

Overview: Masters of Adaptation

- Utah's Great Salt Lake can reach a salt concentration of 32%
- Its pink color comes from living prokaryotes

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Figure 27.1



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- Prokaryotes thrive almost everywhere, including places too acidic, salty, cold, or hot for most other organisms
- Most prokaryotes are microscopic, but what they lack in size they make up for in numbers
- There are more in a handful of fertile soil than the number of people who have ever lived
- Prokaryotes are divided into two domains: bacteria and archaea

PLAY Video: Tubeworms

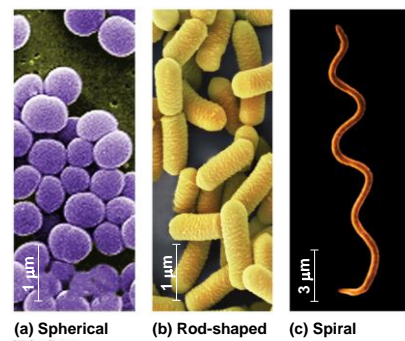
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Concept 27.1: Structural and functional adaptations contribute to prokaryotic success

- Earth's first organisms were likely prokaryotes
- Most prokaryotes are unicellular, although some species form colonies
- Most prokaryotic cells are 0.5–5 μm , much smaller than the 10–100 μm of many eukaryotic cells
- Prokaryotic cells have a variety of shapes
- The three most common shapes are spheres (cocci), rods (bacilli), and spirals

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Figure 27.2



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Figure 27.2a



(a) Spherical

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Figure 27.2b



(b) Rod-shaped

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Figure 27.2c



(c) Spiral

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Cell-Surface Structures

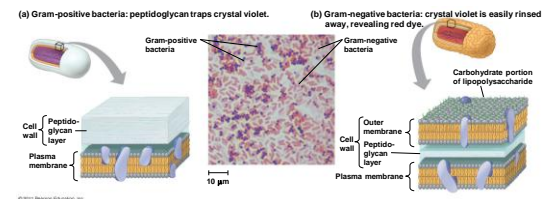
- An important feature of nearly all prokaryotic cells is their cell wall, which maintains cell shape, protects the cell, and prevents it from bursting in a hypotonic environment
- Eukaryote cell walls are made of cellulose or chitin
- Bacterial cell walls contain **peptidoglycan**, a network of sugar polymers cross-linked by polypeptides

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- Archaea contain polysaccharides and proteins but lack peptidoglycan
- Scientists use the **Gram stain** to classify bacteria by cell wall composition
- **Gram-positive** bacteria have simpler walls with a large amount of peptidoglycan
- **Gram-negative** bacteria have less peptidoglycan and an outer membrane that can be toxic

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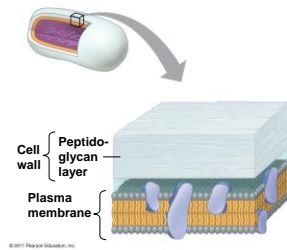
Figure 27.3



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Figure 27.3a

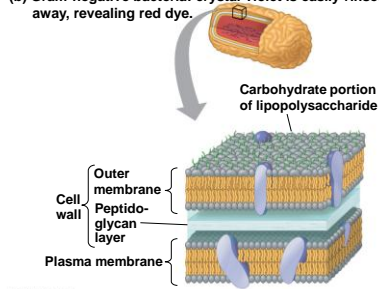
(a) Gram-positive bacteria: peptidoglycan traps crystal violet.



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Figure 27.3b

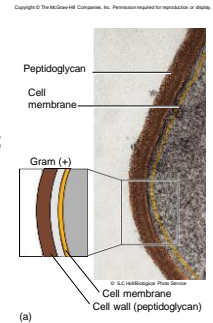
(b) Gram-negative bacteria: crystal violet is easily rinsed away, revealing red dye.



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Gram-Positive Cell Wall

- 20-80 nm thick peptidoglycan
- Includes **teichoic acid** and **lipoteichoic acid**: function in cell wall maintenance and enlargement during cell division; move cations across the cell envelope; stimulate a specific immune response
- Some cells have a **periplasmic space**, between the cell membrane and cell wall

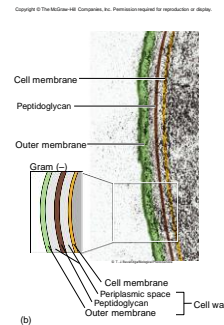


(a)

