Chapter 26: Bacteria and Archaea: The Prokaryotic Domains

- Some bacteria are quite large, 750 μm. (A typical human somatic cell is only about 10 μm.)
- The smallest organisms on Earth are also species of prokaryotes (0.2 μm)
- There are two types of prokaryotes: bacteria and archaea.
- The DNA sequencing of a species of archaea in 1996 provided evidence of substantial differences between archaea and both eukaryotes and bacteria.
- Biologists generally categorize all life first into one of the three domains: Bacteria, Archaea and Eukarya.

I Why Three Domains?

- Members of all three domains metabolize glucose, have double-stranded DNA information molecules, and share a common genetic code.
- Archaea share a more recent common ancestor with eukaryotes than with bacteria.
- The three *domain* names are a higher taxonomic category than *kingdoms*. (See Figure 26.2)
- The common ancestor of all three domains was prokaryotic.
  - It likely had a circular chromosome and structural genes organized into operons.
  - All three domains are over a billion years old.
  - None are "primitive" today, because all cellular life has come from previously existing life, and in essence are the same age.
  - Earliest prokaryotic fossils date back to 3.5 billion years.
  - Prokaryotes were the only life forms for billions of years.
  - See Table 1.

II General Biology of the Prokaryotes

- Prokaryotes live all around and even within us.
  - The bacteria in one person's intestinal tract outnumber all the people who have ever lived.
  - Prokaryotes are important to the biosphere.
    - Some perform key steps in cycling of nitrogen, sulfur, and carbon.
    - Some trap energy from the sun and from inorganic chemical sources.
    - Some help animals digest their food.
- Prokaryotes are found in every conceivable habitat on the planet.
  - They live at extremely hot temperatures.
  - They can survive extreme alkaline and saltiness.
  - Some survive in the presence of oxygen, while others survive without it.
  - Some live at the bottom of the sea.
  - Some live in rocks more than 2 km into Earth's solid crust.

A. Prokaryotes and their association take a few characteristic forms

- Three shapes are common to prokaryotes. (See Figure 26.3)
  - These are spheres, rods and curved or spiral.

    - Those spherical are called coccus. Cocci might live singly or in two or three dimensional arrays of chains, plates, or blocks, depending on the species.
    - Rodshaped prokaryotes are called bacillus. These live in chains or singularly.
- Prokaryotes, with just a few exceptions, are unicellular.
    - Chains and such do not signify multicellularity because each cell is viable independently.
    - The multicellular form associate in chains *and* become enclosed within delicate tubular sheaths.
    - These are called filaments. All the cells of the filament divide simultaneously.

B. Prokaryotes lack nuclei, organelles, and a cytoskeleton

- Most of what is currently known about prokaryotic cellular structure has been learned from bacteria.
- Prokaryotes have no membrane-bound cytoplasmic organelles like mitochondria, endoplasmic reticulum, nuclear envelope and others.
- Some do have plasma membrane infoldings.
- See Figure 26.4.

C. Prokaryotes have distinctive modes of locomotion

- Some prokaryotes are motile. (See Figure 26.5)
    - Some spiral bacteria called spirochetes use a rolling motion.
    - Many cyanobacteria and some other bacteria use a gliding mechanism.
    - Some aquatic prokaryotes move slowly up and down in the water by adjusting the amount of gas in gas vesicles.
    - Bacterial flagella, which are entirely different from those of eukaryotes, consist of a single fibril made of the protein flagellin, projecting from the surface. Prokaryotic flagellum rotate about its base, rather than binding, as eukaryotic flagellum do. (See Figure 26.6)

D. Prokaryotes have distinctive cell walls

- Most prokaryotes have a thick and stiff cell wall of peptidoglycan (amino sugar polymer).
- Archaean cell walls are of a different type.
- The Gram stain, developed by Gram in 1884, separates bacteria into two distinct groups, Gram-positive and Gram-negative, on the nature of their cell walls.
    - See Figure 26.7.
    - To Gram stain, cells on a microscope slide are soaked in violet dye and treated with iodine.
    - The slide is then washed with alcohol and counterstained with safranine.
    - Gram-positive stain violet.
    - Gram-negative stain pink to red.
    - Gram staining correlates with the structure of the cell wall.
    - Gram positive have a thicker layer of peptidoglycan than Gram negative, have a second outer membrane outside the cell wall and the cell wall has only a fifth as much peptidoglycan.

