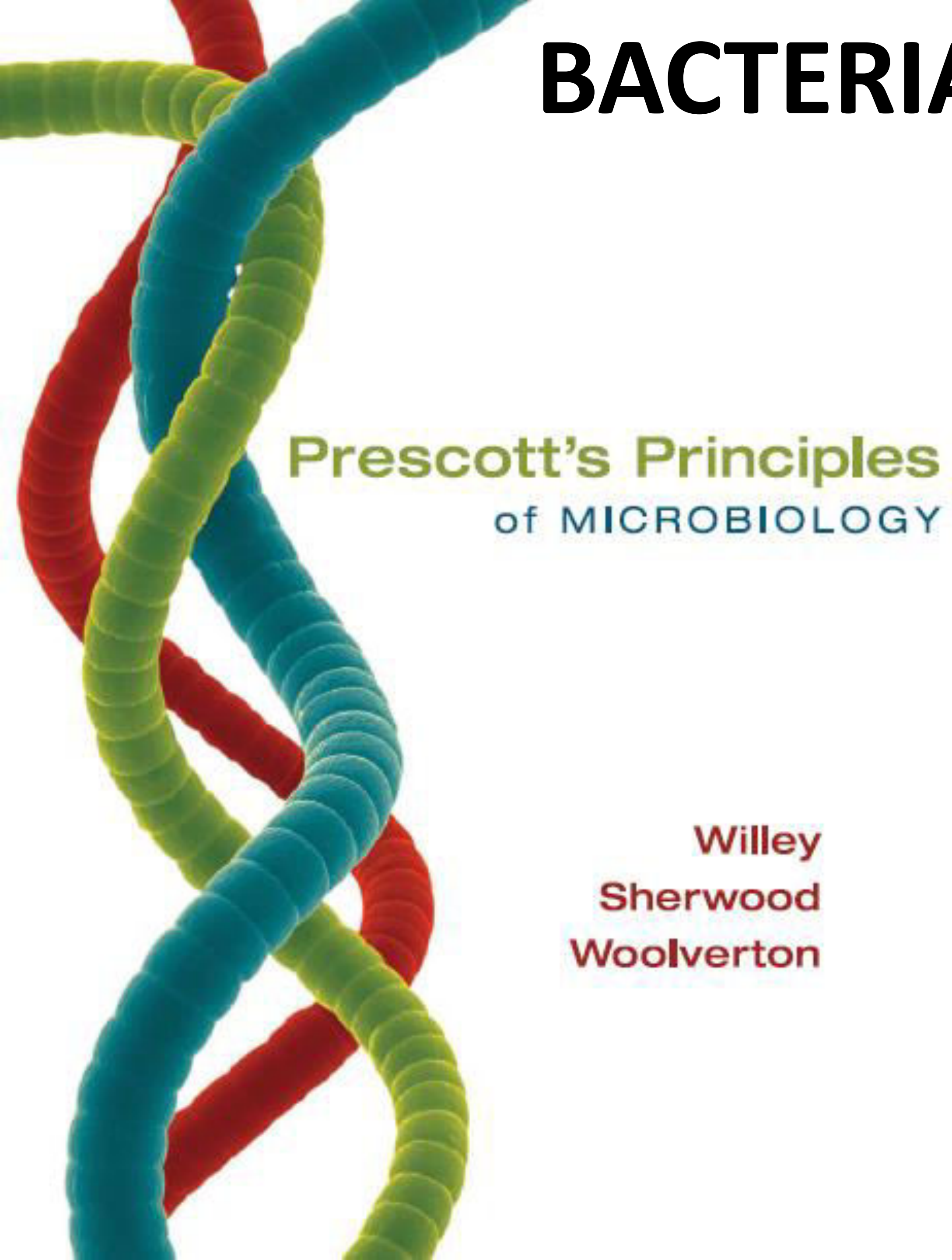
BACTERIAL CLASSIFICATION



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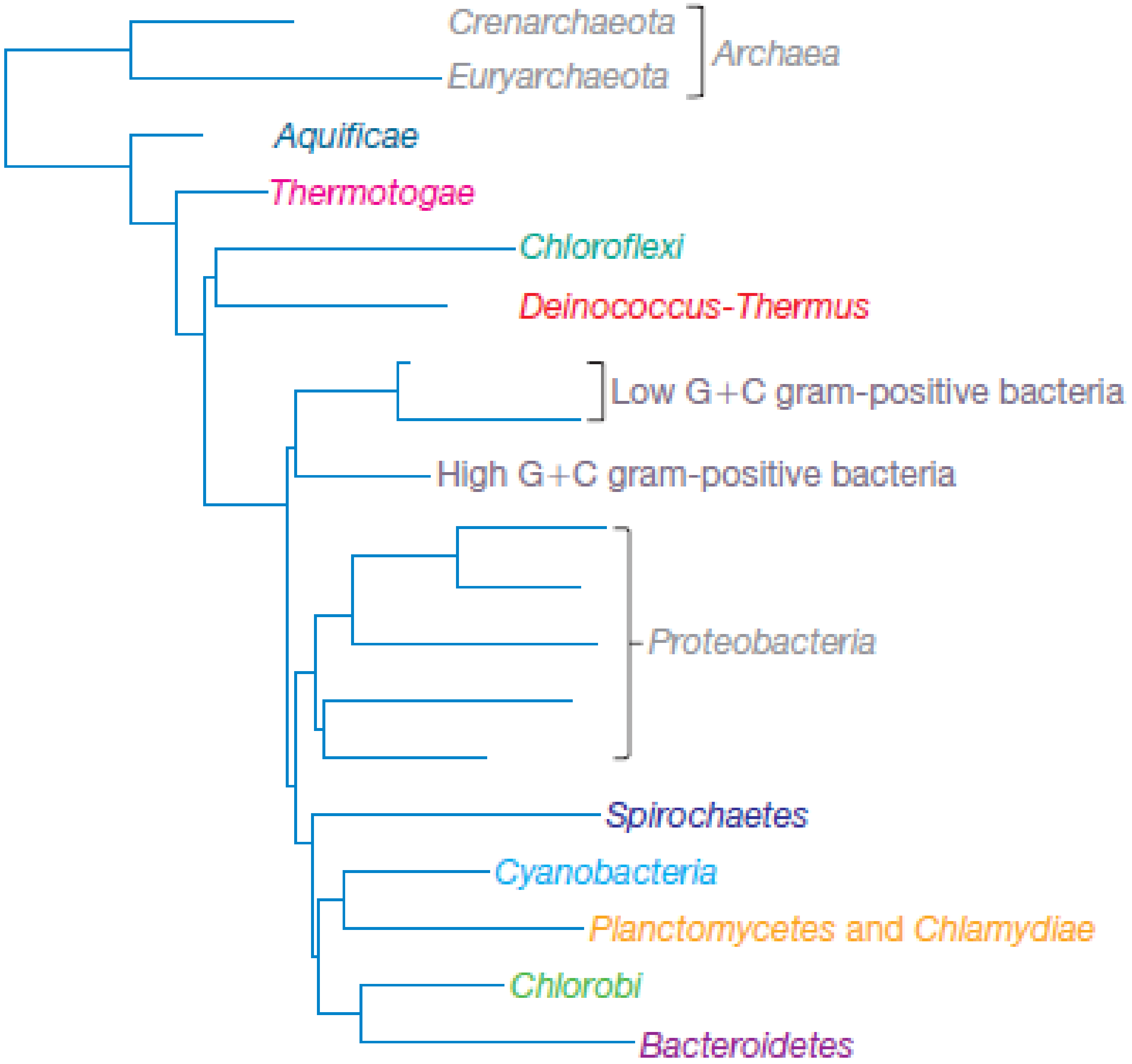
Phylogenetic Relationships Among Procaryotes



