Chapter 20

The Proteobacteria

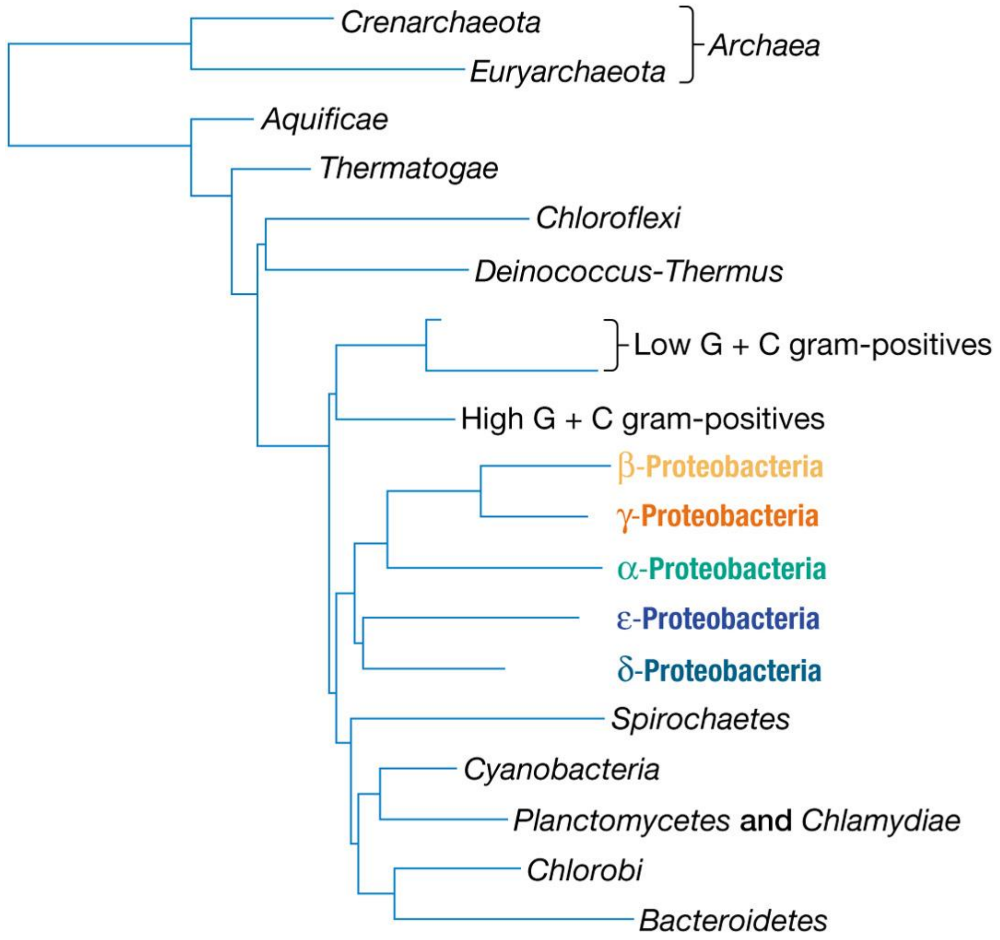
The Phylum *Proteobacteria*

- **the largest phylogenetically coherent bacterial group with more than 500 genera**
- **remarkable diverse morphologically, physiologically, and other ways**
- **volume 2 of *Bergey's Manual (2nd edition*) is devoted to this group of bacteria**

Lineages of Proteobacterium

- **proteobacteria may have arose from a single photosynthetic ancestor**
- **16S rRNA shows five distinct lineages**
- ***Alphaproteobacterium* – α-proteobacteria**
- ***Betaproteobacterium* – β-proteobacteria**
- ***Gammaproteobacterium* – γ-proteobacteria**
- ***Deltaproteobacterium* – δ-proteobacteria**
- ***Epsilonproteobacterium* – Ɛ-proteobacteria**