14

Gram-Negative Cell Wall

- Inner and outer membranes and **periplasmic space** between them contains a thin peptidoglycan layer
- Outer membrane contains **lipopolysaccharides (LPS)**
 - Lipid portion (endotoxin) may become toxic when released during infections
 - May function as receptors and blocking immune response
 - Contain **porin** proteins in upper layer – regulate molecules entering and leaving cell



(b)

16

The Gram Stain

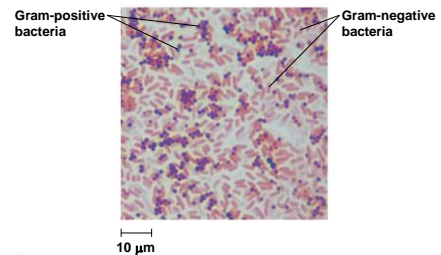
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Step	Microscopic Appearance of Cell		Chemical Reaction in Cell (very magnified view)	
	Gram (+)	Gram (-)	Gram (+)	Gram (-)
1 Crystal Violet (primary dye)				
2 Gram's iodine (mordant)				
3 Alcohol (decolorizer)				
4 Safranin (red dye counterstain)				

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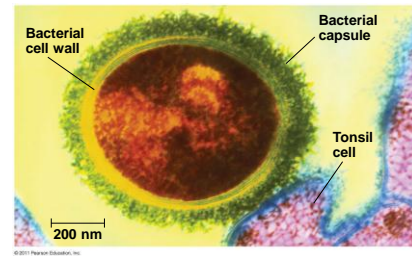
FLEX

Figure 27.3c



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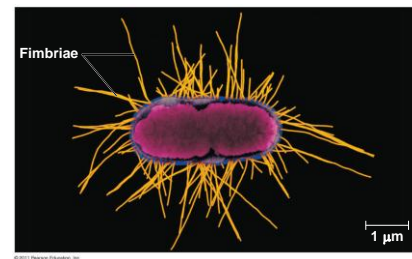
Figure 27.4



- Many antibiotics target peptidoglycan and damage bacterial cell walls
- Gram-negative bacteria are more likely to be antibiotic resistant
- A polysaccharide or protein layer called a **capsule** covers many prokaryotes

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Figure 27.5



- Some prokaryotes have **fimbriae**, which allow them to stick to their substrate or other individuals in a colony
- **Pili** (or sex pili) are longer than fimbriae and allow prokaryotes to exchange DNA

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Motility

- In a heterogeneous environment, many bacteria exhibit **taxis**, the ability to move toward or away from a stimulus
- Chemotaxis is the movement toward or away from a chemical stimulus

- Most motile bacteria propel themselves by flagella scattered about the surface or concentrated at one or both ends
- Flagella of bacteria, archaea, and eukaryotes are composed of different proteins and likely evolved independently

PLAY Video: Prokaryotic Flagella (*Salmonella typhimurium*)

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PLAY Video: Prokaryotic Flagella (*Salmonella typhimurium*)

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Figure 27.6

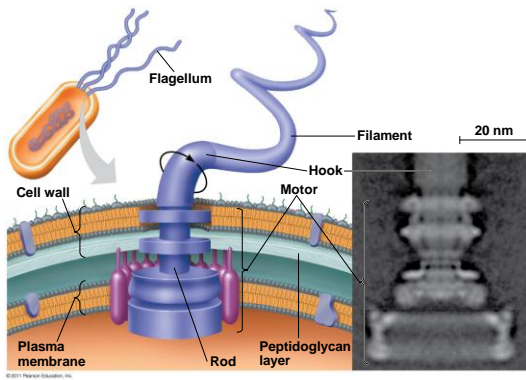
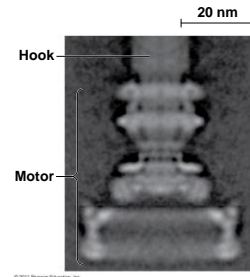


Figure 27.6a



Evolutionary Origins of Bacteria Flagella

- Bacterial flagella are composed of a motor, hook, and filament
- Many of the flagella's proteins are modified versions of proteins that perform other tasks in bacteria
- Flagella likely evolved as existing proteins were added to an ancestral secretory system
- This is an example of exaptation, where existing structures take on new functions through descent with modification

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Internal Organization and DNA

- Prokaryotic cells usually lack complex compartmentalization
- Some prokaryotes do have specialized membranes that perform metabolic functions
- These are usually infoldings of the plasma membrane

