The Microbial World

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The Origin, Evolution and Classification of Microbial Life

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Opalescent Pool in Yellowstone National Park, Wyoming USA. Conditions for life in this environment are similar to Earth over 2 billion years ago. In these types of hot springs, the orange, yellow and brown colors are due to pigmented photosynthetic bacteria which make up the microbial mats. The mats are literally teeming with microbes. Some of these bacteria such as Synechococcus conduct oxygenic photosynthesis, while others, such as Chloroflexus, conduct anoxygenic photosynthesis. Other non-photosynthetic bacteria, as well as thermophilic and acidophilic Archaea, are also residents of the hot spring community.

THE ORIGIN OF CELLULAR LIFE

When life arose on Earth about 4 billion years ago, the first types of cells to evolve were procaryotic cells. For approximately 2 billion years, procaryotic-type cells were the only form of life on Earth. The oldest known sedimentary rocks found in Greenland are about 3.8 billion years old. The oldest known fossils are procaryotic cells, 3.5 billion years in age, found in Western Australia and South Africa. The nature of these fossils, and the chemical composition of the rocks in which they are found, indicates that these first cells made use of simple chemical reactions to produce energy for their metabolism and growth.

The primitive earth's atmospheric gases, such as ammonia (NH₃), hydrogen (H₂) and hydrogen sulfide (H₂S) could be oxidized to produce energy that allowed conversion of CO₂ to cellular (organic) material.
As organic material developed, it became the substrate to support the growth and metabolism of other cells that use simple organic compounds as their source of energy. The use of inorganic chemicals as a source of energy is called **chemolithotrophy**; the use of organic chemicals as energy sources is called **chemoheterotrophy**. Thus, chemolithotrophy and chemoheterotrophy, were the first two types of metabolism to evolve. An important group of archaea that were involved in this process were the **methanogens**, which grow by using H$_2$ as an energy source and CO$_2$ as a carbon source, resulting in the production of the simplest of all organic molecules, methane (CH$_4$). Archaea and bacteria probably arose from a universal ancestor but are thought have split early during the evolution of cellular life into the two groups of procaryotes that we recognize today.

**Photosynthesis** (metabolism which uses of light as an energy source) developed in bacteria about 3.2 billion years ago. The first type of photosynthesis to appear is called **anoxygenic photosynthesis** because it does not produce O$_2$. Anoxygenic photosynthesis preceded **oxygenic photosynthesis** (plant-type photosynthesis, which produces atmospheric O$_2$) by half a billion years. However, oxygenic photosynthesis also arose in procaryotes, specifically in a group of bacteria called **cyanobacteria**, and existed for millions of years before the evolution of plants.

As molecular oxygen (O$_2$) began to appear in the atmosphere, organisms that could use O$_2$ for respiration began their evolution, and "aerobic" respiration became a prevalent form of metabolism among bacteria and some archaea. A time scale for major events in evolution of the first (procaryotic) cells is given in Table 1 below.

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**Table 1. Timescale for some major events in procaryotic evolution.** Battistuzzi, et al. MC Evol Biol. 2004. 4: 44

<table>
<thead>
<tr>
<th>Event</th>
<th>Approximate Time (Ga)</th>
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<tr>
<td>Origin of life</td>
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<tr>
<td>Origin of methanogenesis</td>
<td>3.8 - 4.1 Ga</td>
</tr>
<tr>
<td>Origin of phototrophy</td>
<td>prior to 3.2 Ga</td>
</tr>
<tr>
<td>Divergence of the major groups of Archaea</td>
<td>3.1 - 4.1 Ga</td>
</tr>
<tr>
<td>Origin of anaerobic methanotrophy</td>
<td>after 3.1 Ga</td>
</tr>
<tr>
<td>Colonization of land</td>
<td>2.8 - 3.1 Ga</td>
</tr>
<tr>
<td>Divergence of the major groups of Bacteria</td>
<td>2.5 - 3.2 Ga</td>
</tr>
<tr>
<td>Origin of aerobic methanotrophy</td>
<td>2.5 - 2.8 Ga</td>
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Eucaryotic cells evolved into being between 1.5 and 2 billion years ago. Eucaryotic cells appear to have arisen from procaryotic cells, specifically out of the Archaea. Indeed, there are many similarities in molecular biology of contemporary archaea and eucaryotes. However, the origin of the eucaryotic organelles, specifically chloroplasts and mitochondria, is explained by evolutionary associations between primitive nucleated cells and certain respiratory and photosynthetic bacteria, which led to the development of these organelles and the associated explosion of eucaryotic diversity.