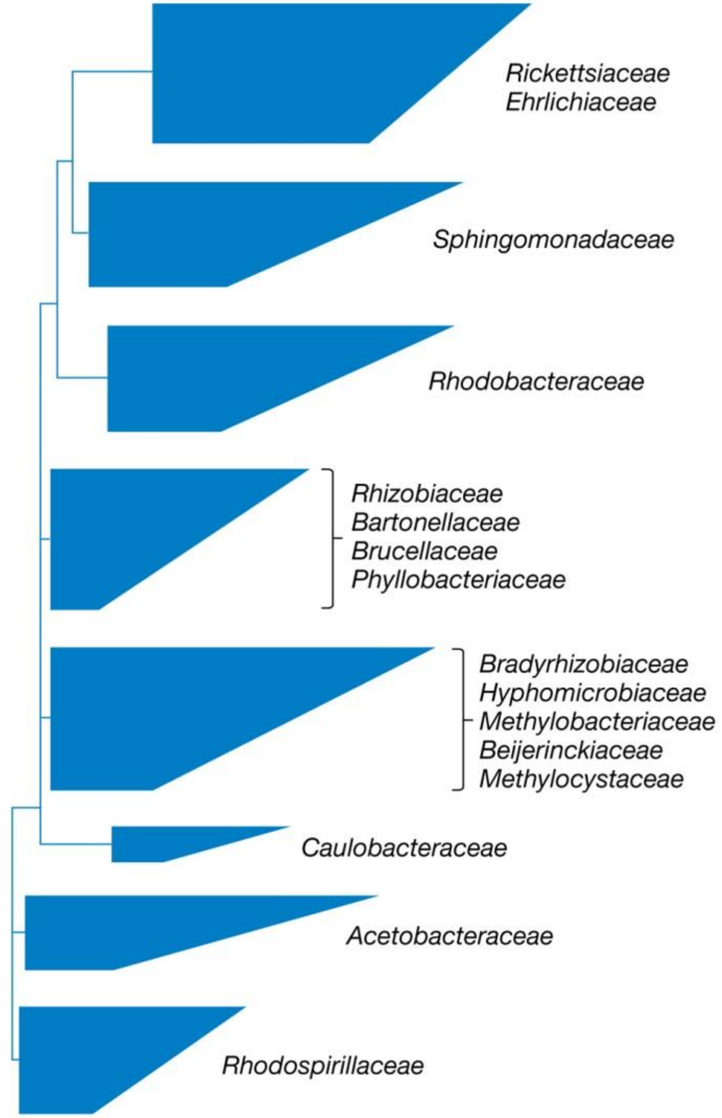
Figure 20.1


Crenarchaeota
Euryarchaeota
Archaea
Aquificae
Thermatogae
Chloroflexi
Deinococcus-Thermus
Low G + C gram-positives
High G + C gram-positives
β-Proteobacteria
γ-Proteobacteria
α-Proteobacteria
ε-Proteobacteria
δ-Proteobacteria
Spirochaetes
Cyanobacteria
Planctomycetes and Chlamydiae
Chlorobi
Bacteroidetes

Class *Alphaproteobacteria*

- **seven orders, 20 families**
- ***Rickettsiales* may have been the earliest α-proteobacteria**
- **most of the oligotrophic (low levels of nutrients) bacteria**
- **most abundant bacteria in oceans**
- **evolved to live within plants and animals resulting in genome reduction or expansion**
- **metabolically diverse**
  - **methylotrophy, chemolithotrophs, nitrogen fixers**

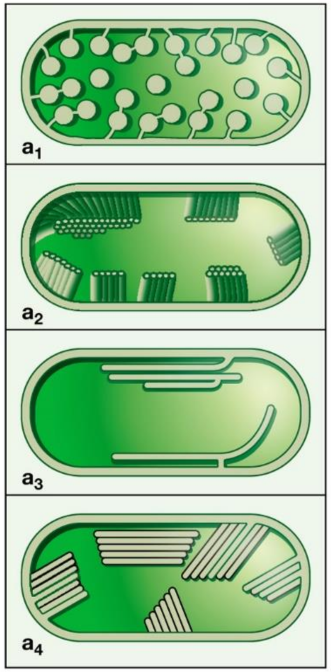
Figure 20.2; phylogenetic relationships among major families within the alpha proteobacteria