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Figure 27.7

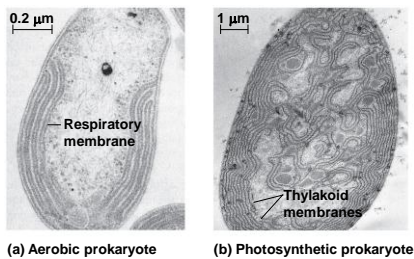


Figure 27.7a

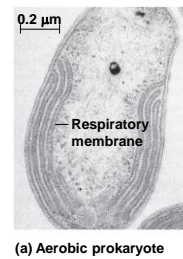


Figure 27.7b

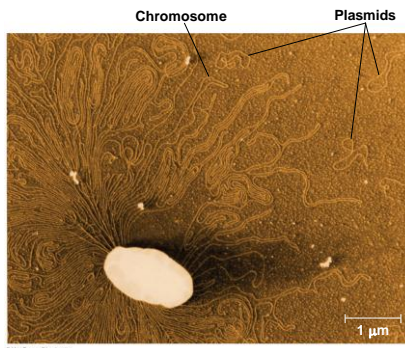


(b) Photosynthetic prokaryote

- The prokaryotic genome has less DNA than the eukaryotic genome
- Most of the genome consists of a circular chromosome
- The chromosome is not surrounded by a membrane; it is located in the **nucleoid** region
- Some species of bacteria also have smaller rings of DNA called **plasmids**

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Figure 27.8



- There are some differences between prokaryotes and eukaryotes in DNA replication, transcription, and translation
- These allow people to use some antibiotics to inhibit bacterial growth without harming themselves

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Reproduction and Adaptation

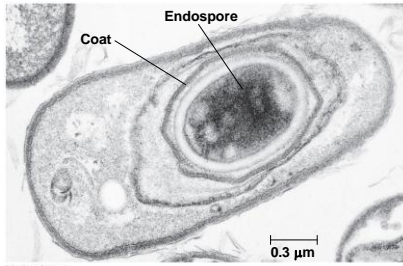
- Prokaryotes reproduce quickly by binary fission and can divide every 1–3 hours
- Key features of prokaryotic reproduction:
 - They are small
 - They reproduce by binary fission
 - They have short generation times

- Many prokaryotes form metabolically inactive **endospores**, which can remain viable in harsh conditions for centuries

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Figure 27.9



- Their short generation time allows prokaryotes to evolve quickly
 - For example, adaptive evolution in a bacterial colony was documented in a lab over 8 years
- Prokaryotes are not “primitive” but are highly evolved

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Figure 27.10

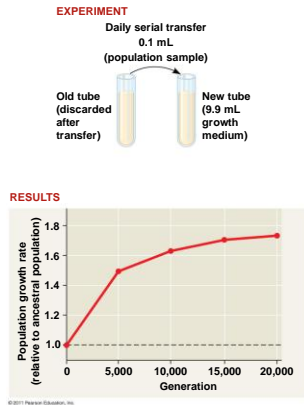


Figure 27.10a

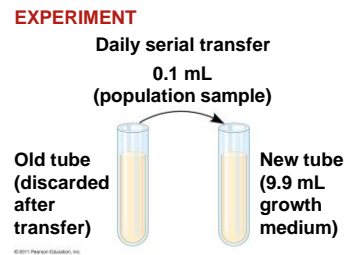
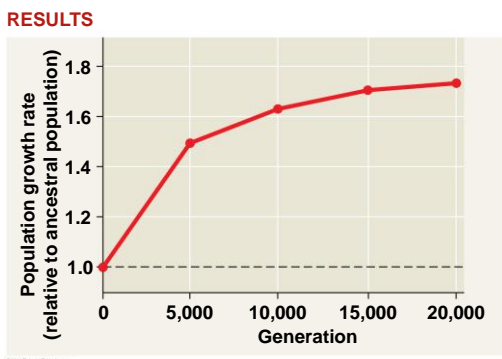


Figure 27.10b



Concept 27.2: Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes

- Prokaryotes have considerable genetic variation
- Three factors contribute to this genetic diversity:
 - Rapid reproduction
 - Mutation
 - Genetic recombination

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Rapid Reproduction and Mutation

- Prokaryotes reproduce by binary fission, and offspring cells are generally identical
- Mutation rates during binary fission are low, but because of rapid reproduction, mutations can accumulate rapidly in a population
- High diversity from mutations allows for rapid evolution

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Genetic Recombination

- Genetic recombination, the combining of DNA from two sources, contributes to diversity
- Prokaryotic DNA from different individuals can be brought together by transformation, transduction, and conjugation
- Movement of genes among individuals from different species is called horizontal gene transfer

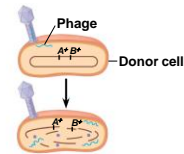
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Transformation and Transduction