AQUIFICAE

- The phyla *Aquificiae* and *Thermotoga* are two examples of bacterial thermophiles.

- The phylum *Aquificae* is thought to represent the deepest or oldest branch of Bacteria.

- It contains one class, one order, and eight genera. Two of the best-studied genera are *Aquifex* and *Hydrogenobacter*.

- *Aquifex pyrophilus* is a gram negative, microaerophilic rod. It is thermophilic with a temperature optimum of 85°C and a maximum of 95°C. *Aquifex* is a chemolithoautotrophy that captures energy by oxidizing hydrogen, thiosulfate, and sulfur with oxygen as the terminal electron.

THERMOTOGAE

- The second deepest branch is the phylum Thermotogae, which has one class, one order, and six genera.

- The members of the genus Thermotoga (Greek therme, heat; Latin toga, outer garment), like Aquifex, are thermophiles with a growth optimum of 80°C and a maximum of 90°C.

- They are gram-negative rods with an outer sheathlike envelope (like a toga) that can extend or balloon out from the ends of the cell.

- They grow in active geothermal areas found in marine hydrothermal systems and terrestrial solfataric springs.

- In contrast to Aquifex, Thermotoga is a chemoheterotroph with a functional glycolytic pathway that can grow anaerobically on carbohydrates and protein digests.

DEINOCOCCUSTHERMUS

- The phylum Deinococcus-Thermus contains the class Deinococci and the orders Deinococcales and Thermales.
- There are **only three genera** in the phylum; the genus Deinococcus is best studied.
- Deinococci are spherical or rod-shaped and nonmotile.
- They often are associated in pairs or tetrads and are aerobic, mesophilic, and catalase positive; usually they can produce acid from only a few sugars.
- Although they stain gram positive, their cell wall is layered with an outer membrane like gram-negative bacteria.

- They also differ from gram-positive cocci in having **l-ornithine** in their peptidoglycan, **lacking teichoic acid**, and having a plasma membrane with large amounts of **palmitoleic acid** rather than phosphatidylglycerol phospholipids.

- Almost all strains are extraordinarily **resistant to both desiccation and radiation**; they can survive as much as 3 to 5 million rad of radiation (an exposure of 100 rad can be lethal to humans).

PHOTOSYNTHETIC BACTERIA

There are three groups of gram-negative photosynthetic bacteria: purple bacteria, green bacteria, and cyanobacteria.

Oxygenic photosynthesis: They have photosystems I and II, use water as an electron donor, and generate oxygen during photosynthesis.

Anoxygenic photosynthesis: In contrast, purple and green bacteria have only one photosystem and use anoxygenic photosynthesis. Because they are unable to use water as an electron source, they employ reduced molecules such as hydrogen sulfide, sulfur, hydrogen, and organic matter as their electron source for the reduction of $NAD(P)^+$ to NAD(P)H.

Table 19.1 Characteristics of the Major Groups of Gram-Negative Photosynthetic Bacteria

	Anoxygenic Photosynthetic Bacteria				Oxygenic Photosynthetic Bacteria
Characteristic	**Green Sulfur[a]**	**Green Nonsulfur[b]**	**Purple Sulfur**	**Purple Nonsulfur**	**Cyanobacteria**
Major photosynthetic pigments	Bacteriochlorophylls *a* plus *c, d,* or *e* (the major pigment)	Bacteriochlorophylls *a* and *c*	Bacteriochlorophyll *a* or *b*	Bacteriochlorophyll *a* or *b*	Chlorophyll *a* plus phycobiliproteins *Prochlorococcus* has divinyl derivatives of chlorophyll *a* and *b*
Morphology of photosynthetic membranes	Photosynthetic system partly in chlorosomes that are independent of the plasma membrane	Chlorosomes present when grown anaerobically	Photosynthetic system contained in spherical or lamellar membrane complexes that are continuous with the plasma membrane	Photosynthetic system contained in spherical or lamellar membrane complexes that are continuous with the plasma membrane	Thylakoid membranes lined with phycobilisomes
Photosynthetic electron donors	H_2, H_2S, S^0	Photoheterotrophic donors—a variety of sugars, amino acids, and organic acids; photoautotrophic donors—H_2S, H_2	H_2, H_2S, S^0	Usually organic molecules: sometimes reduced sulfur compounds or H_2	H_2O

Sulfur deposition	Outside of the cell	N/A[c]	Inside the cell[d]	Outside of the cell in a few cases	N/A
Nature of photosynthesis	Anoxygenic	Anoxygenic	Anoxygenic	Anoxygenic	Oxygenic (some are also facultatively anoxygenic)
General metabolic type	Obligate anaerobic photolithoautotrophs	Usually photoheterotrophic; sometimes photoautotrophic or chemoheterotrophic (when aerobic and in the dark)	Obligate anaerobic photolithoautotrophs	Usually anaerobic photoorgano-heterotrophs; some facultative photolithoautotrophs (in the dark, chemo-organoheterotrophs)	Aerobic photo-lithoautotrophs
Motility	Nonmotile; some have gas vesicles	Gliding	Motile with polar flagella; some are peritrichously flagellated	Motile with polar flagella or nonmotile; some have gas vesicles	Nonmotile, swimming motility without flagella or gliding motility; some have gas vesicles
Percent G + C	48–58	53–55	45–70	61–72	35–71
Phylum or class	*Chlorobi*	*Chloroflexi*	γ-proteobacteria	α-proteobacteria, β-proteobacteria (*Rhodocyclus*)	*Cyanobacteria*

Phylum *Chlorobi*

- The phylum Chlorobi has only one class (Chlorobia), order (Chlorobiales), and family (Chlorobiaceae).

