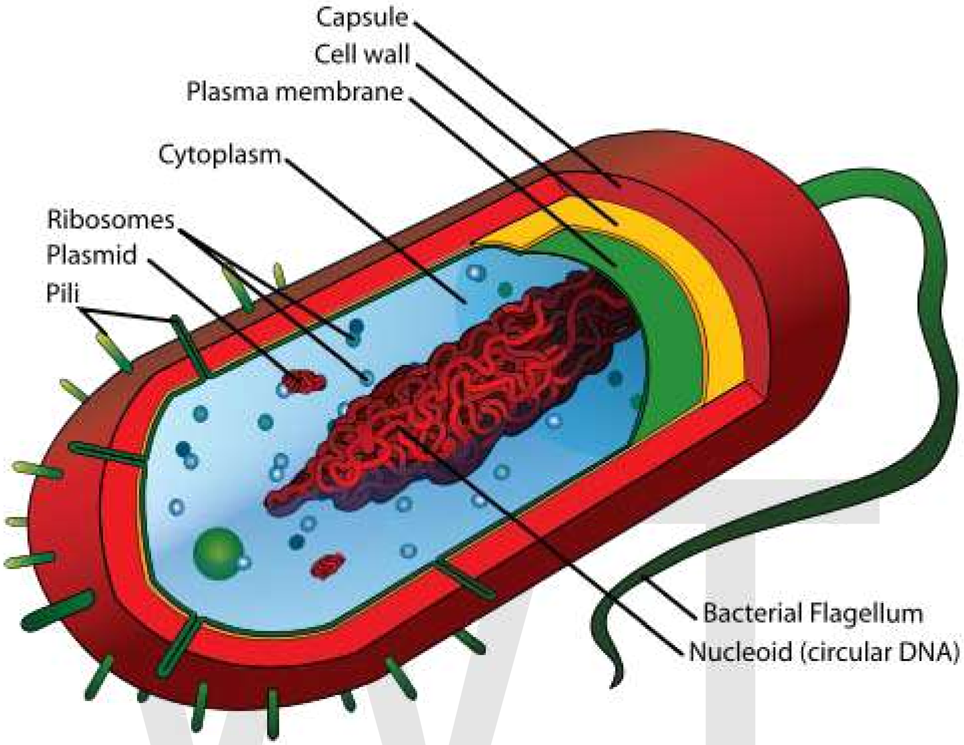
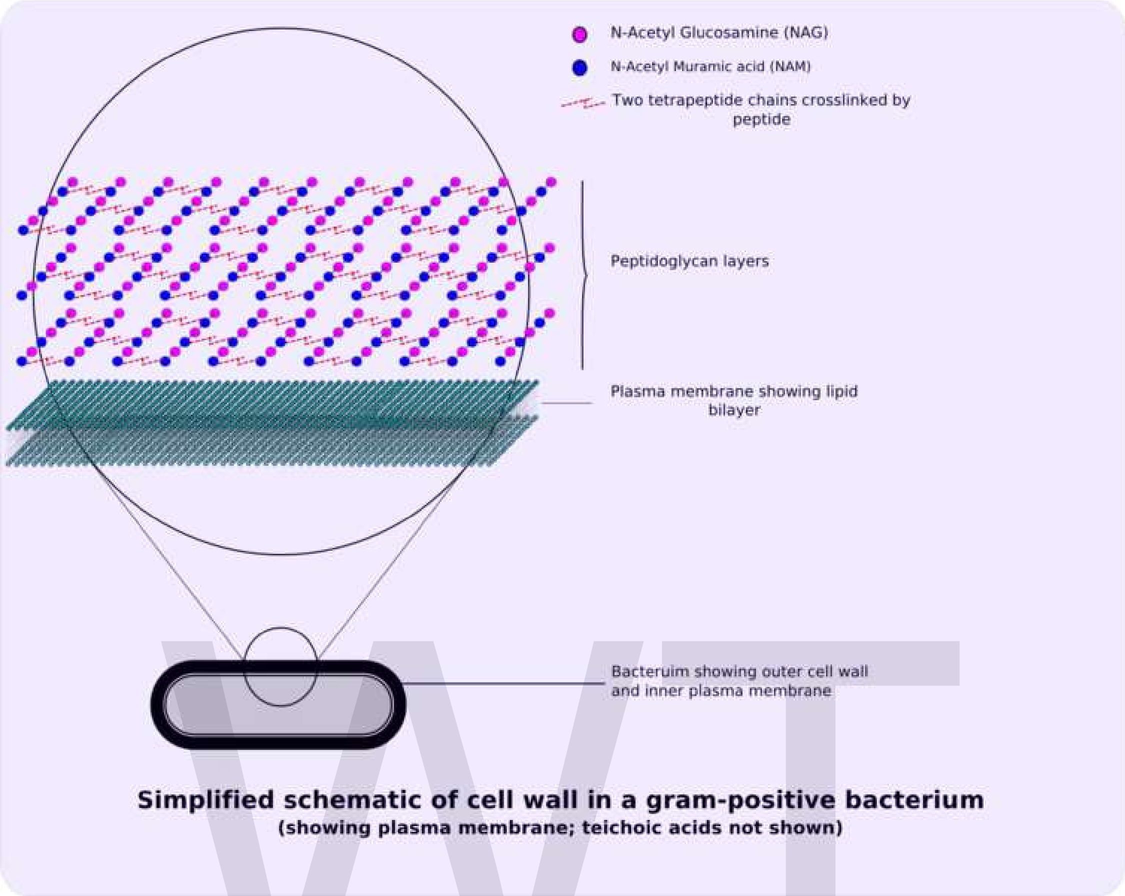


Diagram of a typical gram-negative bacterium, with the thin cell wall sandwiched between the red outer membrane and the thin green plasma membrane



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.

