

CHAPTER 27

PROKARYOTES AND THE ORIGINS OF METABOLIC DIVERSITY

OUTLINE

- I. The World of Prokaryotes
 - A. They're (almost) everywhere! *an overview of prokaryotic life*
 - B. Bacteria and Archaea are the two main branches of prokaryotic evolution
- II. Structure, Function, and Reproduction
 - A. Nearly all prokaryotes have cell walls external to their plasma membranes
 - B. Many prokaryotes are motile
 - C. The cellular and genomic organization of prokaryotes is fundamentally different from that of eukaryotes
 - D. Populations of prokaryotes grow and adapt rapidly
- III. Nutritional and Metabolic Diversity
 - A. Prokaryotes can be grouped into four categories according to how they obtain energy and carbon
 - B. The evolution of prokaryotic metabolism was both cause and effect of changing environments on Earth
- IV. Phylogeny of Prokaryotes
 - A. Molecular systematics is leading to a phylogenetic classification of prokaryotes
- V. Ecological Impact of Prokaryotes
 - A. Prokaryotes are indispensable links in the recycling of chemical elements in the ecosystem
 - B. Many prokaryotes are symbiotic
 - C. Humans use prokaryotes in research and technology

OBJECTIVES

After reading this chapter and attending lecture, the student should be able to:

- 1. List unique characteristics that distinguish archaea from bacteria.
- 2. Describe the three-domain system of classification and explain how it differs from previous systems.
- 3. Using a diagram or micrograph, distinguish among the three most common shapes of prokaryotes.
- 4. Describe the structure and functions of prokaryotic cell walls.
- 5. Distinguish between the structure and staining properties of gram-positive and gram-negative bacteria.
- 6. Explain why disease-causing gram-negative bacterial species are generally more pathogenic than disease-causing gram-positive bacteria.

7. Describe three mechanisms motile bacteria use to move.
8. Explain how prokaryotic flagella work and why they are not considered to be homologous to eukaryotic flagella.
9. Indicate where photosynthesis and cellular respiration take place in prokaryotic cells.
10. Explain how organization of the prokaryotic genome differs from that in eukaryotic cells.
11. Explain what is meant by geometric growth.
12. List the sources of genetic variation in prokaryotes and indicate which one is the major source.
13. Distinguish between autotrophs and heterotrophs.
14. Describe four modes of bacterial nutrition and give examples of each.
15. Distinguish among obligate aerobes, facultative anaerobes and obligate anaerobes.
16. Describe, with supporting evidence, plausible scenarios for the evolution of metabolic diversity of prokaryotes
17. Explain how molecular systematics has been used in developing a classification of prokaryotes.
18. List the three main groups of archaea, describe distinguishing features among the groups and give examples of each.
19. List the major groups of bacteria, describe their mode of nutrition, some characteristic features and representative examples.
20. Explain how endospores are formed and why endospore-forming bacteria are important to the food-canning industry.
21. Explain how the presence of *E. coli* in public water supplies can be used as an indicator of water quality.
22. State which organism is responsible for the most common sexually transmitted disease in the United States.
23. Describe how mycoplasmas are unique from other prokaryotes.
24. Explain why all life on earth depends upon the metabolic diversity of prokaryotes.
25. Distinguish among mutualism, commensalism and parasitism.
26. List Koch's postulates that are used to substantiate a specific pathogen as the cause of a disease.
27. Distinguish between exotoxins and endotoxins.
28. Describe how humans exploit the metabolic diversity of prokaryotes for scientific and commercial purposes.
29. Describe how *Streptomyces* can be used commercially.