- The **green sulfur bacteria** are a small group of **obligately anaerobic photolithoautotrophs** that use hydrogen sulfide, elemental sulfur, and hydrogen as electron sources. The elemental sulfur produced by sulfide oxidation is **deposited outside the cell**.

- Their photosynthetic pigments are located in **ellipsoidal vesicles** called **chlorosomes** or **chlorobium vesicles**, which are attached to the plasma membrane but are not continuous with it.

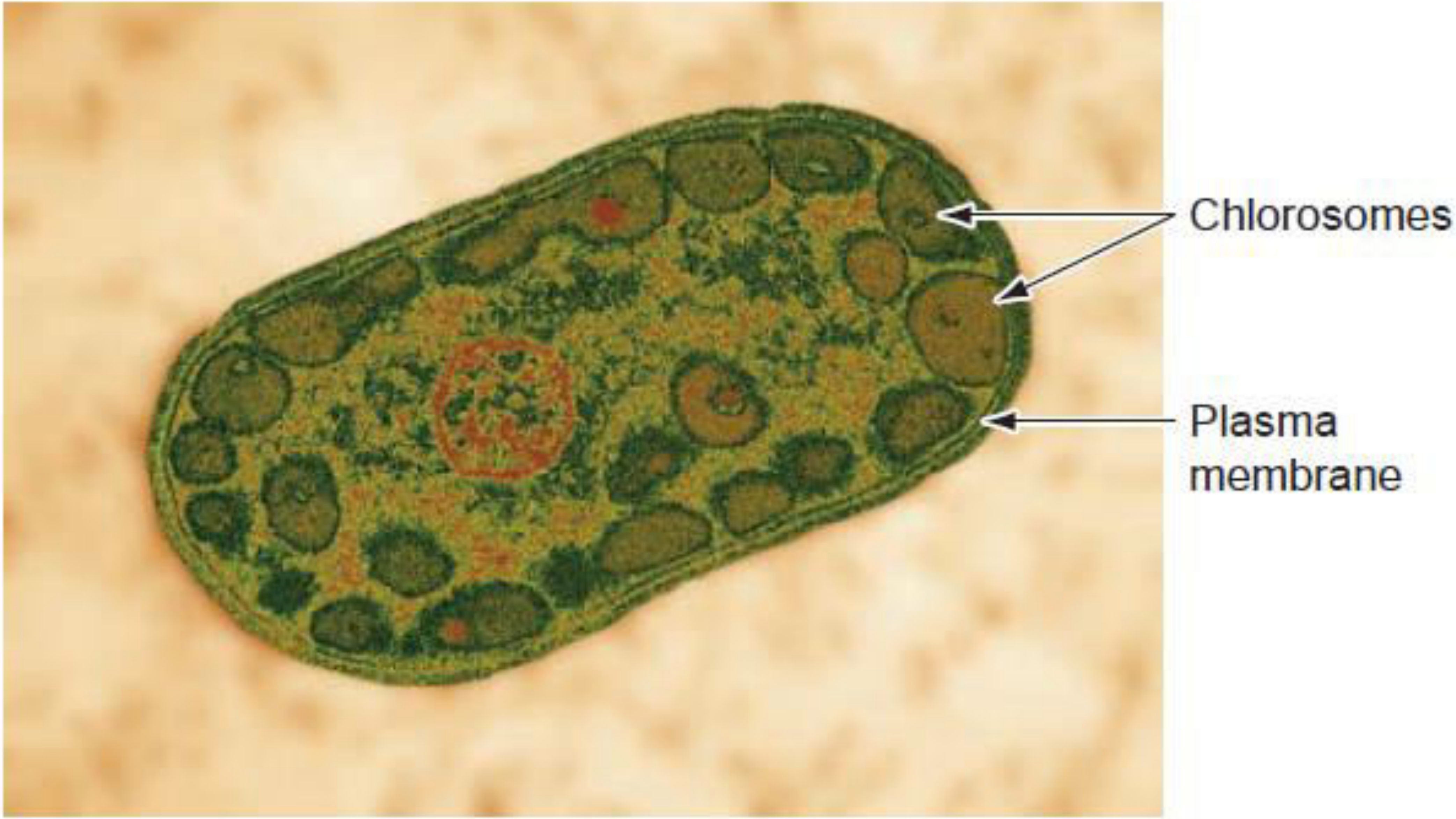
- Chlorosomes are the **most efficient light-harvesting complexes** found in nature. The chlorosome membrane is not a normal lipid bilayer. Instead, bacteriochlorophyll molecules are grouped into lateral arrays held together by carotenoids and lipids.

- Chlorosomes contain **accessory (antenna) Bchl pigments** b, d, or e; reaction centers with Bchl a are located in the plasma membrane, where they obtain energy from chlorosome pigments.

- These bacteria flourish in the anoxic, sulfide-rich zones of lakes. Although they **lack flagella and are nonmotile**, some species have **gas vesicles to adjust their depth for optimal light** and hydrogen sulfide.

- Those without vesicles are found in sulfide-rich muds at the bottom of lakes and ponds. The green sulfur bacteria are very diverse morphologically.

- They may be **rods, cocci, or vibrios**; some grow singly, and others form chains and clusters. They are either grass-green or chocolatebrown in color. Representative genera are *Chlorobium*, *Prosthecochloris*, and *Pelodictyon*.


Chlorosomes
Plasma
membrane

Phylum *Chloroflexi*

- The phylum *Chloroflexi* has both photosynthetic and nonphotosynthetic members. *Chlorofl exus* is the major representative of the photosynthetic **green nonsulfur bacteria.** However, the term green nonsulfur is a misnomer because not all members of this group are green, and some can use sulfur.

- *Chloroflexus* is a filamentous, gliding, thermophilic bacterium that often is isolated from neutral to alkaline hot springs, where it grows in the form of orange-reddish mats, usually in association with cyanobacteria.

- It possesses small chlorosomes with accessory Bchl *c.* Its light-harvesting complexes contain Bchl *a* and are in the plasma membrane. Metabolically, it is similar to that of the purple nonsulfur bacteria. *Chloroflexus* can carry out anoxygenic photosynthesis with organic compounds as carbon sources or grow aerobically as a chemoheterotroph.