- A prokaryotic cell can take up and incorporate foreign DNA from the surrounding environment in a process called **transformation**
- **Transduction** is the movement of genes between bacteria by bacteriophages (viruses that infect bacteria)

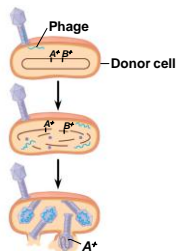
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Figure 27.11-1



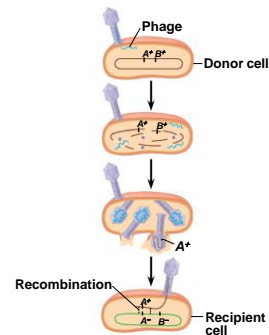
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Figure 27.11-2



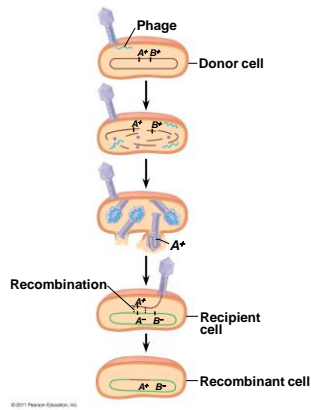
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Figure 27.11-3



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Figure 27.11-4

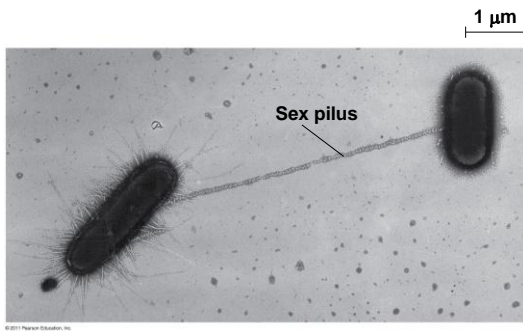


Conjugation and Plasmids

- **Conjugation** is the process where genetic material is transferred between prokaryotic cells
- In bacteria, the DNA transfer is one way
- A donor cell attaches to a recipient by a pilus, pulls it closer, and transfers DNA
- A piece of DNA called the **F factor** is required for the production of pili

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Figure 27.12



The F Factor as a Plasmid

- Cells containing the **F plasmid** function as DNA donors during conjugation
- Cells without the F factor function as DNA recipients during conjugation
- The F factor is transferable during conjugation

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Figure 27.13

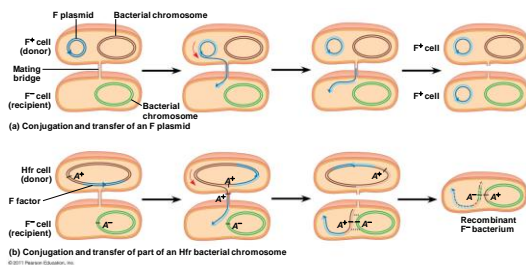


Figure 27.13a-1

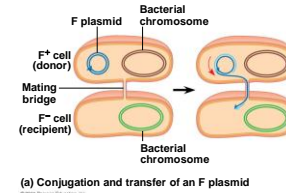
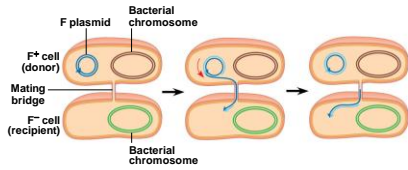
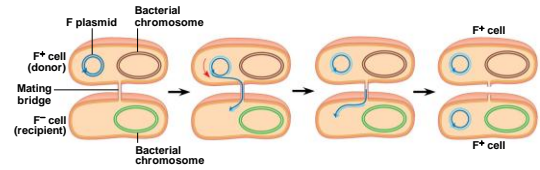


Figure 27.13a-2



(a) Conjugation and transfer of an F plasmid

Figure 27.13a-3

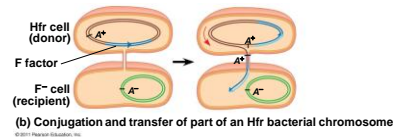


(a) Conjugation and transfer of an F plasmid

Figure 27.13b-1

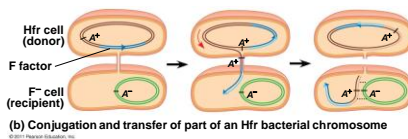
The F Factor in the Chromosome

- A cell with the F factor built into its chromosomes functions as a donor during conjugation
- The recipient becomes a recombinant bacterium, with DNA from two different cells