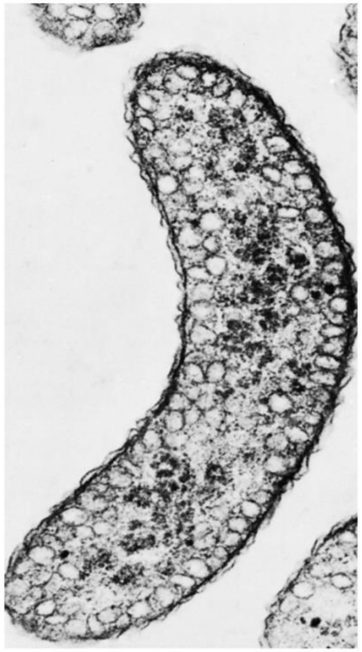
Purple Nonsulfur Bacteria

- **with one exception (genus *Rhodocyclus*) all are α-proteobacteria**
- **metabolically flexible**
  - **normally grow anaerobically as anoxygenic photoorganoheterotrophs**
    - **possess bacteriochlorophylls *a* or *b* in photosystems located in membranes that are continuous with plasma membrane**
    - **some can oxidize sulfide, but not elemental sulfur, to sulfate**

Figure 20.3; photosynthetic apparatus of purple bacteria

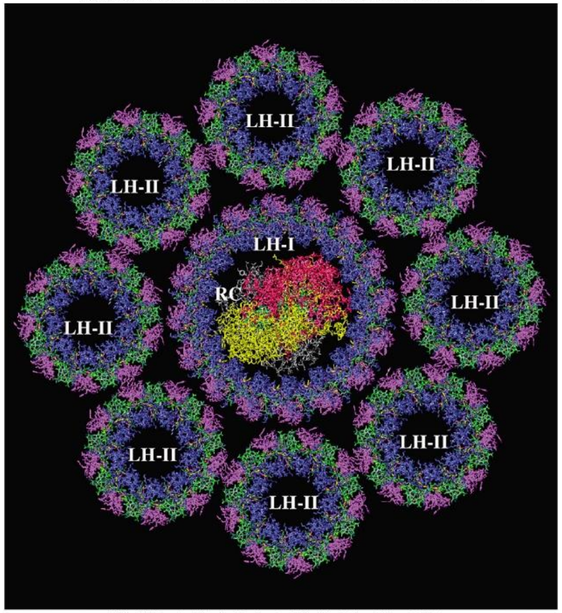


(a) Intracytoplasmic membranes



(b) *R. rubrum*

Reprinted from
The Shorter Bergey's Manual of Determinative Bacteriology, 8e,
John G. Holt, Editor,
1977 © Bergey's Manual Trust.
Published by Williams & Wilkins Baltimore, MD