**Endosymbiosis**

**Endosymbiosis** is the name given to processes wherein one cell lives inside of another cell in a mutualistic fashion. There are many examples of endosymbiosis in the microbial world, usually involving a smaller procaryotic cell living within the cytoplasm of a eucaryotic cell (see [Endosymbiosis.html](#)). Endosymbiotic events between eucaryotic and procaryotic cells has been taking place since the origin of the eucaryotic cell. It is an endosymbiosis between early eucaryotes and bacterial cells that has given rise to eucaryotic chloroplasts and mitochondria as stated above. In fact, possibly all eucaryotic membranous structures may have arisen from procaryotic cells through independent processes of endosymbiosis.
About 1.5 -2 billion years ago, oxygenic photosynthesis and aerobic respiration were predominant types of metabolism in the bacteria. Cyanobacteria produced all of the earth's atmospheric O$_2$, and respiratory bacteria had developed sophisticated membrane systems allowing them to reduce O$_2$ and generate relatively large amounts of energy. If these procaryotes invaded or were captured by primitive eucaryotic cells, which had only sluggish modes of chemoheterotrophic metabolism, they could provide new ways to produce energy from light or during aerobic respiration. In return, the eucaryotic cell could provide nutrients and a protected habitat for its invader or prey. Hence, the two organisms were able to enter into a mutually beneficial and stable relationship, and thus, microbiologists believe that the origin of eucaryotic chloroplasts (organelles for photosynthesis) and mitochondria (organelles for aerobic respiration) are in cyanobacteria and respiratory bacteria that entered into a partnership with eucaryotic cells in the evolutionary past.

If mitochondria and chloroplasts are evolutionary remnants of bacteria, there ought to be some similarities between contemporary eucaryotic organelles and the bacteria from which they arose, and indeed, there are. Mitochondria and chloroplasts are membrane-enclosed structures, the size of procaryotes, that arise from pre-existing structures. They contain their own genome (DNA) and ribosomes, both of which have a bacterial configuration and function. They synthesize their own proteins in the same way as bacteria. Chloroplasts have the same type of chlorophyll, enzymes, and metabolism as cyanobacteria, and mitochondria have the same type of metabolism as respiratory bacteria such as *Pseudomonas*. and other "proteobacteria". Interestingly, on the basis of RNA analysis, the closest relatives of mitochondria are the rickettsia bacteria, which are modern-day intracellular parasites of eucaryotic cells!

For more about endosymbiosis see Kimball's biology page [Endosymbiosis](#).

**Structure of eucaryotic and procaryotic cells**

It is appropriate to review the structure of eucaryotic and procaryotic cells now that we have an idea of how and when they evolved as distinct types of cells. Then we will look at the classification schemes that have
attempted to organize the microbial forms of life in ways that demonstrate their origin and apparent evolutionary relationships.

Procaryotic organisms (archaea and bacteria) and eucaryotic organisms (both unicellular and multicellular forms) have evolved as two distinct types of cells, differing fundamentally in their cell structure. Eucaryotes always contain a membrane-enclosed nucleus, multiple chromosomes, and various other membranous organelles, such as mitochondria, chloroplasts, the golgi apparatus, vacuoles, etc. Procaryotic cells are typically much smaller in size and never contain a nuclear membrane around their genetic material. The fundamental differences between eucaryotic and procaryotic cells, as well as the similarities and differences between eucaryotes, bacteria and archaea, are evidenced by their nuclear organization, their cell wall, cell membrane and ribosome structure, and their modes of protein synthesis, as shown in Figure 2 and Table 2 below.

Figure 2. (above) The structure of a typical procaryotic cell, in this case, a Gram-negative bacterium, compared with (below) a typical eucaryotic cell (plant cell). The procaryote is about 1 micrometer in diameter and about the size of the eucaryotic chloroplast or mitochondrion. Drawings by Vaike Haas, University of Wisconsin-Madison.
Table 2. Phenotypic properties of Bacteria and Archaea compared with Eucarya.