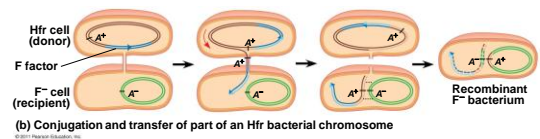
(b) Conjugation and transfer of part of an Hfr bacterial chromosome

Figure 27.13b-2



(b) Conjugation and transfer of part of an Hfr bacterial chromosome

Figure 27.13b-3



(b) Conjugation and transfer of part of an Hfr bacterial chromosome

R Plasmids and Antibiotic Resistance

- **R plasmids** carry genes for antibiotic resistance
- Antibiotics kill sensitive bacteria, but not bacteria with specific R plasmids
- Through natural selection, the fraction of bacteria with genes for resistance increases in a population exposed to antibiotics
- Antibiotic-resistant strains of bacteria are becoming more common

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Concept 27.3: Diverse nutritional and metabolic adaptations have evolved in prokaryotes

- Prokaryotes can be categorized by how they obtain energy and carbon
 - Phototrophs obtain energy from light
 - Chemotrophs obtain energy from chemicals
 - Autotrophs require CO_2 as a carbon source
 - Heterotrophs require an organic nutrient to make organic compounds

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- Energy and carbon sources are combined to give four major modes of nutrition:
 - Photoautotrophy
 - Chemoautotrophy
 - Photoheterotrophy
 - Chemoheterotrophy

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Table 27.1

Mode	Energy Source	Carbon Source	Types of Organisms
AUTOTROPH			
Photoautotroph	Light	CO_2 , HCO_3^- , or related compound	Photosynthetic prokaryotes (for example, cyanobacteria); plants; certain protists (for example, algae)
Chemoautotroph	Inorganic chemicals (such as H_2S , NH_3 , or Fe^{2+})	CO_2 , HCO_3^- , or related compound	Unique to certain prokaryotes (for example, <i>Sulfolobus</i>)
HETEROTROPH			
Photoheterotroph	Light	Organic compounds	Unique to certain aquatic and salt-loving prokaryotes (for example, <i>Rhodobacter</i> , <i>Chloroflexus</i>)
Chemoheterotroph	Organic compounds	Organic compounds	Many prokaryotes (for example, <i>Clostridium</i>) and protists; fungi; animals; some plants

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The Role of Oxygen in Metabolism

- Prokaryotic metabolism varies with respect to O_2
 - **Obligate aerobes** require O_2 for cellular respiration
 - **Obligate anaerobes** are poisoned by O_2 and use fermentation or **anaerobic respiration**
 - **Facultative anaerobes** can survive with or without O_2

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Nitrogen Metabolism

- Nitrogen is essential for the production of amino acids and nucleic acids
- Prokaryotes can metabolize nitrogen in a variety of ways
- In **nitrogen fixation**, some prokaryotes convert atmospheric nitrogen (N_2) to ammonia (NH_3)

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Metabolic Cooperation

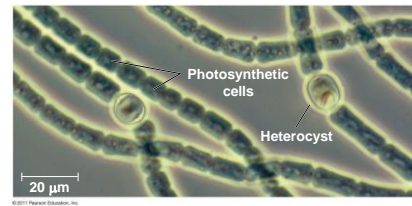
- Cooperation between prokaryotes allows them to use environmental resources they could not use as individual cells
- In the cyanobacterium *Anabaena*, photosynthetic cells and nitrogen-fixing cells called **heterocysts** (or heterocytes) exchange metabolic products



Video: Cyanobacteria (*Oscillatoria*)

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Figure 27.14



Concept 27.4: Molecular systematics is illuminating prokaryotic phylogeny

- In some prokaryotic species, metabolic cooperation occurs in surface-coating colonies called **biofilms**

- Until the late 20th century, systematists based prokaryotic taxonomy on phenotypic criteria
- Applying molecular systematics to the investigation of prokaryotic phylogeny has produced dramatic results

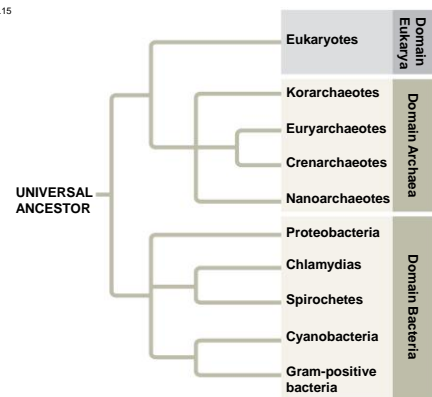
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Lessons from Molecular Systematics