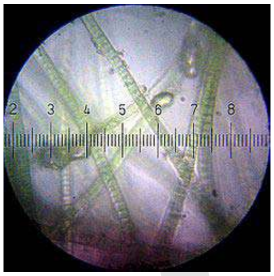
A third type of wall among the Archaea consists of glycoprotein, and occurs in the hyperthermophiles, *Halobacterium*, and some methanogens. In *Halobacterium*, the proteins in the wall have a high content of acidic amino acids, giving the wall an overall negative charge. The result is an unstable structure 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 11

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.

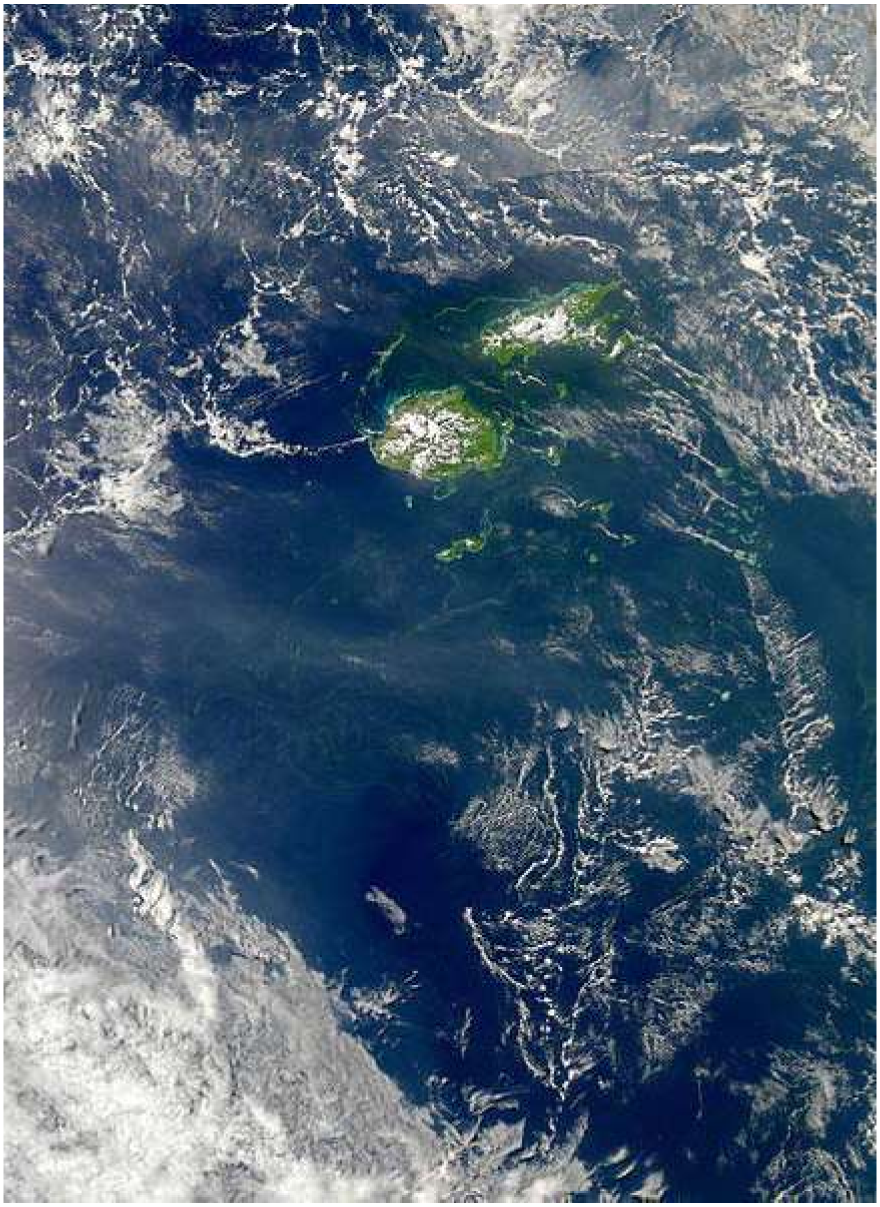
> Cyanobacteria are arguably the most successful group of microorganisms on earth. They are the most genetically diverse; they occupy a broad range of habitats across all latitudes, widespread in freshwater, marine and terrestrial ecosystems, and they are found in the most extreme niches such as hot 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.