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<th>Biological Domain</th>
<th>Archaea</th>
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<tr>
<td>Cell configuration</td>
<td>eucaryotic</td>
<td>procaryotic</td>
<td>procaryotic</td>
</tr>
<tr>
<td>Nuclear membrane</td>
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<td>absent</td>
<td>absent</td>
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<tr>
<td>Number of chromosomes</td>
<td>&gt;1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Chromosome topology</td>
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<td>circular</td>
<td>circular</td>
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<tr>
<td>Murein in cell wall</td>
<td>-</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Cell membrane lipids</td>
<td>ester-linked glycerides; unbranched; polyunsaturated</td>
<td>ester-linked glycerides; unbranched; saturated or monounsaturated</td>
<td>ether-linked branched; saturated</td>
</tr>
<tr>
<td>Cell membrane sterols</td>
<td>present</td>
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<td>absent</td>
</tr>
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<td>Organelles (mitochondria and chloroplasts)</td>
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<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Ribosome size</td>
<td>80S (cytoplasmic)</td>
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<td>70S</td>
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<tr>
<td>Cytoplasmic streaming</td>
<td>+</td>
<td>-</td>
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<td>present</td>
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<tr>
<td>Transcription and translation coupled</td>
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<td>+</td>
<td>+</td>
</tr>
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<td>Amino acid initiating protein synthesis</td>
<td>methionine</td>
<td>N-formyl methionine</td>
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<td>Protein synthesis inhibited by streptomycin and chloramphenicol</td>
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TAXONOMY AND CLASSIFICATION OF MICROBES

Three Kingdom System (1866)
Haeckel (1866), a Swiss naturalist, was the first to create a natural kingdom for the microbes, which had been discovered nearly two centuries before by Antony van Leeuwenhoek. Haeckel placed all unicellular (microscopic) organisms in a new kingdom, "Protista", on the level with the existing kingdoms for plants (Plantae) and animals (Animalia), which are multicellular (macroscopic) organisms.

Figure 3. Haeckel's 3-Kingdom system for the classification of life. Haeckel separated life into three kingdoms and rooted them as a "tree of life". What seemed the most primitive forms of life were closest to the main trunk of the tree, and what seemed the most advanced forms are at the tips of the branches. Also, in keeping with the Darwinian ideas of the day, Haeckel supposed that simpler forms of life lead to more advanced or complicated forms of life. All of the microscopic forms of life are landed in the Protista, and low among the first branches of the Protista are microbial groups that are still recognized today, including bacteria, algae and protozoa.

Four Kingdom System (circa 1950)
The development of the electron microscope in the 1950's revealed a fundamental dichotomy among Haeckel's "Protista": some cells contained a membrane-enclosed nucleus, and some cells lacked this intracellular compartment. The latter were temporarily shifted to a fourth kingdom, Monera (or Moneres), the procaryotes (also called Procaryotae). Protista remained as a kingdom of unicellular eucaryotic microorganisms.

**Five Kingdom System (1967)**

Whittaker, a botanist at the University of California, refined the system into five kingdoms in 1967, by identifying the Fungi as a separate multicellular eucaryotic kingdom of organisms, distinguished by their absorptive mode of nutrition.

![Whittaker's phylogenetic Tree of 1967.](image)

*Figure 4. Whittaker's phylogenetic Tree of 1967. The 5-Kingdom system is based on three levels of organization- procaryotic (Kingdom Monera), eucaryotic unicellular (Kingdom Protista), and eucaryotic multicellular (Kingdoms Plantae, Fungi and Animalia). At the microbial levels there is divergence in relation to principal modes of nutrition - photosynthetic, absorptive and ingestive. Ingestive nutrition is lacking in Monera, but the three modes are continuous along numerous evolutionary lines in Protista giving rise to the three higher Kingdoms of Plantae, Fungi and Animalia. Note that the tree is rooted in the Procaryotes (Monera) and that the more distant an organism is removed from the root, the more highly (and recently) evolved is the organism.*
Carl Woese's Three Domain System (1988)

In the late 1970s, Carl Woese, at the University of Illinois, began phylogenetic analysis of all forms of cellular life based on comparison of nucleotide sequences of the small subunit ribosomal RNA (ssrRNA) that is contained in all organisms. Woese considered other conserved molecules in cells including certain proteins, and conserved genes (DNA), but settled for the ssrRNA for a number of reasons.