- It doesn’t appear closely related to any other bacterial group based on 16S rRNA studies and is a deep and ancient branch of the bacterial tree. Genomic analysis of *Chloroflexus aurantiacus* should help elucidate the origin of photosynthesis.

- The nonphotosynthetic, gliding, rod-shaped or filamentous bacterium *Herpetosiphon* also is included in this phylum.

- *Herpetosiphon* is an aerobic chemoorganotroph with respiratory metabolism that uses oxygen as the electron acceptor. It can be isolated from freshwater and soil habitats.

Phylum *Cyanobacteria*

- The cyanobacteria are the largest and most diverse group of photosynthetic bacteria. Bergey's Manual describes 56 genera.

- Cyanobacterial diversity is reflected in the G+C content of the group, which ranges from 35 to 71%.

- Although cyanobacteria are gram-negative bacteria, their photosynthetic system closely resembles that of the eucaryotes, and endosymbiotic cyanobacteria are thought to have evolved into chloroplasts.

- It follows that all cyanobacteria and most photosynthetic eucaryotes have chlorophyll a and photosystems I and II, and thereby perform oxygenic photosynthesis.

- Cyanobacteria use phycobiliproteins as accessory pigments (just like red algae).

- Photosynthetic pigments and electron transport chain components are located in thylakoid membranes lined with particles called phycobilisomes.

- Carbon dioxide is assimilated through the Calvin cycle; the enzymes needed for this process are thought to be found in internal structures called **carboxysomes**.

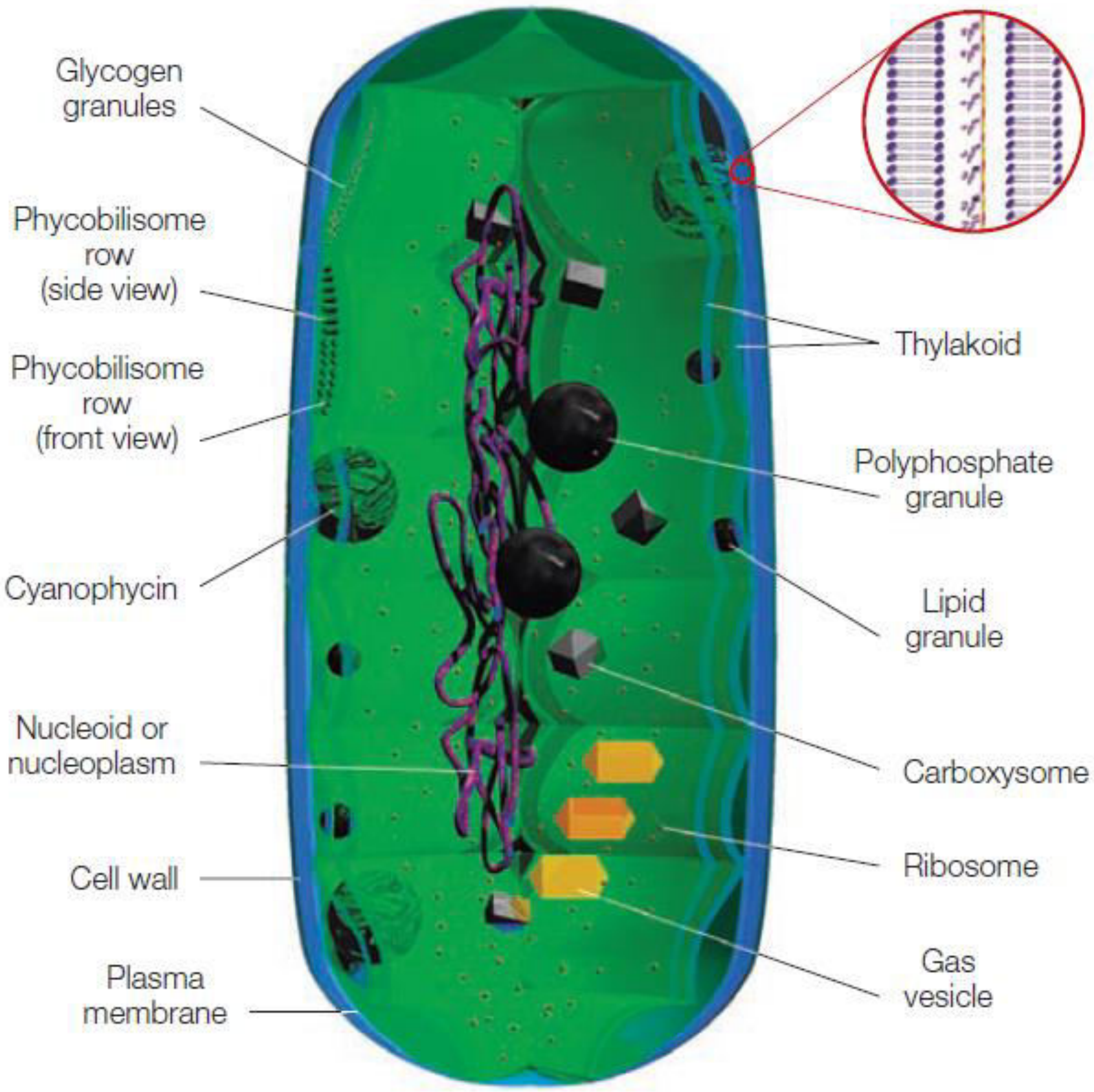
- The reserve carbohydrate is **glycogen**. Sometimes they store extra nitrogen as polymers of arginine and aspartic acid in **cyanophycin granules**.

- Phosphate is stored in **polyphosphate granules**. Because cyanobacteria **lack** the enzyme α-ketoglutarate dehydrogenase, they **do not have** a fully functional citric acid cycle.

- The **pentose phosphate pathway** plays a central role in their carbohydrate metabolism.

- Although many cyanobacteria are obligate **photolithoautotrophs**, a few can grow slowly in the dark as **chemoheterotrophs** by oxidizing glucose and a few other sugars.

- Under anoxic conditions, ***Oscillatoria limnetica*** oxidizes **hydrogen sulfide** instead of water and carries out anoxygenic photosynthesis much like the green photosynthetic bacteria.



- Cyanobacteria also vary greatly in shape and appearance. They range in diameter from about 1 to 10 μm and may be unicellular, exist as colonies of many shapes, or form filaments called **trichomes**.

- A **trichome** is a row of bacterial cells that are in **close contact with one another** over a large area.

- Although many cyanobacteria appear **blue-green** because of **phycocyanin**, isolates from the open ocean are **red or brown** because of the pigment **phycoerythrin**.

- Cyanobacteria modulate the relative amounts of these pigments in a process known as **chromatic adaptation**.