KEY TERMS

| | | | |
|-----------------|-------------------|-----------------------|-------------------|
| bacteria | nucleoid region | parasites | decomposers |
| archaea | binary fission | nitrogen fixation | symbiosis |
| domains | transformation | obligate aerobes | symbionts |
| domain Archaea | conjugation | facultative anaerobes | host |
| domain Bacteria | transduction | obligate anaerobes | mutualism |
| peptidoglycan | endospores | anaerobic respiration | commensalism |
| Gram stain | antibiotics | bacteriorhodopsin | parasitism |
| gram-positive | photoautotrophs | cyanobacteria | parasite |
| gram-negative | chemoautotrophs | signature sequences | Koch's postulates |
| capsule | photoheterotrophs | methanogens | exotoxins |

| | | | |
|---------------------|-------------------|----------------------|------------|
| pili (sing., pilus) | chemoheterotrophs | extreme halophiles | endotoxins |
| taxi | saprobies | extreme thermophiles | |

LECTURE NOTES

Appearing about 3.5 billion years ago, prokaryotes were the earliest living organisms and the only forms of life for 2 billion years.

I. The World of Prokaryotes

A. They're (almost) everywhere! *an overview of prokaryotic life*

Prokaryotes dominate the biosphere; they are the most numerous organisms and can be found in all habitats.

- Approximately 4000 species are currently recognized, however, estimates of the actual diversity range from 400,000 – 4 million species
- They are structurally and metabolically diverse.

Prokaryotic cells differ from eukaryotic cells in several ways:

- Prokaryotes are smaller and lack membrane-bound organelles.
- Prokaryotes have cell walls but the composition and structure differ from those found in plants, fungi and protists.
- Prokaryotes have simpler genomes. They also differ in genetic replication, protein synthesis, and recombination.

Prokaryotes, while very small, have a tremendous impact on the Earth.

- A small percentage cause disease.
- Some are decomposers, key organisms in life-sustaining chemical cycles.
- Many form symbiotic relationships with other prokaryotes and eukaryotes. Mitochondria and chloroplasts may have evolved from such symbioses.

B. Bacteria and Archaea are the two main branches of prokaryotic evolution

The traditional five-kingdom system recognizes one kingdom of prokaryotes (Monera) and four kingdoms of eukaryotes (Protista, Plantae, Fungi, and Animalia).

- This system emphasizes the structural differences between prokaryotic and eukaryotic cells.

Recent research in systematics has resulted in questions about the placement of a group as diverse as the prokaryotes in a single kingdom. Two major branches of prokaryotic evolution have been indicated by comparing ribosomal RNA and other genetic products:

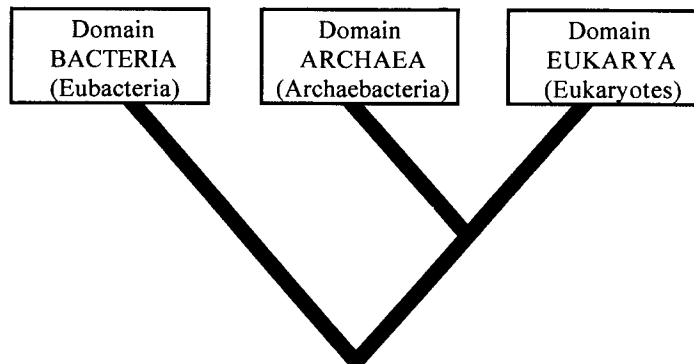
- One branch is called the Archaea (formerly archaebacteria).
 - ⇒ Believed to have evolved from the earliest cells
 - ⇒ Inhabit extreme environments which may resemble the Earth's early habitats (hot springs and salt ponds)
- The second branch is called Bacteria (formerly eubacteria).
 - ⇒ Considered the more "modern" prokaryotes, having evolved later in Earth's history
 - ⇒ More numerous than Archaea
 - ⇒ Differ from Archaea in structural, biochemical, and physiological characteristics

This recently acquired molecular data has led to new proposals for the systematic relationships of organisms.

- Initially, researchers including Carl Woese recognized the distinction between Archaea and Bacteria and proposed a six-kingdom system.

- Because the Archaea and Bacteria diverged so early in the history of life, many systematists now favor organizing life into three *domains*, a taxonomic level higher than kingdom (see Campbell, Figure 27.1).

⇒ Prokaryotes comprise two of these domains: *domain Archaea* and *domain Bacteria*.



II. Structure, Function, and Reproduction

A majority of prokaryotes are unicellular, although some aggregate into two-celled to several-celled groups. Others form true, permanent aggregates and some bacterial species have a simple multicellular form with a division of labor between specialized cells.