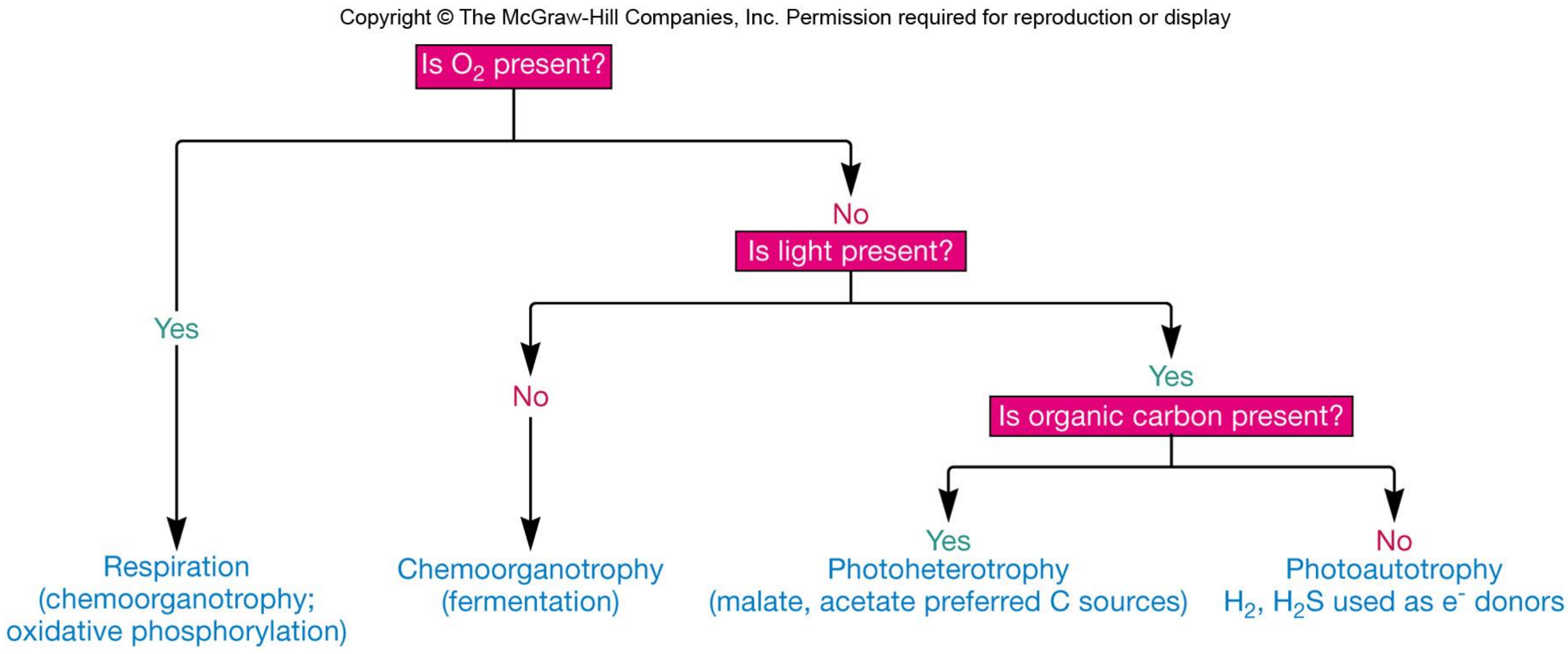


Xiche Hu, Thorsten Ritz, Ana Damjanovic, Felix Autenrieth, and Klaus, Schulten.
Photosynthetic apparatus of purple bacteria.
Quarterly Reviews of Biophysics, 35:1–62, 2002. Cambridge University Press

Purple Nonsulfur Bacteria…

- **in absence of light**
  - **most grow aerobically as chemoorganoheterotrophs**
  - **some carry out fermentation, photoheterotrophy, photoautotrophy, and grow anaerobically**
- ***Rhodosprillum* best studied metabolic diversity**

Figure 20.4; metabolic flexibility of Rodsopririllum



Purple Nonsulfur Bacteria…

- ***Rhodospirillum*** **industrial importance**
  - **produces H_2**
  - **novel biodegradable plastic**
  - **oxidize carbon monoxide to carbon dioxide**
- **morphologically diverse**
  - **most motile by polar flagella**
- **found in mud and water of lakes and ponds with abundant organic matter and low sulfide levels; some marine species**

Purple Nonsulfur Bacteria…

- can produce cellular cysts
  - resting cells
  - resistant to desiccation but less tolerant of heat and UV than bacterial endospores
  - made in response to nutrient limitation
  - have thick outer coat and store polyhydroxybutyrate

Figure 20.5

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(a)

Berleman et al., Hypercyst Mutants in Rhodospirillum centenum Identify Regulatory Loci Involved in Cyst Cell Diff erentiation *J. Bacteriol.* 2004 186, fig. 1, pg. 5836

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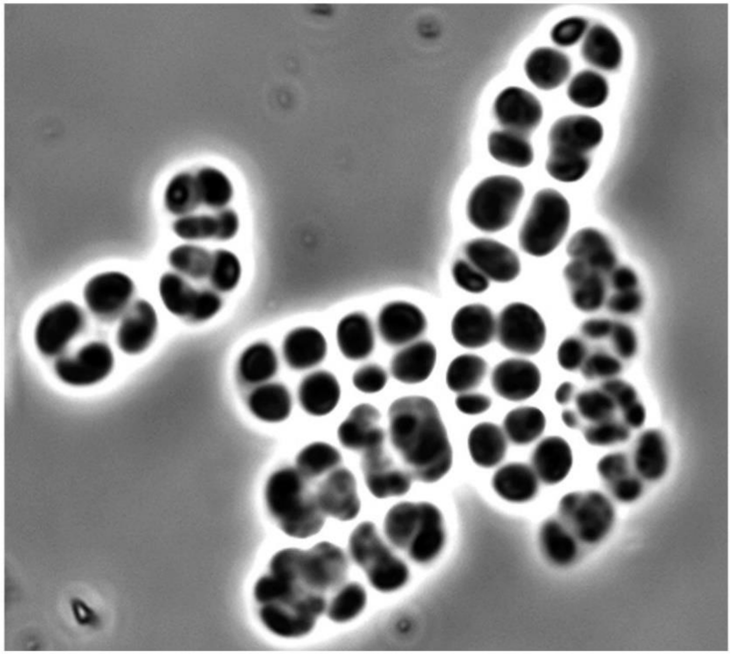