- When orange light is sensed, phycocyanin production is stimulated, while blue and blue-green light promote the production of phycoerythrin.

- Cyanobacteria show great diversity with respect to **reproduction** and employ a variety of mechanisms: **binary fission, budding, fragmentation, and multiple fission**.

- In the last process, a cell enlarges and then divides several times to produce many smaller progeny, which are released upon the rupture of the parental cell.

- Fragmentation of filamentous cyanobacteria can generate small, motile filaments called **hormogonia**.

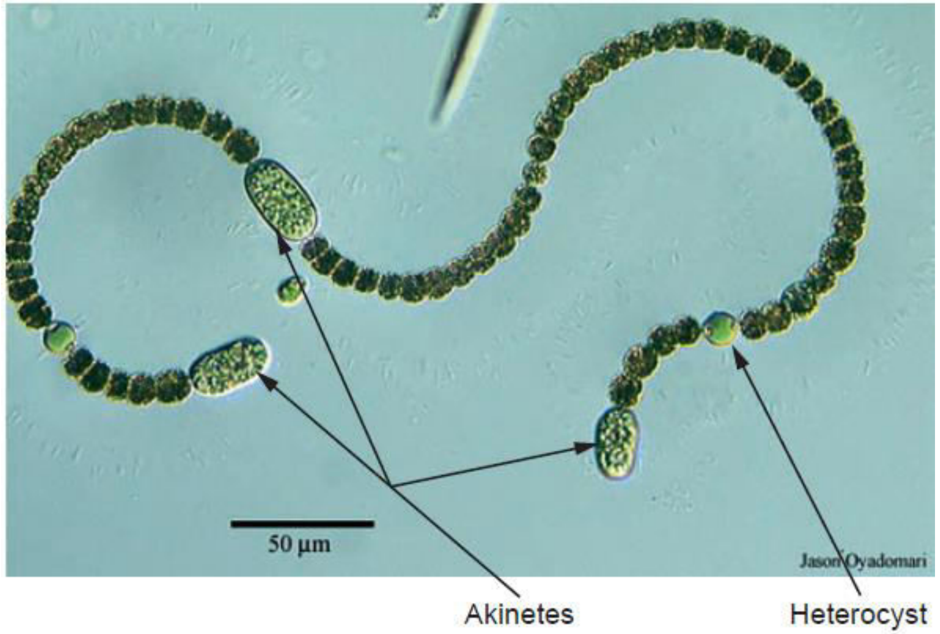
- Some species develop **akinetes**, specialized, **dormant, thick-walled resting cells** that are resistant to desiccation. These later germinate to form new filaments.

- Many filamentous cyanobacteria fix atmospheric nitrogen by means of special cells called **heterocysts**.

- Within these specialized cells, photosynthetic membranes are reorganized and the proteins that make up **photosystem II and phycobilisomes are degraded**. **Photosystem I remains functional to produce ATP**, **but no oxygen is generated**.

- This inability to generate O2 is critical because the enzyme **nitrogenase is extremely oxygen sensitive**.

- Heterocysts develop **thick cell walls**, which slow or **prevent O2 diffusion** into the cell, and any O2 present is consumed during respiration.



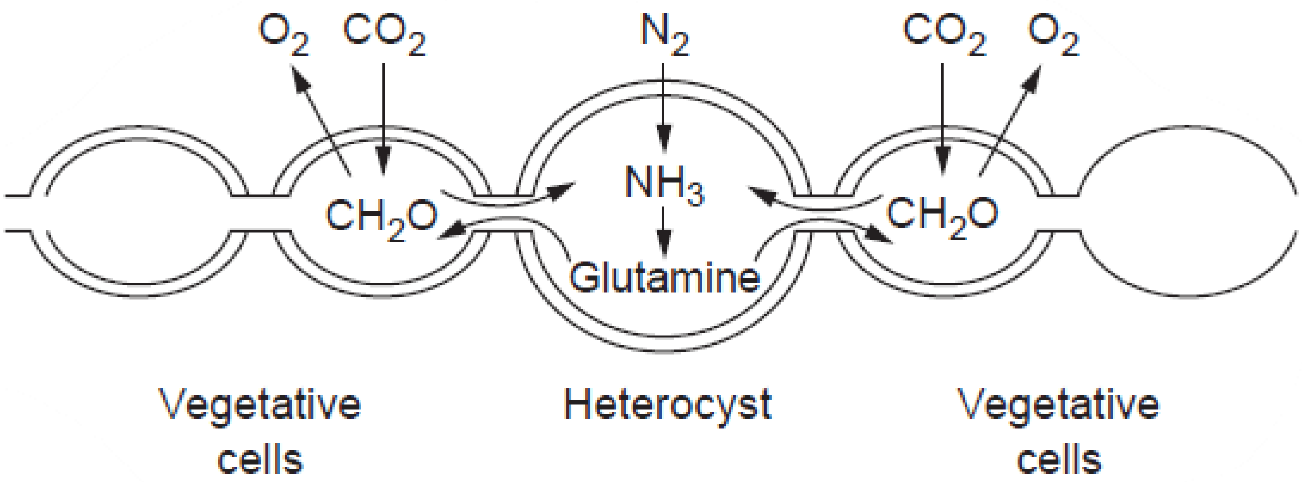


Table 19.2 Characteristics of the Cyanobacterial Subsections

Subsection	General Shape	Reproduction and Growth	Heterocysts	% G + C	Other Properties	Representative Genera
I	Unicellular rods or cocci; nonfilamentous aggregates	Binary fission, budding	–	31–71	Nonmotile or swim without flagella	*Chroococcus* *Gleocapsa* *Prochlorococcus* *Synechococcus*
II	Unicellular rods or cocci; may be held together in aggregates	Multiple fission to form baeocytes	–	40–46	Some baeocytes are motile	*Pleurocapsa* *Dermocarpella* *Chroococcidiopsis*
III	Filamentous, unbranched trichome with only vegetative cells	Binary fission in a single plane, fragmentation	–	34–67	Usually motile	*Lyngbya* *Oscillatoria* *Prochlorothrix* *Spirulina* *Pseudanabaena*
IV	Filamentous, unbranched trichome may contain specialized cells	Binary fission in a single plane, fragmentation to form hormogonia	+	38–47	Often motile, may produce akinetes	*Anabaena* *Cylindrospermum* *Nostoc* *Calothrix*
V	Filamentous trichomes either with branches or composed of more than one row of cells	Binary fission in more than one plane, hormogonia formed	+	42–44	May produce akinetes; greatest morphological complexity and differentiation in cyanobacteria	*Fischerella* *Stigonema* *Geitleria*