- Cells have a diversity of shapes, the most common being spheres (cocci), rods (bacilli), and helices (spirilla and spirochetes).
- One rod-shaped species measures 0.5 mm in length, and is the largest prokaryotic cell known (see Campbell, Figure 27.3).
- Most have diameters of 1–5µm (compared to eukaryotic diameters of 10–100µm).

A. Nearly all prokaryotes have cell walls external to their plasma membranes

A majority of prokaryotes have external cell walls that:

- Maintain the cell shape
- Protect the cell
- Prevent the cell from bursting in a hypotonic environment
- Differ in chemical composition and construction from the cell walls of protists, fungi, and plants

In bacteria, the major cell material is peptidoglycan (cellulose is the main component of plant cell walls); archaea lack peptidoglycan in their cell walls.

- *Peptidoglycan* = Modified sugar polymers cross-linked by short polypeptides
 - Exact composition varies among species.
 - Some antibiotics work by preventing formation of the cross-links in peptidoglycan, thus preventing the formation of a functional cell wall.

Gram stain = A stain used to distinguish two groups of bacteria by virtue of a structural difference in their cell walls

Gram-positive bacteria

- Have simple cell walls with large amounts of peptidoglycan
- Stain blue

Gram-negative bacteria:

- Have more complex cell walls with smaller amounts of peptidoglycan
- Have an outer lipopolysaccharide-containing membrane that covers the cell wall
- Stain pink
- Are more often disease-causing (pathogenic) than gram-positive bacteria
- Lipopolysaccharides:
 - Are often toxic and the outer membrane helps protect these bacteria from host defense systems
 - Impede entry of drugs into the cells, making gram-negative bacteria more resistant to antibiotics

Many prokaryotes also secrete sticky, gelatinous substances that form a layer outside the cell wall called a *capsule*. Capsules also aid in adhesion to other cells (to form prokaryotic aggregates or facilitate attachment to host cells).

Some prokaryotes adhere to one another and/or to a substrate by means of a surface appendage called a *pili*. Some pili are specialized for transferring DNA when bacteria conjugate (see Campbell, Figure 27.4).

B. Many prokaryotes are motile

Motile bacteria (\approx 50% of known species) use one of three mechanisms to move:

1. Flagella

- Prokaryotic flagella differ from eukaryotic flagella in that they are:
 - Unique in structure and function; prokaryotic flagella lack the "9 + 2" microtubular structure and rotate rather than whip back and forth like eukaryotic flagella
 - Not covered by an extension of the plasma membrane
 - One-tenth the width of eukaryotic flagella (see Campbell, Figure 27.5)
- Filaments, composed of chains of the protein *flagellin*, are attached to another protein hook which is inserted into the basal apparatus.
- The basal apparatus consist of 35 different proteins arranged in a system of rings which sit in the various cell wall layers.
- Their rotation is powered by the diffusion of protons into the cell. The proton gradient is maintained by an ATP-driven proton pump.

2. Filaments, which are characteristic of spirochetes, or helical-shaped bacteria

- Several filaments spiral around the cell inside the cell wall.
- Similar to prokaryotic flagella in structure, axial filaments are attached to basal motors at either end of the cell. Filaments attached at opposite ends move relative to each other, rotating the cell like a corkscrew.

3. Gliding

- Some bacteria move by gliding through a layer of slimy chemicals secreted by the organism.
- The movement may result from flagellar motors that lack flagellar filaments.

Prokaryotic movement is fairly random in homogenous environments but may become directional in a heterogenous environment.

Taxis = Movement to or away from a stimulus

- The stimulus can be light (phototaxis), a chemical (chemotaxis), or a magnetic field (magnetotaxis).

- Movement toward a stimulus is a positive taxis (e.g., positive phototaxis = toward light) while movement away from a stimulus is a negative taxis (e.g., negative phototaxis = away from light).

During taxis (directed movement), bacteria move by running and tumbling movements.