1. rRNA is found in all cells.
2. rRNA is present in thousands of copies and is easy to isolate from cells
3. rRNA can be analyzed to determine the exact sequence of nucleotide bases in its makeup.
4. The sequence of bases in RNA is a complementary COPY of the sequence of bases in the gene (DNA) that encodes for RNA.
5. Base sequences in different rRNA molecules can be compared by computer analyses and statistical methods to reveal precise similarities and differences in cellular genomes.

Woese's analysis of RNA molecules from different types of cells revealed a new dichotomy, this time among the procaryotes. There exist two types of procaryotes, as fundamentally unrelated to one another as they are to eucaryotes. Thus, Woese defined three cellular domains of life as they are displayed in Figure 5 (below): Eukaryotes, Eubacteria and Archaeabacteria. Whittaker's Plant, Animal and Fungi kingdoms (all of the multicellular eucaryotes) are at branch tips of the Eukaryote Domain, while other eukaryote branches lead to protists (unicellular algae and protozoa).

Figure 4. Carl Woese's "universal" phylogenetic tree of 1988 determined from ribosomal RNA sequence comparisons. Note the three major domains of living organisms: The Eubacteria (Bacteria), the Archaeabacteria (Archaea) and the Eukaryotes.
(Eucarya). The evolutionary distance between two groups of organisms is proportional to the cumulative distance between the end of the branch and the node that joins the two groups. Compare with the Pace Tree, Figure 5 below.

Although the definitive difference between Woese's Archaea and Bacteria is based on fundamental differences in the nucleotide base sequence in the ssrRNA, there are many biochemical and phenotypic differences between the two groups of procaryotes as shown in Table 2 above. The phylogenetic tree indicates that Archaea are more closely related to Eucarya than are Bacteria. This relatedness seems most evident in the similarities between transcription and translation in the Archaea and the Eucarya. However, it is also evident that the Bacteria have evolved into chloroplasts and mitochondria, so that these eucaryotic organelles derive their lineage from this group of procaryotes. Perhaps the biological success of eucaryotic cells springs from the evolutionary merger of the two procaryotic life forms.

The Universal Tree of Life

On the basis of small subunit ribosomal RNA (ssrRNA) analysis, the Woesean tree of life gives rise to three cellular domains of life: Archaea, Bacteria, and Eucarya (Figure 6). Bacteria (formerly known as eubacteria) and Archaea (formerly called archaebacteria) share the procaryotic type of cellular configuration, but otherwise, they are not related to one another any more closely than they are to the eucaryotic domain, Eucarya. Between the two procaryotes, Archaea are apparently more closely related to Eucarya than are the Bacteria. Eucarya consists of all eucaryotic cell-types, including protista, fungi, plants and animals.

![Figure 6. The Universal Tree of Life as derived from sequencing of ssrRNA. N. Pace. Note the three major domains of living organisms: Archaea, Bacteria and Eucarya. The "evolutionary distance" between two organisms is proportional to the measurable distance between the end of a branch to a node to the end of a comparative branch. For example, in Eucarya, humans (Homo) are more closely related to corn (Zea) than to slime molds (Dictyostelium); or in Bacteria, E. coli is more closely related to Agrobacterium than to Thermus.](image)
Notes on the Tree

It is interesting to note several features of phylogeny and evolution that are revealed in the Unrooted Tree.

- Archaea are the least evolved type of cell (they remain closest to the common point of origin). This helps explain why contemporary Archaea are inhabitants of environments that are something like the earth 3.86 billion years ago (hot, salty, acidic, anaerobic, low in organic material, etc.).

- Eucaryotes (Eucarya) are the most evolved type of cell (they move farthest from the common point of origin). However, the eucaryotes do not begin to diversify (branch) until relatively late in evolution, at a time when the Bacteria diversify into oxygenic photosynthesis (Synechococcus) and aerobic respiration (Agrobacterium).

- Mitochondria and the respiratory bacterium, Agrobacterium, are derived from a common ancestor; likewise, chloroplast and the cyanobacterium, Synechococcus, arise from a common origin. This is good evidence for the idea of evolutionary endosymbiosis, i.e., that the origin of eucaryotic mitochondria and chloroplasts is in procaryotic cells that were either captured by, or which invaded, eucaryotic cells and subsequently entered into a symbiotic association with one cell living inside of the other.