        - The space between the outer membrane and the cell wall is called the periplasmic space.
        - This space contains enzymes important to the transport of some components.
    - Many antibiotics act by disrupting cell wall synthesis.

E. Prokaryotes reproduce asexually, but genetic recombination does occur

- Prokaryotes reproduce asexually by fission. (See Figure 26.1)
- Transformation, conjugation, and transduction are the means used for exchanging genetic information.
- Rates of division vary with species. *E. coli* divides about once every 20 minutes. Shortest for prokaryotes is about 10 minutes. Bacteria living in rock deep in the Earth's crust might not divide for as long as 100 years.

F. Prokaryotes have exploited many metabolic possibilities

- Anaerobic versus aerobic metabolism:
    - Obligate anaerobes live only in the absence of oxygen. Oxygen is toxic to them.
    - Facultative anaerobes can shift between anaerobic and aerobic modes.
    - Some cannot use oxygen but are not damaged by it.
    - Others can shift from aerobic and anaerobic metabolisms.
    - Obligate aerobes are unable to survive for extended periods in the absence of oxygen.
- Nutritional Categories:
    - These include photoautotrophs, photoheterotrophs, chemoautotrophs, and chemoheterotrophs. (See Figure 26.2)
    - Photoautotrophs are photosynthesizers.
    - They use light for energy and carbon dioxide for a carbon source.
    - Cyanobacteria use chlorophyll *a* and produce oxygen as a by-product.
    - Other photosynthetic bacteria use bacteriochlorophyll.
        - They don't produce oxygen.
        - Some produce particles of pure sulfur, because H_2S is used instead of H_2O as an electron donor.
        - Bacteriochlorophyll uses longer wavelengths than chlorophylls. This longer wave length of light penetrates further into water and is not absorbed by plants. (See Figure 26.8)
    - Photoheterotrophs use light as a source of energy but must get carbon from other organisms.
        - They use carbohydrates, fatty acids and alcohols for carbon.
        - Purple nonsulfur bacteria are an example.
    - Chemoautotrophs obtain energy from oxidizing inorganic substances. (See Figure 26.9)
        - They use some of the energy to fix carbon dioxide.
        - Some use pathways to fix CO_2 identical to those of the Calvin cycle.
        - Others use alternative pathways.
        - Some use ammonia as the chemical source of energy, others use hydrogen gas, hydrogen sulfide, sulfur, or methane.
        - Some deep-sea ecosystems are based on chemoautotrophic prokaryotes.

- They form the basis for a food chain that includes giant worms, crabs, and mollusks.
- These bacteria live around the thermal vents of underwater volcanoes.
- Chemoheterotrophs typically obtain energy and carbon atoms from one or more organic compounds. Most known bacteria and archaea are chemoheterotrophs, as are all animal, fungi and many protists.
- Nitrogen and sulfur metabolism:
  - Some bacteria use electron acceptors other than oxygen.
  - Some use oxidized nitrogen such as ammonia, nitrite; or, sulfur such as sulfur or sulfite, as electron acceptors.
  - Denitrifiers return nitrogen to the atmosphere.
  - Nitrogen fixers, are all bacteria.
    - They provide the enzymes and environment to conduct the reaction: $N_2 + 6H \rightarrow 2NH_3$.
    - All organisms require fixed nitrogen for their proteins, nucleic acids and other nitrogen containing compounds.
  - Nitrifiers oxidize ammonia to nitrate.
    - Bacteria of two genera, *Nitrosomona*s and *Nitrosococcus*, convert ammonia to nitrite.
    - *Nitrobacter* oxidizes nitrite to nitrate.
  - The bacteria harvest energy from the conversion of ammonia to nitrite and nitrite to nitrate.
  - See Figure 26.10.

III Prokaryotes in Their Environments

A. Prokaryotes are important players in element cycling

- Plants depend on prokaryotes for sources of nitrogen.
- Prokaryotes that are denitrifiers prevent accumulation of toxic levels of nitrogen in lakes and oceans.
- Cyanobacteria have had a powerful effect on changing the Earth by generating the O_2, which made the evolution of more efficient glucose metabolism possible, and caused the extinction of many of the species that couldn't tolerate oxygen.