- Enabled by rotation of flagella either counterclockwise or clockwise
- Caused by flagella moving coordinately about each other (for a run), or in separate and randomized movements (for a tumble)

C. The cellular and genomic organization of prokaryotes is fundamentally different from that of eukaryotes

Prokaryotes lack the diverse internal membranes characteristic of eukaryotes. Some prokaryotes, however, do have specialized membranes, formed by invaginations of the plasma membranes (see Campbell, Figure 27.6).

- Infoldings of the plasma membrane function in the cellular respiration of aerobic bacteria.
- Cyanobacteria have thylakoid membranes that contain chlorophyll and that function in photosynthesis.

The prokaryotic genome has only 1/1000 as much DNA as the eukaryotic genome.

Genophore = The bacterial chromosome, usually one double-stranded, circular DNA molecule

- This DNA is concentrated in the *nucleoid region*, and is not surrounded by a membrane; therefore, there is no true nucleus.
- Has very little protein associated with the DNA

Many bacteria also have plasmids.

- *Plasmid* = Smaller rings of DNA having supplemental (usually not essential) genes for functions such as antibiotic resistance or metabolism of unusual nutrients
 - Replicate independently of the genophore
 - Can be transferred between partners during conjugation

While prokaryotic and eukaryotic DNA replication and translation are similar, there are some differences. For example,

- Bacterial ribosomes are smaller and have different protein and RNA content than eukaryotic ribosomes.
 - ⇒ This difference permits some antibiotics (e.g., tetracycline) to block bacterial protein synthesis while not inhibiting the process in eukaryotic cells.

D. Populations of prokaryotes grow and adapt rapidly

Neither mitosis nor meiosis occur in the prokaryotes.

- Reproduction is asexual by *binary fission*.
- DNA synthesis is almost continuous.

Although meiosis and syngamy do not occur in prokaryotes, genetic recombination can take place through three mechanisms that transfer variable amounts of DNA:

- *Transformation* = The process by which external DNA is incorporated by bacterial cells
- *Conjugation* = The direct transfer of genes from one bacterium to another
- *Transduction* = The transfer of genes between bacteria by viruses

Growth in the numbers of cells is geometric in an environment with unlimited resources.

- Generation time is usually one to three hours, although it can be 20 minutes in optimal environments.
- At high concentrations of cells, growth slows due to accumulation of toxic wastes, lack of nourishment, among other things.
- Competition in natural environments is reduced by the release of antibiotic chemicals which inhibit the growth of other species.
- Optimal growth requirements vary depending upon the species.

Some bacteria survive adverse environmental conditions and toxins by producing endospores.

- *Endospore* = Resistant cell formed by some bacteria; contains one chromosome copy surrounded by a thick wall
 - When endospores form, the original cell replicates its chromosome and surrounds one copy with a durable wall. The original surrounding cell disintegrates, releasing the resistant endospore.
 - Since some endospores can survive boiling water for a short time, home canners and food canning industry must take special precautions to kill endospores of dangerous bacteria.
 - May remain dormant for many years until proper environmental conditions return.

Short generation times allow prokaryotic populations to adapt to rapidly changing environmental conditions.

- New mutations and genomes (from recombination) are screened by natural selection very quickly.
- This has resulted in the current diversity and success of prokaryotes as well as the variety of nutritional and metabolic mechanisms found in this group.

III. Nutritional and Metabolic Diversity

The prokaryotes exhibit some unique modes of nutrition as well as every type of nutrition found in eukaryotes. In addition, metabolic diversity is greater among prokaryotes than eukaryotes.

A. Prokaryotes can be grouped into four categories according to how they obtain energy and carbon

Prokaryotes exhibit a great diversity in how they obtain the necessary resources (energy and carbon) to synthesize organic compounds.

- Some obtain energy from light (phototrophs), while others use chemicals taken from the environment (chemotrophs).
- Many can utilize CO₂ as a carbon source (autotrophs) and others require at least one organic nutrient as a carbon source (heterotrophs).

