TWELFTH EDITION

CAMPBELL BIOLOGY URRY · CAIN · WASSERMAN MINORSKY · ORR



# Chapter 27

# Bacteria and Archaea

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### What characteristics enable prokaryotes to reach huge population sizes and thrive in diverse environments?



# What characteristics enable prokaryotes to reach huge population sizes and thrive in diverse environments?

- Prokaryotes are single-celled organisms that make up domains Bacteria and Archaea
- Adapted to diverse and extreme environments, they are the most abundant organisms on Earth

# CONCEPT 27.1: Structural and functional adaptations contribute to prokaryotic success

- Prokaryotes were the first organisms to inhabit Earth
- Most are unicellular, but some species form colonies
- Most prokaryotic cells are 0.5–5 µm, much smaller than the 10–100 µm of many eukaryotic cells
- They have a variety of shapes including spheres (cocci), rods (bacilli), and spirals



#### **Cell-Surface Structures**

- The cell wall maintains shape, protects the cell, and prevents it from bursting in a hypotonic environment
- Most prokaryotes lose water and experience plasmolysis in hypertonic environments
- Salt is used as a preservative because water loss slows reproduction of food-spoiling prokaryotes

- Eukaryote cell walls are made of cellulose or chitin
- Most bacterial cell walls instead contain peptidoglycan, a network of sugar polymers crosslinked by polypeptides
- Archaeal walls contain a variety of 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
- The walls of gram-negative bacteria have less peptidoglycan and are more complex with an outer membrane that contains lipopolysaccharides

(a) Gram-positive bacteria (b) Gram-negative bacteria Carbohydrate portion of lipopolysaccharide Outer membrane Peptido-Cell Cell glycan Peptidowall wall layer glycan Plasma layer membrane Plasma membrane

Stain a darker color and have a thick cell wall of peptidoglycan

Gram-positive bacteria



Have a thinner layer of peptidoglycan between plasma and outer membranes

, Gram-negative bacteria

- Gram-negative bacteria tend to be more resistant to antibiotics than gram-positive bacteria
- Many antibiotics target peptidoglycan and damage gram-positive bacterial cell walls
- Human cells lack peptidoglycan and are unaffected by antibiotics

- Many prokaryotes have a sticky layer of polysaccharide or protein surrounding the cell wall
- It is called a capsule if it is dense and well-defined, or a slime layer if it is not well organized
- Both types enable adherence to the substrate or other individuals, prevent dehydration, and protect the cell from the host's immune system



- Some bacteria form metabolically inactive endospores when water or nutrients are lacking
- The cell copies its chromosome and surrounds it with a multilayered structure
- Endospores can withstand extreme conditions and remain viable for centuries



- Some prokaryotes have hairlike appendages called fimbriae that allow them to stick to their substrate or other individuals in a colony
- **Pili** (or *sex pili*) are longer than fimbriae and function to pull cells together enabling the exchange of DNA



#### Motility

- About half of all prokaryotes exhibit taxis, the ability to move toward or away from a stimulus
  - For example, *chemotaxis* is the movement toward or away from a chemical stimulus

- Flagella are the most common structures used by prokaryotes for movement
- They may be scattered over the entire surface or concentrated at the ends of the cell
- Flagella of prokaryotes and eukaryotes differ in structure, mechanism of propulsion, and molecular composition



#### Video: Prokaryotic flagella



#### **Evolutionary Origins of Bacterial Flagella**

- Bacterial flagella are composed of 42 different kinds of proteins that form a motor, hook, and filament
- Bacterial flagella likely originated as simpler structures that were modified stepwise over time

- Only half of the flagellum's proteins are essential
- About half of those are modified versions of proteins with different functions
- Proteins forming the rod, hook, and filament are all descended from a protein that formed a pilus-like tube

- Flagella likely evolved as existing proteins were added to an ancestral secretory system
- This is an example of exaptation, where structures adapted for one function take on new functions through descent with modification

#### **Internal Organization and DNA**

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



(a) Aerobic prokaryote

(b) Photosynthetic prokaryote

- Prokaryotes have less DNA and produce fewer proteins than the eukaryotes
- Prokaryotes have one circular chromosome; eukaryotes have multiple linear chromosomes
- Prokaryotes lack a nucleus; the chromosome is in the nucleoid, a region with no membrane
- Prokaryotes may also have smaller rings of independently replicating DNA called plasmids