B. Prokaryotes live on and in other organisms

- Mitochondria and chloroplasts are assumed to be descendants of free-living bacteria.
- Cows depend on prokaryotes in their digestive tract to digest cellulose that makes up the bulk of their plant food.
- Humans use vitamins B12 and K produced by our intestinal bacteria.

C. A small minority of bacteria are pathogens

- In the late nineteenth century, Robert Koch formulated rules for determining that a particular microorganism causes a particular disease.
  - The microorganism must always be found in individuals with disease.
  - The microorganism can be taken from the host and grown in pure culture.

    - A sample of the culture produces the disease when injected into a new, healthy host.
    - The newly infected host yields a new, pure culture of microorganisms identical to those obtained in the second step.
    - These are called Koch's postulates.
- Only a tiny proportion of prokaryotic species are pathogens.
- For an organism to be a pathogen it must:
    - Arrive at the body surface;
    - Enter the body;
    - Evade detection and defenses;
    - Multiply inside the host;
    - Infect new hosts.
- For the host, the seriousness of the infection depends on:
    - The invasiveness;
    - The toxigenicity.
    - *Corynebacterium diphtheriae* has low invasiveness but produces powerful toxins.
    - *Bacillus anthracis*, which causes anthrax, has low toxigenicity, but is so invasive, the bloodstream of infected animals teams with organisms.
- There are two major types of toxins.
    - Endotoxins are lipopolysaccharides from the outer membrane of Gram-negatives, which cause vomiting, fever and diarrhea.
    - *Salmonella* and *Escherichia* produce endotoxins.
    - Exotoxins are produced and released by living, multiplying bacteria.
        - These can be highly toxic, even fatal.
        - They don't cause fever.
        - Tetanus (from *Clostridium tetani*), botulism (from *Clostridium botulinum*), Cholera (from *Vibrio cholerae*) and plague (from *Yersinia pestis*) are all examples of exotoxins.

IV Prokaryote Phylogeny and Diversity

A. Nucleotide sequences of prokaryotes reveal their evolutionary relationships

- Three primary motivations for classification schemes are to help identify unknown organisms, reveal evolutionary relationships and provide names.
- In the past, phenotypic characters such as color, shape, antibiotic resistance and staining were used.
- These were the best clues available in the past.
    - Now, nucleic acid sequencing is providing clues to evolutionary relationships.
    - Ribosomal RNA's (rRNA's) have been studied.
        - rRNA is evolutionarily ancient
        - All organisms have them.
        - They function the same in all organisms.
        - They change slowly enough so that similarities exist between groups of organisms.
    - Signature sequences are compared.

- The sequence AAACUUAAAG occurs about 910 bases from one end in all Archaea and Eukarya but it fails to exist as such in any bacteria.
- Results so far have provided some surprises.

B. Lateral gene transfer muddied the phylogenetic waters

- Lateral gene transfer among bacteria of different species has complicated the use of sequencing information for determining the evolutionary relationships of bacteria.
- There is currently great controversy over prokaryotic phylogeny.
- See Figure 26.11 for an abridged, but current ancestral tree.

C. Mutations are the most important source of prokaryotic variation

- The rapid multiplication of many prokaryotes coupled with mutation, selection and genetic drift causes rapid changes.
- An example is the acquiring of resistance to antibiotics.

V The Bacteria

A. Some bacteria are heat lovers

- Three of the bacterial groups that may have branched out earliest are all thermophiles.

B. The Proteobacteria are a large and diverse group

- Proteobacteria, sometimes called purple bacteria, is the largest group in terms of the number of species.
- Some are Gram-negative, bacteriochlorophyll-containing, and sulfur-using photoautotrophics.
- Mitochondrin are derived from proteobacteria.
- See Figure 26.12 for a comparison of proteobacterial metabolisms.
- The common ancestor to all proteobacteria was probably a photoautotroph.
- In two groups most members have lost the ability to photosynthesize and became chemoheterotrophs.
- There are also chemoautotrophs in all three groups.
- Some fix nitrogen (*Rhizobium*) and some help cycle nitrogen and sulfur.
- *E. coli*, *Yersinia pestis*, *Vibrio cholerae* and *Salmonella typhimurium* are all proteobacterium.
- *Agrobacterium tumeficiens*, which causes crown gall, and which is currently being used by plant molecular biologists as a vector for gene transfer in plants due to its Ti plasmid(see Chapter 17), is a proteobacteria. (See Figure 26.13)

C. The Cyanobacteria are important photoautotrophs

- Cyanobacteria (blue-green bacteria) require only water, N_2, CO_2, a few mineral elements, light and O_2 (This, they actually produce from water.).
- Cyanobacteria have highly organized internal membranes called photosynthetic lamellae. (See Figure 26.14)
- Chloroplasts are derived from an endosymbiotic cyanobacterium.
- Cyanobacteria grow free or in colonies.