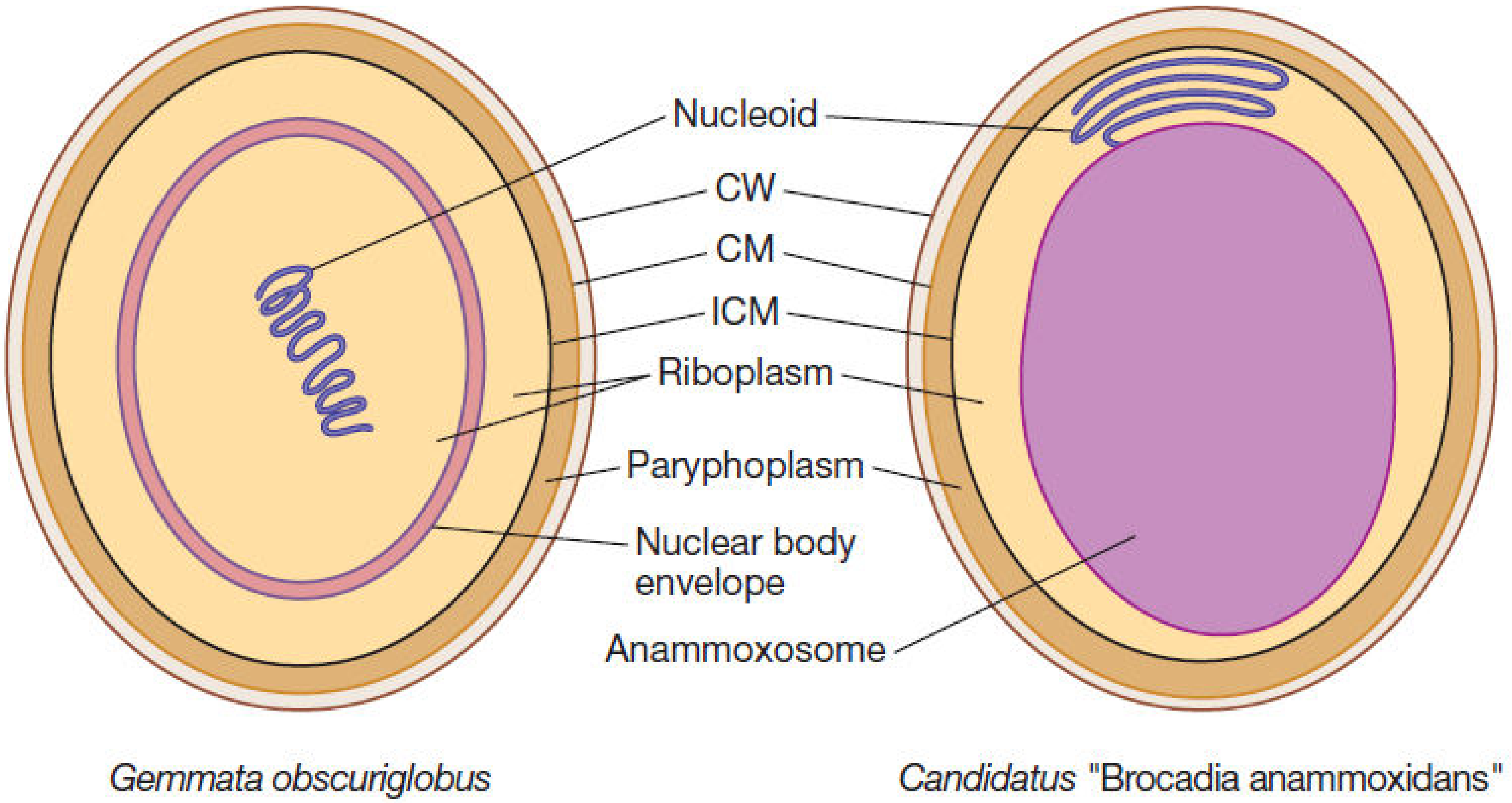
PHYLUM *PLANCTOMYCETES*

- The phylum *Planctomycetes* contains one class, one order, and four genera.
- The planctomycetes are morphologically unique bacteria, having compartmentalized cells.
- Although each species is unique, all follow a basic cellular organization that includes a plasma membrane closely surrounded by the cell wall, which **lacks peptidoglycan**.
- The largest internal compartment, the intracytoplasmic membrane, is separated from the plasma membrane by a peripheral, **ribosome-free region called the paryphoplasm**.
- The nucleoid of the planctomycete ***Gemmata obscuriglobus*** is located in the nuclear body, which is enclosed in a double membrane.
- The species ***Candidatus*** "**Brocadia anammoxidans**" **does not localize its DNA**

- This is the site of **anaerobic ammonia oxidation**, a unique and recently discovered form of chemolithotrophy in which **ammonium ion (NH_4) serves as the electron donor and nitrite (NO_2) as the terminal electron acceptor** it is reduced to nitrogen gas (N_2).

- The genus ***Planctomyces*** **attaches to surfaces through a stalk and holdfast**; the other genera in the order lack stalks. Most of these bacteria have life cycles in which sessile cells bud to produce motile swarmer cells.

- The swarmer cells are **flagellated** and **swim for a while before attaching to a substrate** and beginning reproduction.


Nucleoid
CW
CM
ICM
Riboplasm
Paryphoplasm
Nuclear body envelope
Anammoxosome
Gemmata obscuriglobus
Candidatus "Brocadia anammoxidans"

PHYLUM *CHLAMYDIAE*

- The gram-negative chlamydiae are **obligate intracellular parasites**. That is, they must grow and reproduce within host cells.
- Although their **ability to cause disease** is widely recognized, many species grow within protists and animal cells without important and best studied; it is the focus of our attention.
- Chlamydiae are **nonmotile**, **coccoid** bacteria, ranging in size **from 0.2 to 1.5 µm**.
- They **reproduce** only **within cytoplasmic vesicles of host cells by a unique developmental cycle** involving the formation of two cell types: **elementary bodies** and **reticulate bodies**.
- Although their envelope resembles that of other gram-negative bacteria, the **cell wall differs in** lacking **muramic acid and a peptidoglycan layer**.

- **Elementary bodies** achieve **osmotic stability** by cross-linking their outer membrane proteins, and possibly periplasmic proteins, with **disulfide bonds**. Chlamydiae are extremely limited metabolically, relying on their host cells for key metabolites.

- This is reflected in the size of their genome. It is relatively small at **1.0 to 1.3 Mb**; the **G+C content is 41 to 44%**.