- Diversification in Eucarya is mainly within the Protista (unicellular protozoa, algae). The only multicellular eucaryotes on the Tree are Zea (plants), Homo (animals) and some fungi. Since the protists, along with the archaea and bacteria, constitute the microbial (“microorganismal”) community of the planet, this helps to substantiate the claim that microorganisms are the predominant and most diverse form of life on Earth.

- Humans (Homo) are more closely related to yeast (Saccharomyces) than the are to corn (Zea). There are more genetic differences between E. coli and Bacillus than there are between humans and a paramecium. The protozoan Trichomonas is more closely related to the archaea than it is to fellow protozoan, Trypanosoma. When the tree branches are amplified there many other surprising relationships to biologists.

- Most biology and anthropology students have been presented with fossil and other structural evidence that humans (Homo) emerged a very short time ago on the evolutionary clock. The Tree confirms this evidence on the basis of comparative molecular genetic analysis.

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TAXONOMY AND CLASSIFICATION OF PROCARYOTES

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In the 1980's, Woese began phylogenetic analysis of all forms of cellular life based on comparative sequencing of the small subunit ribosomal RNA (ssrRNA) that is contained in all organisms. A new dichotomy was revealed, this time among the procaryotes: there existed two types of procaryotes, as

Figure 9 (above) The structure of a typical procaryotic cell, in this case, a Gram-negative bacterium, compared with (below) a typical eucaryotic cell (plant cell). The procaryote is about 1 micrometer in diameter and about the size of the eucaryotic chloroplast or mitochondrion. Drawings by Vaike Haas, University of Wisconsin-Madison.
fundamentally unrelated to one another as they are to eucaryotes. Thus, Woese defined the three cellular Domains of life as they are displayed in Figure 3 (above): Eucarya, Bacteria and Archaea. Whittaker's Plant, Animal and Fungal Kingdoms (all of the multicellular eucaryotes) are at the end of a very small branch of the tree of life, and all other branches lead to microorganisms, either procaryotes (Bacteria and Archaea), or protists (unicellular algae and protozoa), thus establishing clearly that microbial life is the predominant form of life on the planet.

Sequence analysis of macromolecules such as the small subunit ribosomal RNA found in all cells has allowed bacteriologists to classify bacteria into a typical hierarchal scheme based on genetic relatedness. The current edition (2001) of Bergey's Manual of Systematic Bacteriology has established 24 phyla of bacteria, systematically ordered into class, order, family, genus and species. For example, *E. coli* is in the Domain Bacteria, Phylum Proteobacteria, Class Gamma Proteobacteria, Order Enterobacteriales, Family Enterobacteriaceae, Genus Escherichia, Species *E. coli*. You can download Bergey's 400-page taxonomic outline of the procaryotes at Bergey's Manual of Systematic Bacteriology 2nd ed (2001), or you can back in to a taxonomic outline of bacteria in Wikipedia by looking up the scientific name of any well-known bacterium and viewing the right-hand frame, Scientific classification.

Although the definitive difference between Woese's Archaea and Bacteria is based on fundamental differences in the nucleotide base sequence in the 16S ribosomal RNA, there are many biochemical and phenotypic differences between the two groups of procaryotes. (Table 1). The phylogenetic tree indicates that Archaea are more closely related to Eucarya than are Bacteria. This relatedness seems most evident in the similarities between transcription and translation in the Archaea and the Eucarya. However, it is also evident that the Bacteria have evolved into chloroplasts and mitochondria, so that these eucaryotic organelles derive their lineage from this group of procaryotes. Perhaps the biological success of eucaryotic cells springs from the evolutionary merger of the two procaryotic life forms.

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**IDENTIFICATION OF BACTERIA**
Classic Methods

The criteria used for microscopic identification of procaryotes include cell shape and grouping, Gram-stain reaction, and motility. Bacterial cells almost invariably take one of three forms: rod (bacillus), sphere (coccus), or spiral (spirilla and spirochetes). Rods that are curved are called vibrios. Fixed bacterial cells stain either Gram-positive (purple) or Gram-negative (pink); motility is easily determined by observing living specimens. Bacilli may occur singly or form chains of cells; cocci may form chains (streptococci) or grape-like clusters (staphylococci); spiral shape cells are almost always motile; cocci are almost never motile. This nomenclature ignores the actinomycetes, a prominent group of branched bacteria which occur in the soil. But they are easily recognized by their colonies and their microscopic appearance.