Depending upon the energy source and the carbon source, prokaryotes have four possible nutritional modes (see Campbell, Table 27.1):

1. *Photoautotrophs* - Use light energy to synthesize organic compounds from CO₂. Include the cyanobacteria. (Actually all photosynthetic eukaryotes fit in this category.)
2. *Chemoautotrophs* - Require only CO₂ as a carbon source and obtain energy by oxidizing inorganic compounds such as H₂S, NH₃ and Fe²⁺. This mode of nutrition is unique to certain prokaryotes (i.e. archaea of the genus *Sulfolobus*).
3. *Photoheterotrophs* - Use light to generate ATP from an organic carbon source. This mode of nutrition is unique to certain prokaryotes.
4. *Chemoheterotrophs* - Must obtain organic molecules for energy and as a source of carbon. Found in many bacteria as well as most eukaryotes.

1. Nutritional diversity among chemoheterotrophs

Most bacteria are chemoheterotrophs and can be divided into two subgroups: *saprobies* and *parasites*.

- Saprobes are decomposers that absorb nutrients from dead organic matter.
- Parasites are bacteria that absorb nutrients from body fluids of living hosts.

The chemoheterotrophs are a very diverse group, some have very strict requirements, while others are extremely versatile.

- *Lactobacillus* will grow well only when the medium contains all 20 amino acids, several vitamins, and other organic compounds.
- *E. coli* will grow on a medium which contains only a single organic ingredient (e.g., glucose or some other substitute).

Almost any organic molecule can serve as a carbon source for some species.

- Some bacteria are capable of degrading petroleum and are used to clean oil spills.
- Those compounds that cannot be used as a carbon source by bacteria are considered non-biodegradable (e.g., some plastics).

2. Nitrogen metabolism

While eukaryotes can only use some forms of nitrogen to produce proteins and nucleic acid, prokaryotes can metabolize most nitrogen compounds.

Prokaryotes are extremely important to the cycling of nitrogen through ecosystems.

- Some chemoautotrophic bacteria (*Nitrosomonas*) convert $\text{NH}_3 \rightarrow \text{NO}_2^-$.
- Other bacteria, such as *Pseudomonas*, denitrify NO_2^- or NO_3^- to atmospheric N_2 .
- *Nitrogen fixation* ($\text{N}_2 \rightarrow \text{NH}_3$) is unique to certain prokaryotes (cyanobacteria) and is the only mechanism that makes atmospheric nitrogen available to organisms for incorporation into organic compounds.
- The nitrogen-fixing cyanobacteria are very self-sufficient, they need only light energy, CO_2 , N_2 , water, and a few minerals to grow.

3. Metabolic relationships to oxygen

Prokaryotes differ in their growth response to the presence of oxygen.

- *Obligate aerobes* = Prokaryotes that need O_2 for cellular respiration
- *Facultative anaerobes* = Prokaryotes that use O_2 when present, but in its absence can grow using fermentation
- *Obligate anaerobes* = Prokaryotes that are poisoned by oxygen
 - Some species live exclusively by fermentation.
 - Other species use inorganic molecules (other than O_2) as electron acceptors during anaerobic respiration.

B. The evolution of prokaryotic metabolism was both cause and effect of changing environments on Earth

Prokaryotes evolved all forms of nutrition and most metabolic pathways eons before eukaryotes arose.

- Evolution of these new metabolic capabilities was a response to the changing environment of the early atmosphere.
- As these new capabilities evolved, they changed the environment for subsequent prokaryotic communities.

Information from molecular systematics, comparisons of energy metabolism, and geological studies about Earth's early atmosphere have resulted in many hypotheses about the evolution of prokaryotes and their metabolic diversity.

1. The origins of metabolism

The first prokaryotes, which evolved 3.5 - 4.0 billion years ago, probably had few enzymes and were very simple. Moreover, living in an environment with virtually no oxygen, they would have been anaerobes.

The universal role of ATP implies that prokaryotes used that molecule for energy very early in their evolution.

- As ATP supplies were depleted, natural selection favored those prokaryotes that could regenerate ATP from ADP, leading to step-by-step evolution of glycolysis and other catabolic pathways.

Glycolysis is the only metabolic pathway common to all modern organisms and does not require O_2 (which was not abundant on early Earth).

- Some extant archaea and other obligate anaerobes that live by fermentation have forms of nutrition believed to be similar to those of the original prokaryotes.