- There are minor differences in DNA replication, transcription, and translation between eukaryotes and prokaryotes
- These differences allow antibiotics to kill or inhibit bacterial cell growth without harming human cells

#### Reproduction

- Prokaryotes reproduce quickly by binary fission and can divide every 1–3 hours under optimal conditions
- There are three key features of prokaryote biology:
  - They are small
  - They reproduce by binary fission
  - They have short generation times

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

- Three factors contribute to the high levels of genetic diversity observed in prokaryote populations:
  - Rapid reproduction
  - Mutation
  - Genetic recombination

#### **Rapid Reproduction and Mutation**

- Cells produced by binary fission are generally identical, but differences can arise through mutation
- Mutation rates are typically low, but mutations accumulate rapidly with short generation times and large populations



Data from V. S. Cooper and R. E. Lenski, The population genetics of ecological specialization in evolving *Escherichia coli* populations, *Nature* 407:736–739 (2000).

- Rapid production of genetic diversity in prokaryote populations enables rapid adaptation by natural selection
- Though structurally simpler than eukaryote cells, prokaryotes are highly evolved

#### **Genetic Recombination**

- Genetic recombination, the combining of DNA from two sources, contributes to prokaryote diversity
- DNA from different individuals can be combined by transformation, transduction, or conjugation
- Movement of genes between individual prokaryotes of different species is called horizontal gene transfer

#### **Transformation and Transduction**

- In transformation, prokaryotic cells incorporate foreign DNA taken up from their surroundings
  - For example, a nonpathogenic cell could take up a piece of DNA carrying an allele for pathogenicity and replace its own allele with the foreign allele
  - The resulting recombinant cell would be pathogenic
- In transduction, phages (from "bacteriophages," viruses that infect bacteria) carry prokaryotic genes from one host cell to another
- Transduction is generally an unintended result of the phage replicative cycle



#### **Conjugation and Plasmids**

- Conjugation is the process through which DNA is transferred between two prokaryotic cells
- In bacteria, the DNA transfer is always one way:
  One cell donates the DNA and the other receives it

- In *E. coli*, conjugation occurs by the following steps:
  - A pilus of the donor cell attaches to the recipient
  - The pilus retracts, pulling the two cells together
  - DNA is transferred through a temporary structure called the "mating bridge"



- A piece of DNA called the F factor (F for fertility) is required for the production of pili
- The F factor can exist either as a plasmid or a segment of DNA within the bacterial chromosome

#### The F Factor as a Plasmid

- Cells containing the F plasmid (F<sup>+</sup> cells) function as DNA donors
- Cells lacking the F factor (F<sup>-</sup> cells) are recipients
- An F<sup>+</sup> cell can convert an F<sup>-</sup> cell to an F<sup>+</sup> cell if it transfers an entire F plasmid to the F<sup>-</sup> cell
- If only part of the F plasmid's DNA is transferred, the recipient cell will be recombinant



(a) Conjugation and transfer of an F plasmid

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#### The F Factor in the Chromosome

- Cells that have the F factor in their chromosome (Hfr cells, named for <u>high frequency of</u> <u>recombination</u>) function as donors during conjugation
- Homologous segments of the chromosomal DNA from the Hfr cell recombines with that of the F<sup>-</sup> cell
- The recombinant recipient cell becomes a new genetic variant on which evolution can act



(b) Conjugation and transfer of part of an Hfr bacterial chromosome, resulting in recombination



(a) Conjugation and transfer of an F plasmid



(b) Conjugation and transfer of part of an Hfr bacterial chromosome, resulting in recombination

#### **R Plasmids and Antibiotic Resistance**

- Antibiotics kill most bacteria, but not those with R plasmids, plasmids that carry resistance genes
- Some R plasmids carry genes for resistance to multiple antibiotics
- R plasmids also have genes that encode the pili used to transfer DNA between cells, enabling the rapid spread of resistance

# 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<sub>2</sub> or related compounds as a carbon source
  - Heterotrophs require an organic nutrient to make other organic compounds

- Energy and carbon sources are combined to give four major modes of nutrition:
  - Photoautotroph
  - Chemoautotroph
  - Photoheterotroph
  - Chemoheterotroph

Table 27.1

Mode	Energy Source	Carbon Source	Types of Organisms
AUTOTROPH			
Photoautotroph	Light	CO <sub>2</sub> , HCO <sub>3</sub> -, or related compound	Photosynthetic prokaryotes (for example, cyanobacteria); plants; certain protists (for example, algae)
Chemoautotroph	Inorganic chemicals (such as $H_2S$ , NH <sub>3</sub> , or Fe <sup>2+</sup> )	CO <sub>2</sub> , HCO <sub>3</sub> -, or related compound	Unique to cer- tain 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 prokary- otes (for exam- ple, <i>Clostridium</i> ) and protists; fungi; animals; some plants