Such easily-made microscopic observations, combined with knowing the natural environment of the organism, are important aids to identify the group, if not the exact genus, of a bacterium - providing, of course, that one has an effective key. Such a key is Bergey's Manual of Determinative Bacteriology 9th ed, the "field guide" to identification of the bacteria. Bergey's Manual describes affiliated groups of Bacteria and Archaea based on a few easily observed microscopic and physiologic characteristics. Further identification requires biochemical tests which will distinguish genera among families and species among genera. Strains within a single species are usually distinguished by genetic or immunological criteria.
Molecular Techniques

The sciences of genomics and bioinformatics have led to a radical reclassification of procaryotes based on comparative analysis of organismal DNA. **Genomics** involves the study of all of the nucleotide sequences, including structural genes, regulatory sequences, and noncoding DNA segments, in the chromosomes of an organism. To date over 200 bacterial genomes have been sequenced. We have seen how highly conserved genetic sequences, such as those that encode for the small subunit ribosomal RNAs (16S rRNA) of an organism, can be analyzed to specifically relate two organisms. So can the identification of certain genes provide information about specific properties of an organism, and analysis of specific nucleotide sequences may be used to indicate identity and degrees of genetic relatedness among organisms.

The newest editions of Bergey's Manual are adapted to the new phylogenetic classification. This has resulted in the formation of several new taxa of bacteria and archaea at every hierarchical level. Occasionally, organisms thought to be more or less distantly related become unified; but more likely, organisms thought to be closely-related due to similar phenotypic properties are found to be genetically distinct and warrant separation into a new taxa.

**Metagenomics.** Sequencing of 16S rRNA genes obtained from environmental samples produces a broad profile of microbial diversity and reveals that the vast majority of microbes present have been missed by reliance on cultivation-based methods. This observation has given rise to the field of metagenomics. Metagenomics (also called environmental genomics) is the application of modern genomics techniques to the study of communities of microorganisms directly in their natural environments, bypassing the need for isolation and lab cultivation of individual species. Metagenomics provides a means to identify and quantify microbes from environmental samples based on the presence of distinctive genes. This enables studies of organisms that are not easily cultured in the laboratory, as well as studies of organisms in their natural environment.

"Shotgun" metagenomics is capable of sequencing nearly complete microbial genomes directly from the environment. Because the collection of DNA from an environment is largely uncontrolled, the most abundant organisms in a sample are most highly represented in the resulting sequence data. To achieve the high coverage needed to fully resolve the genomes of underrepresented community members, large samples,
Shotgun sequencing and screens of clone libraries reveal genes present in environmental samples. This provides information both on which organisms are present and what metabolic processes are possible in the community. This can be helpful in understanding the ecology of a community, particularly if multiple samples are compared to one other.

**BACTERIAL REPRODUCTION AND GENETICS**

Most bacteria reproduce by a relatively simple asexual process called **binary fission**: each cell increases in size and divides into two cells. During this process there is an orderly increase in cellular structures and components, replication and segregation of the bacterial DNA, followed by formation of a **septum** or cross wall which divides the cell into two. The process is evidently coordinated by activities associated with the cell membrane. The DNA molecule is believed to be attached to a point on the membrane where it is replicated. The two DNA molecules remain attached at points side-by-side on the membrane while new membrane material is synthesized between the two points. This draws the DNA molecules in opposite directions while new cell wall and membrane are laid down as a septum between the two chromosomal compartments. When septum formation is complete the cell splits into two progeny cells. The time interval required for a bacterial cell to divide or for a population of cells to double is called the **generation time**. Generation times for bacterial species growing in nature may be as short as 15 minutes or as long as several days.