- Filamentous colonies differentiate into three cell types: vegetative cells, spores, and heterocysts.
- Heterocysts are specialized for nitrogen fixation.
- See Figure 26.15.

D. Spirochetes look like corkscrews
- Spirochetes are Gram-negative bacteria with axial filaments, which are fibrils running through the periplasmic space.
- See Figure 26.5a.
- The cell body is a long cylinder coiled into a spiral.
- Many spirochetes live in humans as parasites. Others live free in mud or water.
- See Figure 26.16.

E. Chlamydias are extremely small
- Chlamydias are among the smallest bacteria (0.2 -1.5μm in diameter).
- They are intracellular parasites.
- They change form during their life cycle. See Figure 26.17.
- In humans, they cause eye infections, sexually transmitted disease and some forms of pneumonia.

F. Most Firmicutes are Gram-positive
- Most are Gram-positive but some are negative. (See Figure 26.19)
- Some produce endospores, which are heat resistant resting structures.
  - The bacteria replicates its DNA.
  - It encapsulates one copy in a tough cell wall, thickened with peptidoglycan, covered with a spore coat. (See Figure 26.18)
  - The parent cell then breaks down, releasing the endospore.
  - Some endospores can be reactivated after more than a thousand years of dormancy.
  - Members of this endospore-forming group include *Bacillus* and Clostridium.
  - Just 1 μg of toxin from Clostridium botulinum is lethal to a human.
  - *Staphylococcus* includes pathogens that cause boils on skin, as well as respiratory, intestinal and wound infections.
  - *Actinomycetes* are firmicutes that develop an elaborately branched system of filaments. (See Figure 26.20)
    - Some form chains of spores at the tips of filaments.
    - *Mycobacterium* tuberculosis causes tuberculosis.
    - *Streptomyces* produces the antibiotic streptomycin, as well as hundreds of other antibiotics.
    - Most of our antibiotics are from members of actinomycetes.
  - *Mycoplasmas* have the least amount of DNA and are the smallest bacterias.
    - They lack cell walls.
    - Some are 0.2μm in size.
    - See Figure 26.21.

VI The Archaea

A. The Archaea share some unique characteristics

- These lack peptidoglycan in their cell walls.
- They have distinctive lipids.
- See figure 26.22.
- When biologists sequenced the first archaean genome, of its 1,738 genes, more than half were unique to any found in the other two domains.
- Long fatty acids are bonded to glycerol via an ether linkage instead of ester linkage found in other organisms.

B. Most Crenarchaeota live in hot, acidic places

- Most Crenarchaeota are both thermophilic and acidophilic.
- The genus *Sulfolobus* live in hot sulfur springs at temperatures of 70 - 75^{o}C.
- They die of "cold" at 55^{o}C (131^{o}F).
- They grow best at pH 2 to 3 but can survive pH 0.9.

C. The Euryarchaeota live in many amazing places

- Some Euryarchaeota produce methane from CO_2.
- All methanogenes are obligate anaerobes.
- Methanogens release approximately 2 billion tons of methane gas into Earth's atmosphere.
- Approximately a third of this methane comes from methanogens in the guts of grazing herbivores.
- *Methanopyrus* lives on the ocean bottom near volcanic vents. These can live at 110^{o}C.
- Some Euryarchaeota, called extreme halophiles, live exclusively in very salty environments.
- These grow in the Dead Sea. (See Figure 26.24)
- Some of these organisms survive a pH of 11.5.
- Some of the extreme halophiles use bacteriorhodopsin to make ATP using a chemiosmotic mechanism.
- Thermoplasma is thermophilic and acidophilic.
    - It is aerobic and lives in coal deposits.
    - It has the smallest genome of any archaea, 1,100,000 base pairs.