# The Role of Oxygen in Metabolism

- Prokaryotic metabolism varies with respect to O<sub>2</sub>
  - Obligate aerobes require O<sub>2</sub> for cellular respiration
  - Obligate anaerobes are poisoned by O<sub>2</sub> and live by fermentation or use substances other than O<sub>2</sub> for anaerobic respiration
  - Facultative anaerobes can use O<sub>2</sub> if it is present or carry out fermentation or anaerobic respiration if not

#### Nitrogen Metabolism

- Nitrogen is essential for the production of amino acids and nucleic acids in all organisms
- Prokaryotes metabolize nitrogen in many forms
  - For example, some prokaryotes convert atmospheric nitrogen (N<sub>2</sub>) to ammonia (NH<sub>3</sub>) in a process called **nitrogen fixation**

#### **Metabolic Cooperation**

- Prokaryote cells may cooperate to use resources unavailable to individual cells
  - For example, in the filamentous cyanobacterium
    Anabaena, cells are specialized for nitrogen-fixation
    or photosynthesis
  - Nitrogen-fixation is isolated in cells called
    heterocysts that prevent oxygen penetration
  - Photosynthetic cells exchange carbohydrates for the fixed nitrogen produced by the heterocysts



- Cells of one or more prokaryote species cooperate to form surface-coating colonies called **biofilms**
- Cells near the edge release signaling molecules to recruit new cells
- Channels in the biofilm allow nutrients to reach cells in the interior and wastes to be expelled

- Biofilms are common in nature, but can cause many problems for humans including
  - Corrosion of industrial structures and products
  - Contamination of medical devices
  - Tooth decay
  - Chronic, antibiotic-resistant infections



# CONCEPT 27.4: Prokaryotes have radiated into a diverse set of lineages

- Prokaryotes date back to 3.5 billion years ago
- They now inhabit every environment known to support life
- Advances in genomics are just beginning to reveal the extent of prokaryotic diversity

### An Overview of Prokaryotic Diversity

- Genetic analysis conducted in the 1970s led to the division of prokaryotes into Bacteria and Archaea
- Analysis of over 1,700 genomes indicates a few of the traditional groups are monophyletic, but others are scattered throughout several lineages



# An Overview of Prokaryotic Diversity

- In the past, the polymerase chain reaction (PCR) was used to analyze individual prokaryote genes
- Today, metagenomics is used to obtain entire prokaryotic genomes from environmental samples
- Though only 16,000 prokaryote species have been named, a handful of soil can contain 10,000 species

- Horizontal gene transfer has played a key role in the evolution of prokaryotes
- Significant portions of the genomes of prokaryotes are mosaics of genes imported from other species
  - For example, in a study of 329 bacterial genomes, an average of 75% of the genes in each genome had been horizontally transferred at some point

#### Bacteria

- Bacteria include the vast majority of prokaryotic species familiar to most people
- Every major mode of nutrition and metabolism is represented among bacteria

Figure 27.UN01



Known species of bacteria (16,000)

Estimated number of undiscovered species of bacteria

Spirochetes



Leptospira





Thiomargarita namibiensis (LM)

#### Cyanobacteria



Cylindrospermum

#### Chlamydias



Chlamydia (TEM)

#### Gram-positive bacteria



5 µm

Streptomyces

# Figure 27.17 Exploring bacterial diversity

- There are about 16,000 known species of bacteria
- The actual number is estimated to be 700,000–1.4 million species



#### Proteobacteria

- Gram-negative bacteria including photoautotrophs, chemoautotrophs, and heterotrophs
  - For example, the sulfur bacterium *Thiomargarita namibiensis*, is an autotroph that obtains energy by oxidizing H<sub>2</sub>S and producing sulfur as a waste product

#### Proteobacteria



#### Thiomargarita namibiensis (LM)

- Heterotrophic proteobacteria include several pathogens
  - Neisseria gonorrhoeae causes gonorrhea
  - Vibrio cholerae causes cholera
  - Helicobacter pylori causes stomach ulcers

#### Chlamydias

- All species parasitize animal cells and have gramnegative walls lacking peptidoglycan
  - For example, *Chlamydia trachomatis* causes nongonococcal urethritis, the most common sexually transmitted disease in the United States
#### Chlamydias