Chemiosmotic ATP synthesis is also an ancient process since it is common to all three domains of life, but it more likely emerged later in prokaryotic evolution.

Many biologists believe that environmental conditions on early Earth would not have generated enough ATP or other organic molecules by abiotic synthesis to support chemoheterotrophs (see Campbell, Figure 27.8).

The most widely accepted view is that the first prokaryotes were chemoautotrophs that obtained their energy from inorganic chemicals and made their own energy currency molecules instead of absorbing ATP.

- Hydrogen sulfide and iron compounds were abundant and early cells could have obtained energy with their use.

2. The origin of photosynthesis

As the supply of free ATP and abiotically produced organic molecules was depleted, natural selection may have favored organisms that could make their own organic molecules from inorganic resources.

Light absorbing pigments in the earliest prokaryotes may have provided protection to the cells by absorbing excess light energy, especially ultraviolet, that could be harmful.

- These energized pigments may have then been coupled with electron transport systems to power ATP synthesis.
- *Bacteriorhodopsin*, the light-energy capturing pigment in the membrane of extreme halophiles (a group of archaea), uses light energy to pump H^+ out of the cell to produce a gradient of hydrogen ions. This gradient provides the power for production of ATP.
- This mechanism is being studied as a model system of solar energy conversion.

Components of electron transport chains that functioned in anaerobic respiration in other prokaryotes also may have been co-opted to provide reducing power. For example, H_2S could be used as a source of electrons and hydrogen for fixing CO_2 .

- The nutritional modes of modern purple and green sulfur bacteria are believed the most similar to early prokaryotes.
- The colors of these bacteria are due to bacteriochlorophyll, their main photosynthetic pigment.

3. Cyanobacteria, the oxygen revolution, and the origins of cellular respiration

Eventually, some prokaryotes evolved that could use H_2O as the electron source. Thus evolved *cyanobacteria*, which released oxygen (see Campbell, Figure 27.9).

- Cyanobacteria evolved between 2.5 and 3.4 billion years ago.
- They lived with other bacteria in colonies that resulted in the formation of the stromatolites.

Oxygen released by photosynthesis may have first reacted with dissolved iron ions to precipitate as iron oxide (supported by geological evidence of deposits), preventing accumulation of free O_2 .

- Precipitation of iron oxide would have eventually depleted the supply of dissolved iron and O_2 would have accumulated in the seas.
- As seas became saturated with O_2 , the gas was released into the atmosphere.
- As O_2 accumulated, many species became extinct while others survived in anaerobic environments (including some archaea) and others evolved with antioxidant mechanisms.
- Aerobic respiration may have originated as a modification of electron transport chains used in photosynthesis. The purple nonsulfur bacteria are photoheterotrophs that still use a hybrid electron transport system between a photosynthetic and respiratory system.
- Other bacterial lineages reverted to chemoheterotrophic nutrition with electron transport chains adapted only to aerobic respiration.

All major forms of nutrition evolved among prokaryotes before the first eukaryotes arose.

IV. Phylogeny of Prokaryotes

A. Molecular systematics is leading to a phylogenetic classification of prokaryotes

The use of molecular systematics (especially ribosomal RNA comparisons) has shown that prokaryotes diverged into the archaea and bacteria lineages very early in prokaryotic evolution.

- Studies of ribosomal RNA indicate the presence of signature sequences.
 - *Signature sequences* = Domain-specific base sequences at comparable locations in ribosomal RNA or other nucleic acids
- Numerous other characteristics differentiate these two domains (see Campbell, Table 27.2).
- A somewhat surprising result of these types of studies has been the realization that archaea have at least as much in common with eukaryotes as they do with bacteria.

1. Domain Archaea

Some unique characteristics of archaea include:

- Cell walls lack peptidoglycan.
- Plasma membranes have a unique lipid composition.
- RNA polymerase and ribosomal protein are more like those of eukaryotes than of bacteria.

The archaea inhabit the most extreme environments of the Earth. Studies of these organisms have identified three main groups:

1. *Methanogens* are named for their unique form of energy metabolism.
 - They use H_2 to reduce CO_2 to CH_4 and are strict anaerobes.