Figure 13. A pair of dividing streptococci. The chromosome has been replicated and is partially segregated as septum
Genetic Exchange in Bacteria

Although procaryotes do not undergo sexual reproduction, they are not without the ability to exchange genes and undergo genetic recombination. Bacteria are known to exchange genes in nature by three fundamental processes: conjugation, transduction and transformation. Conjugation requires cell-to-cell contact for DNA to be transferred from a donor to a recipient. During transduction, a virus transfers the genes between mating bacteria. In transformation, DNA is acquired directly from the environment, having been released from another cell. Genetic recombination can follow the transfer of DNA from one cell to another leading to the emergence of a new genotype (recombinant). It is common for DNA to be transferred as plasmids between mating bacteria. Since bacteria usually develop their genes for drug resistance on plasmids (called resistance transfer factors, or RTFs), they are able to spread drug resistance to other strains and species during genetic exchange processes. The genetic engineering of bacterial cells in the research or biotechnology laboratory is often based on the use of plasmids as vectors. The genetic systems of the Archaea are poorly characterized at this point, although the entire genome of Methanosarcina has been sequenced which opens up the possibilities for genetic analysis of the group.

Evolution of Bacteria and Archaea

For most procaryotes, mutation is a major source of variability that allows the species to adapt to new conditions. The mutation rate for most procaryotic genes is in the neighborhood of $10^{-8}$. This means that if a bacterial population doubles from $10^8$ cells to $2 \times 10^8$ cells, there is likely to be a mutant present for any given gene. Since procaryotes grow to reach population densities far in excess of $10^9$ cells, such a mutant could develop from a single generation during 15 minutes of growth. The evolution of procaryotes, driven by such Darwinian principles of evolution (mutation and selection) is called vertical evolution.

However, as a result of the processes of genetic exchange described above, the bacteria and archaea can also undergo a process of horizontal evolution, also called horizontal gene transfer (HGT). In this case, genes are transferred laterally from one organism to another, including between members of different Kingdoms, which allows the recipient to experiment with a new genetic trait. Horizontal gene transfer is becoming realized to be a significant force in driving cellular evolution.

The combined effects of fast growth rates, high concentrations of cells, genetic processes of mutation and selection, and the ability to exchange genes, account for the extraordinary rates of adaptation and evolution that can be observed in the procaryotes.

ECOLOGY OF BACTERIA AND ARCHAEA

Bacteria and Archaea are present in all environments that support life. They may be free-living, or living in associations with "higher forms" of life (plants and animals), and they are found in environments that support no other form of life. Procaryotes have the usual nutritional requirements for growth of cells, but many of the ways that they utilize and transform their nutrients are unique. This bears directly on their habitat and their ecology.

Nutritional Types of Organisms

In terms of carbon utilization a cell may be heterotrophic or autotrophic. Heterotrophs obtain their carbon and energy for growth from organic compounds in nature. Autotrophs use $\text{CO}_2$ as a sole source of carbon for growth and obtain their energy from light (e.g. photoautotrophs) or from the oxidation of inorganic compounds.
compounds (e.g. lithoautotrophs).

Most heterotrophic bacteria are saprophytes, meaning that they obtain their nourishment from dead organic matter. In the soil, saprophytic bacteria and fungi are responsible for biodegradation of organic material. Ultimately, organic molecules, no matter how complex, can be degraded to CO$_2$ (plus H$_2$ and H$_2$O). Probably no naturally-occurring organic substance cannot be degraded by the combined activities of the bacteria and fungi. Hence, most organic matter in nature is converted by heterotrophs to CO$_2$, only to be converted back into organic material by autotrophs that die and nourish heterotrophs to complete the carbon cycle.

Lithotrophic procaryotes have a type of energy-producing metabolism which is unique. Lithotrophs (also called lithoautotrophs or chemoautotrophs) use inorganic compounds as sources of energy, i.e., they oxidize compounds such as H$_2$ or H$_2$S or NH$_3$ to obtain electrons to feed into an electron transport system and to produce ATP. Lithotrophs are found in soil and aquatic environments wherever their energy source is present. Most lithotrophs are autotrophs so they can grow in the absence of any organic material. Lithotrophic species are found among the Bacteria and the Archaea. Sulfur-oxidizing lithotrophs convert H$_2$S to S$^\circ$ and S$^\circ$ to SO$_4$. Nitrifying bacteria convert NH$_3$ to NO$_2$ and NO$_2$ to NO$_3$; methanogenic archaea strip electrons off of H$_2$ as a source of energy and add them to CO$_2$ to form CH$_4$ (methane). Lithotrophs have an obvious impact on the sulfur, nitrogen and carbon cycles in the biosphere.