(b)

Berleman et al., Hypercyst Mutants in Rhodospirillum centenum Identify Regulatory Loci Involved in Cyst Cell Diff erentiation *J. Bacteriol.* 2004 186, fig. 1, pg. 5836

Rickettsia

- **genus *Rickettsia***
  - **order *Rickettsiales*; family *Rickettsiaceae***
- **very small, gram-negative, non-flagellated, diverse morphology**
- **all species are parasitic or mutualistic**
  - **grows in vertebrate erythrocytes, macrophages, vascular endothelial cells**
  - **live in blood sucking arthropods – vectors or primary hosts**

Rickettsia...

- **genome sequence similar to mitochondria**
  - **arose from endosymbiotic association**
    - **free living, aerobic bacterium became intracellular parasite of proto-eukaryotic cell that lacked organelles**
    - **gene reduction occurred and loss of free living ability**

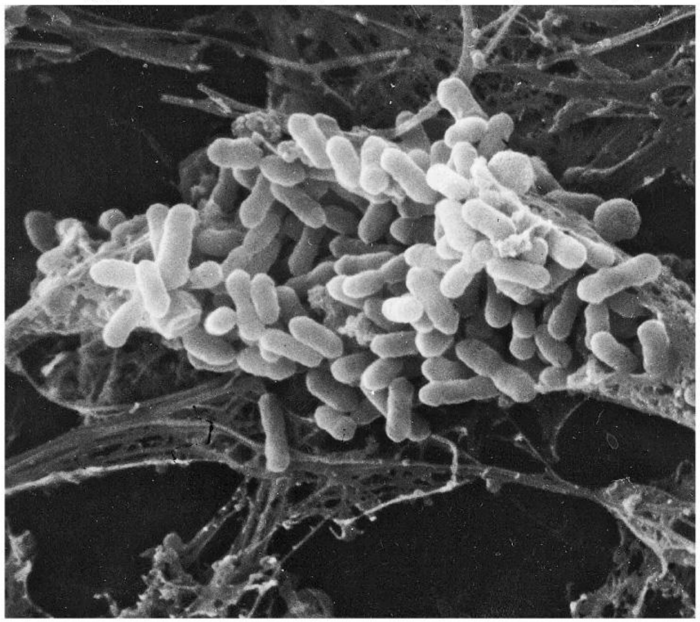
Rickettsia Metabolism

- lack glycolytic pathway
  - do not use glucose as energy source
- oxidize glutamate and TCA cycle intermediates (e.g., succinate)
- take up and use ATP and other materials from host cell

Important Pathogens

- ***Rickettsia prowazekii*** **and** ***Rickettsia typhi*** **– typhus fever**
- ***Rickettsia rickettsii*** **– Rocky Mountain Spotted Fever**
- **reproduction**
  - **enters host by phagocytosis**
  - **escapes phagosome**
  - **reproduces in cytoplasm**
  - **host cell bursts**

Figure 20.6



(a)

David J. Silverman, Anna Waddell In Vitro Studies of Rickettsia-Host Cell Interactions: Ultrastructural Study of Rickettsia prowazekii-Infected Chicken Embryo Fibroblasts, *Infect Immun*. 1980 August; 29(2): 778–790

(b)

ASM MicrobeLibrary.org © Walker

Caulobacteraceae and *Hyphomicrobiaceae*

- **rods or cocci with an appendage**
- **life cycle**
  - **prostheca (pl., prosthecae) or stalk**
    - **extension of cell, including plasma membrane, that is narrower than mature cell**
  - **reproduction by budding**
    - **progeny cell is a bud that first appears as a small protrusion on parent cell and enlarges to form mature cell**

Genus *Hyphomicrobium*

- **prosthecate, budding bacteria**
- **aerobic chemoheterotrophs**
  - **grow on ethanol, acetate, and one-carbon molecules (facultative methylotroph)**
    - **e.g., methanol, formate, and formaldehyde**
- **frequently attach to solid objects in aquatic and terrestrial environments**
  - **may be 25% of total bacterial population in oligotrophic (nutrient-poor) freshwater habitats**