- Molecular systematics led to the splitting of prokaryotes into bacteria and archaea
- Molecular systematists continue to work on the phylogeny of prokaryotes

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- The use of polymerase chain reaction (PCR) has allowed for more rapid sequencing of prokaryote genomes
- A handful of soil may contain 10,000 prokaryotic species
- Horizontal gene transfer between prokaryotes obscures the root of the tree of life

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Archaea

- Archaea share certain traits with bacteria and other traits with eukaryotes

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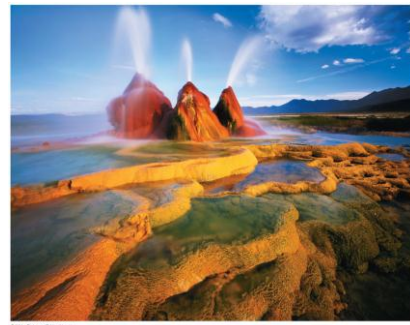
Figure 27.UN01



Table 27.2

CHARACTERISTIC	DOMAIN		
	Bacteria	Archaea	Eukarya
Nuclear envelope	Absent	Absent	Present
Membrane-enclosed organelles	Absent	Absent	Present
Peptidoglycan in cell wall	Present	Absent	Absent
Membrane lipids	Unbranched hydrocarbons	Some branched hydrocarbons	Unbranched hydrocarbons
RNA polymerase	One kind	Several kinds	Several kinds
Initiator amino acid for protein synthesis	Formyl-methionine	Methionine	Methionine
Introns in genes	Very rare	Present in some genes	Present in many genes
Response to the antibiotics streptomycin and chloramphenicol	Growth inhibited	Growth not inhibited	Growth not inhibited
Histones associated with DNA	Absent	Present in some species	Present
Circular chromosome	Present	Present	Absent
Growth at temperatures > 100°C	No	Some species	No

Figure 27.16



- Some archaea live in extreme environments and are called **extremophiles**
- **Extreme halophiles** live in highly saline environments
- **Extreme thermophiles** thrive in very hot environments

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- **Methanogens** live in swamps and marshes and produce methane as a waste product
- Methanogens are strict anaerobes and are poisoned by O_2
- In recent years, genetic prospecting has revealed many new groups of archaea
- Some of these may offer clues to the early evolution of life on Earth

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Figure 27.UN02



Bacteria

- Bacteria include the vast majority of prokaryotes of which most people are aware
- Diverse nutritional types are scattered among the major groups of bacteria

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Proteobacteria

- These gram-negative bacteria include photoautotrophs, chemoautotrophs, and heterotrophs
- Some are anaerobic, and others aerobic

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Figure 27.17-a

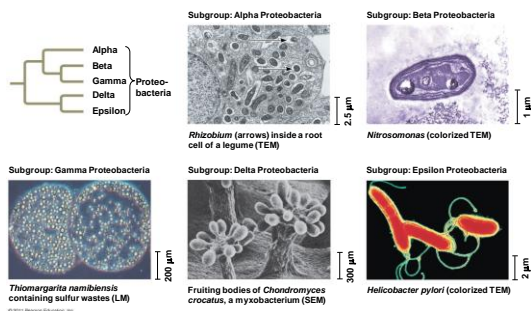
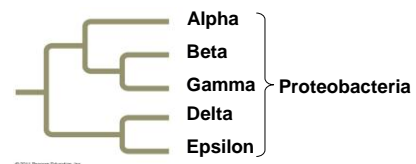


Figure 27.17a



Subgroup: Alpha Proteobacteria

- Many species are closely associated with eukaryotic hosts
- Scientists hypothesize that mitochondria evolved from aerobic alpha proteobacteria through endosymbiosis

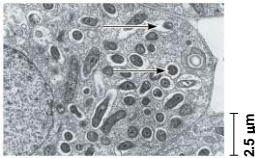
- Example: *Rhizobium*, which forms root nodules in legumes and fixes atmospheric N_2
- Example: *Agrobacterium*, which produces tumors in plants and is used in genetic engineering

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Figure 27.17b

Subgroup: Alpha Proteobacteria



Rhizobium (arrows) inside a root cell of a legume (TEM)

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Figure 27.17c

Subgroup: Beta Proteobacteria



Nitrosomonas (colorized TEM)

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Subgroup: Beta Proteobacteria

- Example: the soil bacterium *Nitrosomonas*, which converts NH_4^+ to NO_2^-

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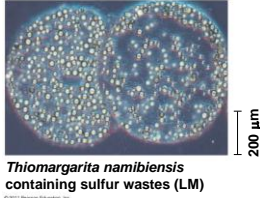
Subgroup: Gamma Proteobacteria