### Chlamydia (inside an animal cell; TEM)

## **Spirochetes**

- These bacteria are helical gram-negative heterotrophs that spiral through the environment by rotating internal filaments
- Many are free-living, but others are pathogens
  - For example, *Treponema pallidum*, causes syphilis, and *Borrelia burgdorferi*, causes Lyme disease

## **Spirochetes**



5 µm

# Leptospira

## Cyanobacteria

- These bacteria are gram-negative photoautotrophs
- Plant chloroplasts likely evolved from cyanobacteria by the process of endosymbiosis
- Solitary and filamentous cyanobacteria are abundant components of freshwater and marine phytoplankton

## Cyanobacteria



# Cylindrospermum

## Video: Cyanobacteria (Oscillatoria)



#### **Gram-Positive Bacteria**

- Gram-positive bacteria are a diverse group
  - Actinomycetes are colony forming bacteria including pathogens and soil decomposers
  - Soil-dwelling species of *Streptomyces* are cultured as a source of antibiotics, including tetracycline
  - Other subgroups include pathogens such as Staphylococcus aureus; Bacillus anthracis, the cause of anthrax; and Clostridium botulinum, the cause of botulism

#### **Gram-positive bacteria**



#### Streptomyces

## Archaea

- Archaea share certain traits with bacteria and other traits with eukaryotes
- They also have many unique characteristics



	DOMAIN		
CHARACTERISTIC	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

- **Extremophiles** are archaea that live in extreme environments, uninhabitable for most organisms
  - Extreme halophiles either tolerate or require highly saline environments
  - Extreme thermophiles have adaptations that make their DNA and proteins stable at high temperatures (even above 100°C)



- Methanogens are obligate anaerobes that produce methane as a by-product of their metabolism
- They are found in diverse environments
  - Under kilometers of ice in Greenland
  - In swamps and marshes
  - In the guts of cattle, termites, and other herbivores

- Euryarchaeota is the clade that includes many of the extreme halophiles, most methanogens, and some extreme thermophiles
- Most of the extreme thermophiles belong to another clade

- TACK is a supergroup composed of the remaining, closely-related clades of archaea
- The group is named for its component clades
  - <u>T</u>haumarchaeota
  - <u>A</u>igarchaeota
  - <u>Crenarchaeota</u>—includes most extreme thermophiles
  - Korarchaeota

- Lokiarchaeotes are a recently discovered group, closely related to the TACK archaea, that may represent the sister group of the eukaryotes
- Characteristics of this group could shed light on how eukaryotes arose from their prokaryotic ancestors

# **CONCEPT 27.5: Prokaryotes play crucial roles** in the biosphere

 If prokaryotes were to disappear, the prospects for any other life surviving on Earth would be dim

# **Chemical Recycling**

- Prokaryotes play a major role in the recycling of chemical elements between the living and nonliving components of the environment
  - For example, some chemoheterotrophic prokaryotes are **decomposers**, they break down dead organisms and wastes and release carbon and other elements

- Prokaryotes can convert some molecules to forms that are taken up by other organisms
  - Autotrophic prokaryotes use  $CO_2$  to produce sugars and  $O_2$  that are consumed by other organisms
  - Nitrogen-fixing bacteria transform atmospheric nitrogen into forms available to other organisms
  - Some prokaryotes can increase the availability of soil nutrients that plants require for growth



 Prokaryotes can also "immobilize" or decrease the availability of nutrients by using them within their own cells

# **Ecological Interactions**

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

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



- The existence of some ecosystems depends on prokaryotes
  - For example, the ecological communities of hydrothermal vents depend on chemoautotrophic bacteria for energy

# CONCEPT 27.6: Prokaryotes have both beneficial and harmful impacts on humans

- The best-known prokaryotes are human pathogens, but they represent a small fraction of prokaryotes
- Many others have positive interactions with people; some play essential roles in agriculture and industry

# **Mutualistic Bacteria**

- Human intestines are home to about 500–1,000 species of bacteria
- Intestinal bacteria cells collectively outnumber all human cells in the body by a factor of ten

- Many intestinal bacteria are mutualists
  - For example, *Bacteroides thetaiotaomicron*, has genes involved in synthesizing carbohydrates, vitamins, and other important nutrients
  - It also produces signals that activate human genes involved in absorption and antimicrobial production