- Some species are important decomposers in marshes and swamps (form marsh gas) and some are used in sewage treatment.
 - Other species are important digestive system symbionts in termites and herbivores that subsist on cellulose diets.
2. *Extreme halophiles* inhabit high salinity (15–20%) environments (e.g., Dead Sea).
 - Some species simply tolerate extreme salinities while others require such conditions (see Campbell, Figure 27.10).
 - They have the pigment bacteriorhodopsin in their plasma membrane which absorbs light to pump H^+ ions out of the cell.
 - This pigment is also responsible for the purple-red color of the colonies.
 3. *Extreme thermophiles* inhabit hot environments.
 - They live in habitats of 60 – 80°C.
 - One sulfur-metabolizing thermophile inhabits water of 105°C near deep sea hydrothermal vents.

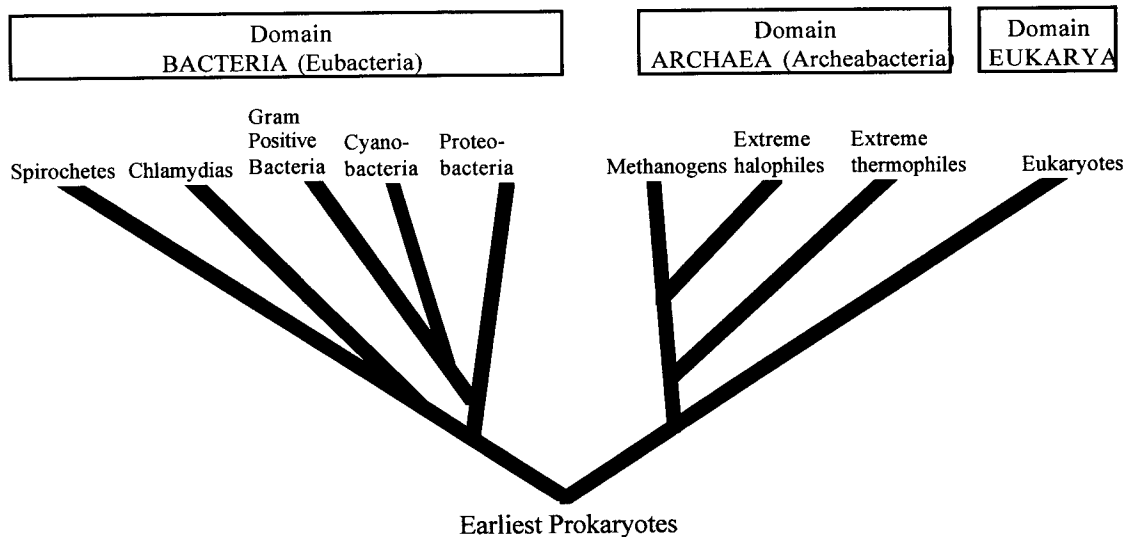
2. Domain Bacteria

Bacteria comprise a majority of the prokaryotes.

The major groups of bacteria include a very diverse assemblage of organisms.

Among the thousands of known species are forms which exhibit every known mode of nutrition and energy metabolism.

Molecular systematics has provided an increased understanding of the once hazy relationships among members of this taxon. At present, most prokaryotic systematists recognize a dozen groups of bacteria (see Campbell, Figures 27.11 and Table 27.3).



V. Ecological Impact of Prokaryotes

A. Prokaryotes are indispensable links in the recycling of chemical elements in ecosystems

Prokaryotes are critical links in the recycling of chemical elements between the biological and physical components of ecosystems—a critical element in the continuation of life.

Decomposers = Prokaryotes that decompose dead organisms and waste of live organisms

- Return elements such as carbon and nitrogen to the environment in inorganic forms needed for reassimilation by other organisms, many of which are also prokaryotes.

Autotrophic bacteria = Bacteria that fix CO₂, thus supporting food chains through which organic nutrients pass

Cyanobacteria supplement plants in restoring oxygen to the atmosphere as well as fixing nitrogen into nitrogenous compounds used by other organisms.