- Examples include sulfur bacteria such as *Chromatium* and pathogens such as *Legionella*, *Salmonella*, and *Vibrio cholerae*
- *Escherichia coli* resides in the intestines of many mammals and is not normally pathogenic

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Figure 27.17d

Subgroup: Gamma Proteobacteria



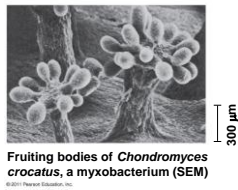
Subgroup: Delta Proteobacteria

- Example: the slime-secreting myxobacteria

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Figure 27.17e

Subgroup: Delta Proteobacteria



Subgroup: Epsilon Proteobacteria

- This group contains many pathogens including *Campylobacter*, which causes blood poisoning, and *Helicobacter pylori*, which causes stomach ulcers

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Figure 27.17f

Subgroup: Epsilon Proteobacteria

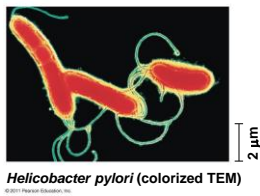


Figure 27.17-b

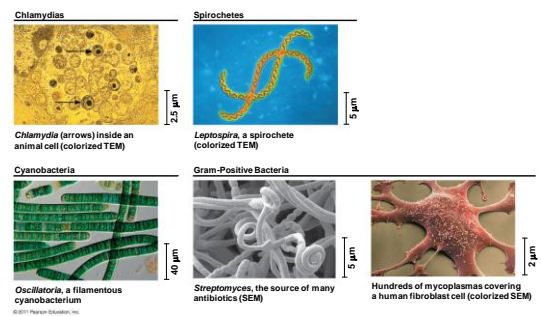
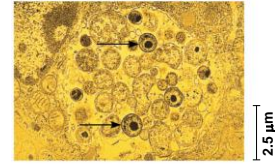


Figure 27.17g

Chlamydias

- These bacteria are parasites that live within animal cells
- *Chlamydia trachomatis* causes blindness and nongonococcal urethritis by sexual transmission

Chlamydias



Chlamydia (arrows) inside an animal cell (colorized TEM)

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Figure 27.17h

Spirochetes

- These bacteria are helical heterotrophs
- Some are parasites, including *Treponema pallidum*, which causes syphilis, and *Borrelia burgdorferi*, which causes Lyme disease

Spirochetes



Leptospira, a spirochete (colorized TEM)

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Figure 27.17i

Cyanobacteria

- These are photoautotrophs that generate O₂
- Plant chloroplasts likely evolved from cyanobacteria by the process of endosymbiosis

Cyanobacteria



Oscillatoria, a filamentous cyanobacterium

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Figure 27.17j

Gram-Positive Bacteria

- Gram-positive bacteria include
 - Actinomycetes, which decompose soil
 - Bacillus anthracis*, the cause of anthrax
 - Clostridium botulinum*, the cause of botulism
 - Some *Staphylococcus* and *Streptococcus*, which can be pathogenic
 - Mycoplasmas, the smallest known cells

Gram-Positive Bacteria



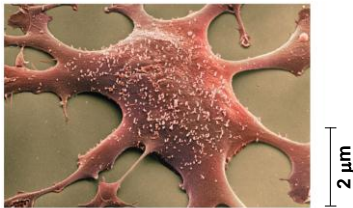
Streptomyces, the source of many antibiotics (SEM)

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Figure 27.17k

Gram-Positive Bacteria



Hundreds of mycoplasmas covering a human fibroblast cell (colorized SEM)

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Concept 27.5: Prokaryotes play crucial roles in the biosphere

- Prokaryotes are so important that if they were to disappear the prospects for any other life surviving would be dim

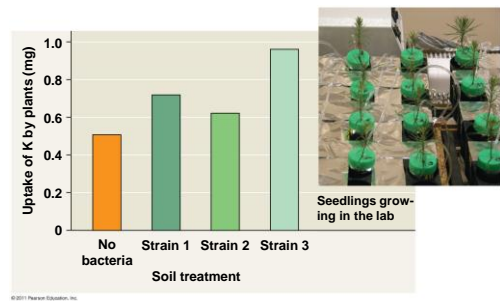
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Chemical Recycling

- Prokaryotes play a major role in the recycling of chemical elements between the living and nonliving components of ecosystems
- Chemoheterotrophic prokaryotes function as **decomposers**, breaking down dead organisms and waste products
- Prokaryotes can sometimes increase the availability of nitrogen, phosphorus, and potassium for plant growth