Photosynthetic bacteria convert light energy into chemical energy for growth. Most phototrophic bacteria are autotrophs so their role in the carbon cycle is analogous to that of plants. The planktonic cyanobacteria are the "grass of the sea" and their form of oxygenic photosynthesis generates a substantial amount of O$_2$ in the biosphere. However, among the photosynthetic bacteria are types of photosynthetic metabolism not seen in eucaryotes, including photoheterotrophy (using light as an energy source while assimilating organic compounds as a source of carbon), anoxygenic photosynthesis, and unique mechanisms of CO$_2$ fixation (autotrophy).

Photosynthesis has not been found to occur among the Archaea, but one archaeal species employs a light-driven non photosynthetic means of energy generation based on the use of a chromophore called bacteriorhodopsin.

Adaptations to Environmental Conditions

Most procaryotes, whether they have been cultured and studied in the laboratory, or observed growing in their natural habitats, seem to be highly adapted to their specific environment by means of their macromolecular structure and/or their physiologic (metabolic) capabilities. The nutritional quality of the environment determines whether a particular organism will be present, but so do various physical parameters such as the availability of light and O$_2$, as well as the pH, temperature and salinity of the environment. As examples, the range of procaryotic responses to oxygen and temperature are discussed below.

Procaryotes vary widely in their response to O$_2$ (molecular oxygen). Organisms that require O$_2$ for growth are called obligate aerobes; those which are inhibited or killed by O$_2$, and which grow only in its absence, are called obligate anaerobes; organisms which grow either in the presence or absence of O$_2$ are called facultative anaerobes. Whether or not a particular organism can exist in the presence of O$_2$ depends upon the distribution of certain enzymes such as superoxide dismutase and catalase that are required to detoxify lethal oxygen radicals that are always generated by living systems in the presence of O$_2$

Procaryotes also vary widely in their response to temperature. Those that live at very cold temperatures (0
degrees or lower) are called **psychrophiles**; those which flourish at room temperature (25 degrees) or at the temperature of warm-blooded animals (37 degrees) are called **mesophiles**; those that live at high temperatures (greater than 45 degrees) are **thermophiles**. The only limit that seems to be placed on growth of certain procaryotes in nature relative to temperature is whether liquid water exists. Hence, growing procaryotic cells can be found in supercooled environments (ice does not form) as low as -20 degrees and superheated environments (steam does not form) as high as 120 degrees. Archaea have been detected around thermal vents on the ocean floor where the temperature is as high as 320 degrees!

**Symbiosis**

The biomass of procaryotic cells in the biosphere, their metabolic diversity, and their persistence in all habitats that support life, ensures that these microbe will play a crucial role in the cycles of elements and the functioning of the world ecosystem. However, the procaryotes affect the world ecology in another significant way through their inevitable interactions with insects, plants and animals. Some bacteria are required to associate with insects, animals or plants for the latter to survive. For example, the sex of offspring of certain insects is determined by endosymbiotic bacteria. Ruminant animals (cows, sheep, etc.), whose diet is mainly cellulose (plant material), must have cellulose-digesting bacteria in their intestine to convert the cellulose to a form of carbon that the animal can assimilate. Leguminous plants grow poorly in nitrogen-deprived soils unless they are colonized by nitrogen-fixing bacteria which can supply them with a biologically-useful form of nitrogen.

**Bacterial Pathogenicity**

Some bacteria are **parasites** of plants or animals, meaning that they grow at the expense of their eucaryotic host and may damage, harm, or even kill it in the process. Such bacteria that cause disease in plants or animals are **pathogens**. Human diseases caused by bacterial pathogens include tuberculosis, whooping cough, diphtheria, tetanus, gonorrhea, syphilis, pneumonia, cholera and typhoid fever, to name a few. The bacteria that cause these diseases have special structural or biochemical properties that determine their virulence or pathogenicity. These include: (1) ability to colonize and invade their host; (2) ability to resist or withstand the antibacterial defenses of the host; (3) ability to produce various toxic substances that damage the host. Plant diseases, likewise, may be caused by bacterial pathogens. More than 200 species of bacteria are associated with plant diseases, but a very small handful of genera are involved.

![Image](https://via.placeholder.com/150)

**Figure 14. Borrelia burgdorferi.** This spirochete is the bacterial parasite that causes Lyme disease. CDC.

**APPLICATIONS OF BACTERIA IN INDUSTRY AND BIOTECHNOLOGY**