Other prokaryotes also support cycling of nitrogen, sulfur, iron and hydrogen.

B. Many prokaryotes are symbiotic

Most prokaryotes form associations with other organisms; usually with other bacterial species possessing complementary metabolisms.

Symbiosis = Ecological relationships between organisms of different species that are in direct contact

- Usually the smaller organism, the *symbiont*, lives within or on the larger *host*.

Three categories of symbiosis:

1. *Mutualism* = Symbiosis in which both symbionts benefit

Example: Nitrogen-fixing bacteria in root nodules of certain plants fix nitrogen to be used by the plant, which in turn furnishes sugar and other nutrients to the bacteria.

2. *Commensalism* = Symbiosis in which one symbiont benefits while neither helping nor harming the other symbiont
3. *Parasitism* = Symbiosis in which one symbiont (the *parasite*) benefits at the expense of the host

Symbiosis is believed to have played a major role not only in the evolution of prokaryotes, but also in the origin of early eukaryotes.

1. Prokaryotes and disease

About one-half of all of human disease is caused by bacteria. To cause a disease, the bacteria must invade, evade, or resist the host's internal defenses, long enough to grow and harm the host.

Some pathogens are opportunistic.

- *Opportunistic* = Normal inhabitants of the body that become pathogenic only when defenses are weakened by other factors such as poor nutrition or other infections

Example: *Streptococcus pneumoniae* lives in the throat of most healthy humans, but can cause pneumonia if the host's defenses are weakened.

Louis Pasteur, Joseph Lister, and others began linking disease to pathogenic microbes in the late 1800s, but Robert Koch was the first to determine a direct connection between specific bacteria and certain diseases.

- Koch identified the bacteria responsible for anthrax and tuberculosis, and his methods established the four criteria to use as guidelines in medical microbiology.
- *Koch's postulates* = Four criteria to substantiate a specific pathogen as the cause for a disease; they are:
 1. Find the same pathogen in each diseased individual.
 2. Isolate the pathogen from a diseased subject and grow it in a pure culture.

3. Use cultured pathogen to induce the disease in experimental animals.
4. Isolate the same pathogen in the diseased experimental animal.

Some pathogens cause disease by growth and invasion of tissues which disrupts the physiology of the host, while others cause disease by production of a toxin. Two major types of toxins have been found:

- *Exotoxins* = Proteins secreted by bacterial cells
 - Can cause disease without the organism itself being present; the toxin is enough
 - Among the most potent poisons known
 - Elicits specific symptoms

Examples: Botulism toxin from *Clostridium botulinum* and cholera toxin from *Vibrio cholerae*

- *Endotoxins* = Toxic component of outer membranes of some gram-negative bacteria
 - All induce the general symptoms of fever and aches

Examples: *Salmonella typhi* (typhoid fever) and other species of *Salmonella* that cause food poisoning

Improved sanitation measures and development of antibiotics have greatly reduced mortality due to bacterial diseases.

- Many of the antibiotics now in use are produced naturally by members of the genus *Streptomyces*. In its natural habitat (soil) such materials would reduce competition from other prokaryotes.
- Although beneficial, the excessive and improper use of antibiotics has resulted in the evolution of many antibiotic-resistant bacterial species, which now pose a major health problem.

C. Humans use prokaryotes in research and technology

Humans use the metabolic diversity of bacteria for a multitude of purposes. The range of these purposes has increased through the application of recombinant DNA technology.

- Pharmaceutical companies use cultured bacteria to make vitamins and antibiotics. More than half of the antibiotics used to treat bacterial diseases come from cultures of various species of *Streptomyces* maintained by pharmaceutical companies.
- As simple models of life to learn about metabolism and molecular biology. (*E. coli* is the best understood of all organisms.)
- Methanogens are used to digest organic wastes at sewage treatment plants.
- Some species of pseudomonads are used to decompose pesticides and other synthetic compounds (see Campbell, Figure 27.12).
- Industry uses bacterial cultures to produce products such as acetone and butanol.
- The food industry uses bacteria to convert milk into yogurt and cheese.

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