- Chlamydial **reproduction is unique**. Although they undergo **binary fission**, **Chlamydia** is one of only a few bacteria that **lacks the cell division protein FtsZ**.

- **Reproduction** begins with the attachment of an elementary body (EB) to the host cell surface. Elementary bodies are 0.2 to 0.6 µm in diameter, contain electron-dense nuclear material and a rigid cell wall, and are infectious.

- The host cell phagocytoses the EB, which is held in inclusion bodies where the EB reorganizes to form a reticulate body (RB). The RB is specialized for reproduction rather than infection.

PHYLUM *SPIROCHAETES*

The phylum Spirochaetes (Greek spira, a coil, and chaete, hair) contains gram-negative, **chemoheterotrophic bacteria** distinguished by their structure and mechanism of motility.

Bergey's Manual divides the phylum Spirochaetes into one class, one order (Spirochaetales), and three families (Spirochaetaceae, Serpulinaceae, and Leptospiraceae). At present, there are 13 genera in the phylum.

Spirochetes can be anaerobic, facultatively anaerobic, or aerobic.

Carbohydrates, amino acids, long-chain fatty acids, and long-chain fatty alcohols may serve as carbon and energy sources.

- Spirochetes are **morphologically unique**. They are slender, long bacteria (0.1 to 3.0 µm by 5 to 250 µm) with a flexible, helical shape.

- The central **protoplasmic cylinder**, which contains cytoplasm and **the nucleoid**, is bounded by a plasma membrane and a **gram-negative cell wall**.

- **Two to more than a hundred flagella, called axial fibrils or periplasmic flagella**, extend from both ends of the cylinder and often overlap one another in the center third of the cell.

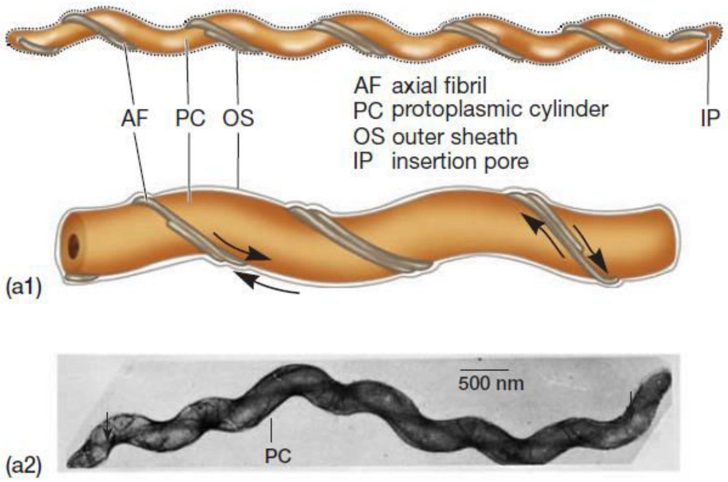
- The whole complex of **periplasmic flagella**, called the **axial filament**, lies inside a **flexible outer sheath**. The outer sheath contains lipid, protein, and carbohydrate and varies in structure between different genera.

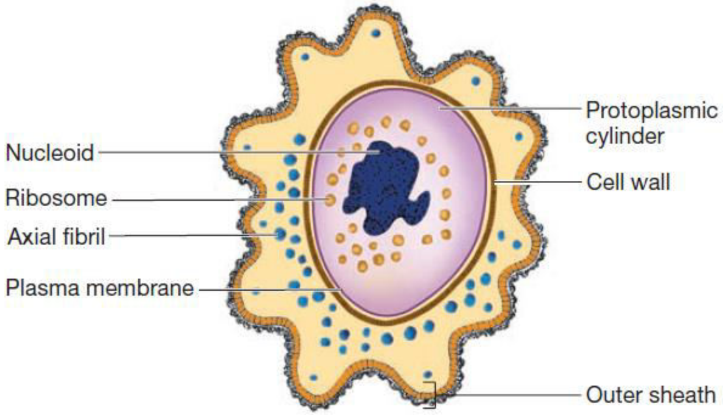
- Its precise function is unknown, but the sheath is essential because spirochetes die if it is damaged or removed. The outer sheath of Treponema pallidum has few proteins exposed on its surface. This allows the syphilis spirochete to avoid attack by host antibodies.

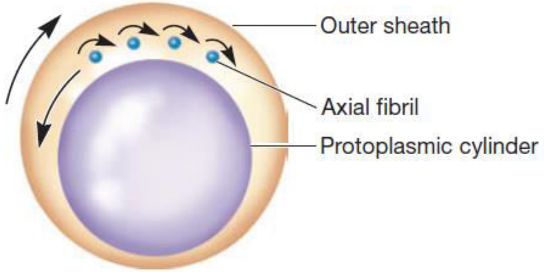
- Motility in the spirochetes is uniquely adapted to movement through viscous solutions. Like the external flagella of other bacteria, the axial fibrils rotate.

- This results in the rotation of the outer sheath in the opposite direction relative to the periplasmic cylinder, and the cell moves in a corkscrewlike movement through the medium.

- Fibril rotation can also enable cell flexing and crawling on solid substrates. Thus, unlike other bacteria flagella, axial fibrils mediate movement through liquids and on solid surfaces.







PHYLUM *BACTEROIDETES*

- The phylum Bacteroidetes is very diverse and seems most closely related to the phylum Chlorobi.

- The phylum has three classes (Bacteroides, Flavobacteria, and Sphingobacteria), 12 families, and 63 genera.

- The class Bacteroides contains **anaerobic, gram-negative, nonsporing, motile or nonmotile rods of various shapes**.

- These bacteria are **chemoheterotrophic** and usually produce a mixture of organic acids as fermentation end products.

- They do not reduce sulfate or other sulfur compounds. The genera are identified using properties such as general shape, motility and flagellation pattern, and fermentation end products.

- These bacteria grow in habitats such as the **oral cavity** and **intestinal tract** of vertebrates and the rumen of ruminants.

- Although difficulty culturing these anaerobes has hindered our understanding of them, they are clearly widespread and important.

- Often they benefit their host. Bacteroides ruminicola is a major component of the rumen flora; it ferments starch, pectin, and other carbohydrates.

- About 30% of the bacteria isolated from human feces are members of the genus Bacteroides, and these organisms may provide extra nutrition by degrading cellulose, pectins, and other complex carbohydrates.

- The family also is involved in human disease. Members of the genus Bacteroides are associated with diseases of major organ systems, ranging from the central nervous system to the skeletal system. B. fragilis is a particularly common anaerobic pathogen found abdominal, pelvic, pulmonary, and blood infections.