# **Pathogenic Bacteria**

- All known pathogenic prokaryotes are bacteria
- Bacteria cause about half of all human diseases
  - For example, more than 1.5 million people die each year of tuberculosis, a lung disease caused by *Mycobacterium tuberculosis*

- Some bacterial diseases are transmitted by other species
  - For example, Lyme disease, which can cause arthritis, heart disease, nervous disorders, and death, infects about 300,000 people per year in the United States
  - It is caused by a bacterium that is carried by ticks



- Pathogenic prokaryotes typically cause disease by releasing exotoxins or endotoxins
- Exotoxins are proteins secreted by bacteria that can cause disease even if the bacteria are no longer present
  - For example, cholera is a diarrheal disease caused by an exotoxin secreted by a *Vibrio cholerae*

- Endotoxins are lipopolysaccharide components of the outer membrane of gram-negative bacteria
- They are released only when bacteria die and their cell walls break down
  - For example, endotoxins released by species in the genus Salmonella cause food poisoning

- Horizontal gene transfer can spread genes associated with virulence to normally harmless bacteria
  - For example, pathogenic strains of the intestinal bacteria *E. coli* were produced by phase-mediated transfer of genes from pathogenic species

# **Antibiotic Resistance**

- Since their introduction in the 1940s, resistance to antibiotics has evolved rapidly in many bacteria
- Discovery of new antibiotics has not kept pace with the rate at which bacteria have evolved resistance
- For every antibiotic now in use, at least one species of bacteria has developed resistance to it


- Rapid reproduction enables bacterial cells carrying resistance genes to quickly produce large numbers of resistant offspring
- Resistance genes spread rapidly within and among bacterial species by horizontal gene transfer

- Highly lethal, drug-resistant strains of the tuberculosis bacterium have arisen since 2006
- By 2017, more than 100 countries had confirmed cases of the resistant strain
- Few treatment options are available, and they are more toxic than treatments for standard strains

- A new class of antibiotics called *malacidins* was recently discovered through metagenomic analysis of soil bacteria
- Malacidins are effective against multidrug-resistant gram-positive pathogens



 Virus-like particles capable of targeting and killing particular species of multidrug-resistant bacteria were developed in 2018

## **Prokaryotes in Research and Technology**

- Humans reap many benefits from bacteria including the production of many foods:
  - Cheese and yogurt from milk
  - Beer and wine
  - Pepperoni
  - Fermented cabbage (sauerkraut)
  - Soy sauce

- Experiments using prokaryotes have led to important advances in DNA technology
  - E. coli is used in gene cloning
  - DNA polymerase from *Pyrococcus furiosus* is used in the PCR technique

- The CRISPR-Cas9 system, which helps prokaryotes defend against viral attack, has been developed as a gene altering tool
- This system has been used to study HIV, the virus that causes AIDS



### (a) Control cells

### (b) Experimental cells

- Bacteria can be used to produce natural plastics
  - For example, some bacteria synthesize PHA, a polymer used to store chemical energy
  - PHA can be extracted, formed into pellets, and used to make durable, biodegradable plastics



 Engineering bacteria to produce ethanol from agricultural waste, switchgrass, and corn can help reduce dependence on petroleum

- Prokaryotes can also be used in bioremediation, the use of organisms to remove pollutants from soil, air, or water
  - For example, bacteria that metabolize oil can be used to increase the breakdown of oil following a spill



#### **Data from the Experiment**

Treatment	Dose (mg/kg)	Log of Number of Colonies	Mean ( <del>x</del> )
Control		9.0, 9.5, 9.0, 8.9	
Vancomycin	1.0	8.5, 8.4, 8.2	
	5.0	5.3, 5.9, 4.7	
Teixobactin	1.0	8.5, 6.0, 8.4, 6.0	
	5.0	3.8, 4.9, 5.2, 4.9	

**Data from** L. Ling et al. A new antibiotic kills pathogens without detectable resistance, *Nature* 517:455–459 (2015).



# Plastic chip used to grow soil bacteria



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Rhizobium strain	1	2	3	4	5	6			
Plant mass (g)	0.91	0.06	1.56	1.72	0.14	1.03			
Data from J. J. Burdon et al., Variation in the effectiveness of symbiotic associations between native rhizobia and temperate Australian Acacia: within species interactions, <i>Journal of Applied Ecology</i> 36:398–408 (1999).									
<i>Note:</i> Without <i>Rhizobium</i> , after 12 weeks, <i>Acacia</i> plants have a mass of about 0.1 g.									