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Figure 27.18



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Figure 27.18a



Seedlings growing in the lab

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- Prokaryotes can also “immobilize” or decrease the availability of nutrients

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Ecological Interactions

- **Symbiosis** is an ecological relationship in which two species live in close contact: a larger **host** and smaller **symbiont**
- Prokaryotes often form symbiotic relationships with larger organisms

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- In **mutualism**, both symbiotic organisms benefit
- In **commensalism**, one organism benefits while neither harming nor helping the other in any significant way
- In **parasitism**, an organism called a **parasite** harms but does not kill its host
- Parasites that cause disease are called **pathogens**

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Figure 27.19



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- The ecological communities of hydrothermal vents depend on chemoautotrophic bacteria for energy

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Concept 27.6: Prokaryotes have both beneficial and harmful impacts on humans

- Some prokaryotes are human pathogens, but others have positive interactions with humans

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Mutualistic Bacteria

- Human intestines are home to about 500–1,000 species of bacteria
- Many of these are mutualists and break down food that is undigested by our intestines

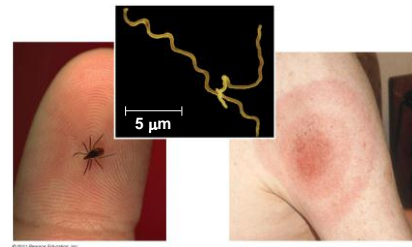
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Pathogenic Bacteria

- Prokaryotes cause about half of all human diseases
 - For example, Lyme disease is caused by a bacterium and carried by ticks

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Figure 27.20



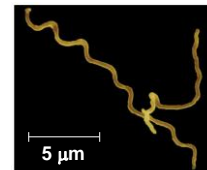
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Figure 27.20a



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Figure 27.20b



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Figure 27.20c



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- Pathogenic prokaryotes typically cause disease by releasing exotoxins or endotoxins
- **Exotoxins** are secreted and cause disease even if the prokaryotes that produce them are not present
- **Endotoxins** are released only when bacteria die and their cell walls break down

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- Horizontal gene transfer can spread genes associated with virulence
- Some pathogenic bacteria are potential weapons of bioterrorism

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Prokaryotes in Research and Technology

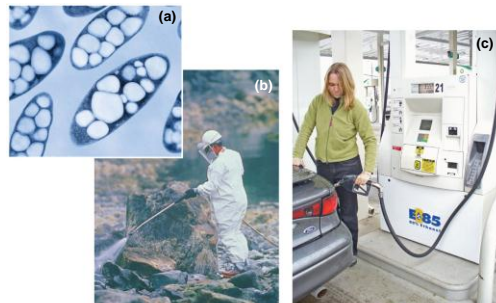
- Experiments using prokaryotes have led to important advances in DNA technology
 - For example, *E. coli* is used in gene cloning
 - For example, *Agrobacterium tumefaciens* is used to produce transgenic plants
- Bacteria can now be used to make natural plastics

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- Prokaryotes are the principal agents in **bioremediation**, the use of organisms to remove pollutants from the environment
- Bacteria can be engineered to produce vitamins, antibiotics, and hormones
- Bacteria are also being engineered to produce ethanol from waste biomass

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Figure 27.21



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Figure 27.21a

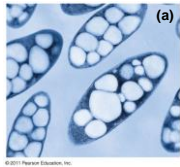


Figure 27.21b



Figure 27.21c



Figure 27.UN03

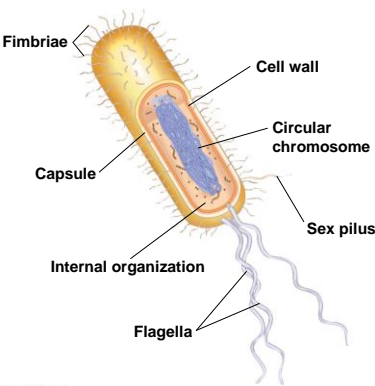


Figure 27.UN04

Rhizobium strain	1	2	3	4	5	6
Plant mass (g)	0.91	0.06	1.56	1.72	0.14	1.03

Source: J. J. Burdon et al., Variation in the effectiveness of symbiotic associations between native rhizobia and temperate Australian *Acacia*: within species interactions, *Journal of Applied Ecology* 36:398–408 (1999).

Note: Without *Rhizobium*, after 12 weeks, *Acacia* plants have a mass of about 0.1 g.

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Figure 27.UN05