The proteobacteria

- In this chapter, we introduce the bacteria that are covered in **volume 2** of the second edition of Bergey’s Manual of Systematic Bacteriology.

- This volume is devoted entirely to the proteobacteria . This is the largest and most diverse group of bacteria; there are over 500 known genera.

- Although 16S rRNA studies show that they are phylogenetically related, proteobacteria are remarkably diverse.

- The morphology of these gram-negative bacteria ranges from simple rods and cocci to genera with prosthecae, buds, and even fruiting bodies.

- Physiologically, they include photoautotrophs, chemolithotrophs, and chemoheterotrophs. No obvious overall pattern in metabolism, morphology, or reproductive strategy characterizes proteobacteria.

CLASS *ALPHA -PROTEO BACTERIA*

- The class Alphaproteobacteria has seven orders and 20 families.
- The class includes most of the oligotrophic proteobacteria (those capable of growing at low nutrient levels).
- Some have unusual metabolic modes such as methylotrophy- the ability to grow using methane as a carbon source (Methylobacterium), chemolithotrophy (Nitrobacter), and the ability to fix nitrogen (Rhizobium).
- Members of genera such as Rickettsia and Brucella are important pathogens.
- Purple Nonsulfur Bacteria

CLASS *BETAPROTEOBACTERIA*

- The β-proteobacteria overlap the α-proteobacteria metabolically but tend to use substances that diffuse from organic decomposition in anoxic habitats.
- Some of these bacteria use hydrogen, ammonia, methane, volatile fatty acids, and similar substances.
- As with the α -proteobacteria, there is considerable metabolic diversity; the β -proteobacteria may be chemoheterotrophs, photolithotrophs, methylotrophs, and chemolithotrophs.
- The class Beta-proteobacteria has seven orders and 12 families.
- *Neisseria, Nitrosomonas, Thiobacillus*

CLASS *GAMMAPROTEO BACTERIA*

The γ-proteobacteria constitute the largest subgroup of proteobacteria with an extraordinary variety of physiological types.

Many important genera are chemoorganotrophic and facultatively anaerobic. Other genera contain aerobic chemoorganotrophs, photolithotrophs, chemolithotrophs, or methylotrophs.

According to some DNA-rRNA hybridization studies, the γ-proteobacteria are composed of several deeply branching groups. One consists of the purple sulfur bacteria; a second includes the intracellular parasites Legionella and Coxiella.

The two largest groups contain a wide variety of nonphotosynthetic genera.

Ribosomal RNA superfamily I includes the families Vibrionaceae, Enterobacteriaceae, and Pasteurellaceae.

- These bacteria use the Embden-Meyerhof and pentose phosphate pathways to catabolize carbohydrates.
- Most are facultative anaerobes. Ribosomal RNA superfamily II contains mostly aerobes that often use the Entner-Doudoroff and pentose phosphate pathways to catabolize many different kinds of organic molecules.
- The genera Pseudomonas, Azotobacter, Moraxella, and Acinetobacter belong to this superfamily.
- The exceptional diversity of these bacteria is evident from the fact that Bergey's Manual divides the class -proteobacteria into 14 orders and 28 families

CLASS *DELTAPROTEO BACTERIA*

- Although the -proteobacteria are **not a large** assemblage of genera, they show considerable morphological and physiological diversity.
- These bacteria can be divided into two general groups, all of them chemoorganotrophs.
- Some genera are predators, such as the bdellovibrios and myxobacteria. Others are anaerobes that generate sulfide from sulfate and sulfur while oxidizing organic nutrients.
- The class has eight orders and 20 families.

CLASS *EPSILONPROTEOBACTERIA*

- The **-proteobacteria** are the smallest of the five proteobacterial classes.

- They all are slender gram-negative rods, which can be straight, curved, or helical. The -proteobacteria have one order, *Campylobacterales,* and three families: *Campylobacteraceae, Helicobacteraceae,* and the recently added *Nautiliaceae.*

- Two pathogenic genera, *Campylobacter* and *Helicobacter,* are microaerophilic, motile, helical or vibrioid, gram-negative rods.

- The genus *Campylobacter* contains both nonpathogens and species pathogenic for humans and other animals. *C. fetus* causes reproductive disease and abortions in cattle and sheep.

- It is associated with a variety of conditions in humans ranging from septicemia (pathogens or their toxins in the blood) to enteritis (infl ammation of the intestinal tract).

- It causes an estimated 2 million human cases of ***Campylobacter*** **gastroenteritis** — inflammation of the intestine or **campylobacteriosis** and subsequent diarrhea in the United States each year.

- Studies with chickens, turkeys, and cattle have shown that as much as 50 to 100% of a flock or herd of these birds or animals excrete *C. jejuni.*

- These bacteria also can be isolated in high numbers from surface waters. They are transmitted to humans by contaminated food and water, contact with infected animals, or anal-oral sexual activity.

Low G+C gram-positive bacteria (phylum *Firmicutes*)

- The low G C gram-positive bacteria are placed in the phylum *Firmicutes* and divided into three classes: *Clostridia, Mollicutes,* and *Bacilli.*

- The phylum *Firmicutes* is large and complex; it has 10 orders and 34 families.

- The mycoplasmas, class *Mollicutes,* are also considered low G+C gram positives despite their lack of a cell wall.

- Ribosomal RNA data indicate that the mycoplasmas are closely related to the lactobacilli.

High G+C gram-positive bacteria (phylum *Actinomycetes*)

Actinomycetes are gram-positive, aerobic bacteria but are distinctive because they have filamentous hyphae that differentiate to produce asexual spores.

They are the source of most of the antibiotics used in medicine today. They also produce metabolites that are used as anticancer drugs, anti-helminthics (e.g., ivermectin given to dogs to prevent heartworm).

This practical aspect of the actinomycetes is linked very closely to their mode of growth.

The actinomycetes have a complex life cycle. The life cycle of many actinomycetes includes the development of filamentous cells, called hyphae , and spores.

When growing on a solid substratum such as soil or agar, the actinomycetes develop a branching network of hyphae. The hyphae grow both on the surface of the substratum and into it to form a dense hyphal mat called a **substrate mycelium** .

Septae usually divide the hyphae into long cells (20 µm and longer) containing several nucleoids.

In many actinomycetes, substrate hyphae differentiate into upwardly growing hyphae to form an **aerial mycelium** that extends above the substratum that extends above the substratum.

It is at this time that medically useful compounds are formed. Because the physiology of the actinomycete has switched from actively growing vegetative cells into this special cell type, these compounds are often called secondary metabolites .