Figure 20.7

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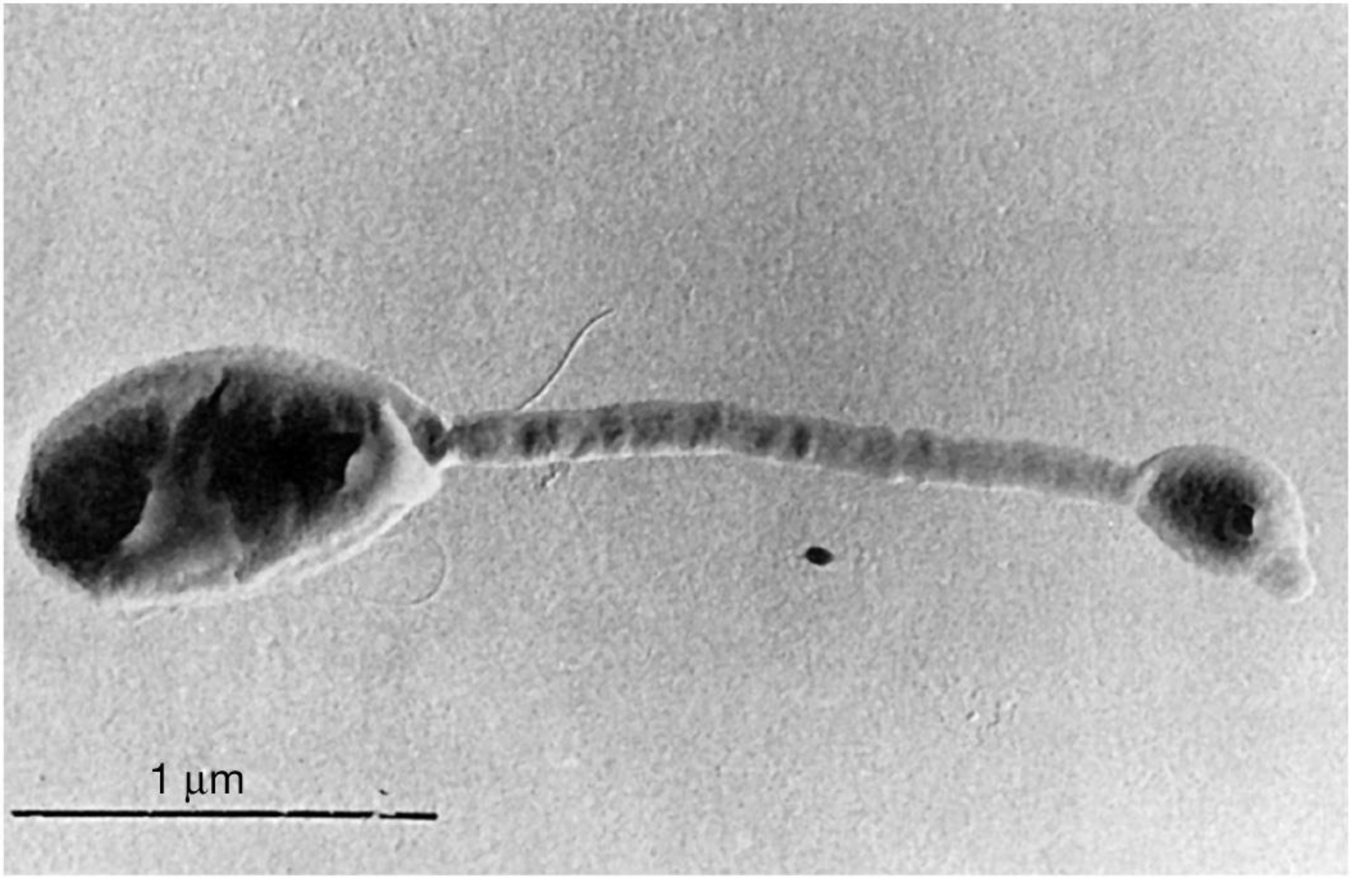

From J.T. Staley, M.P. Bryant, N. Pfenning and J.G. Holt (Eds), *Bergey's Manual of Systematic Bacteriology*, Vol. 3.

Figure 20.8

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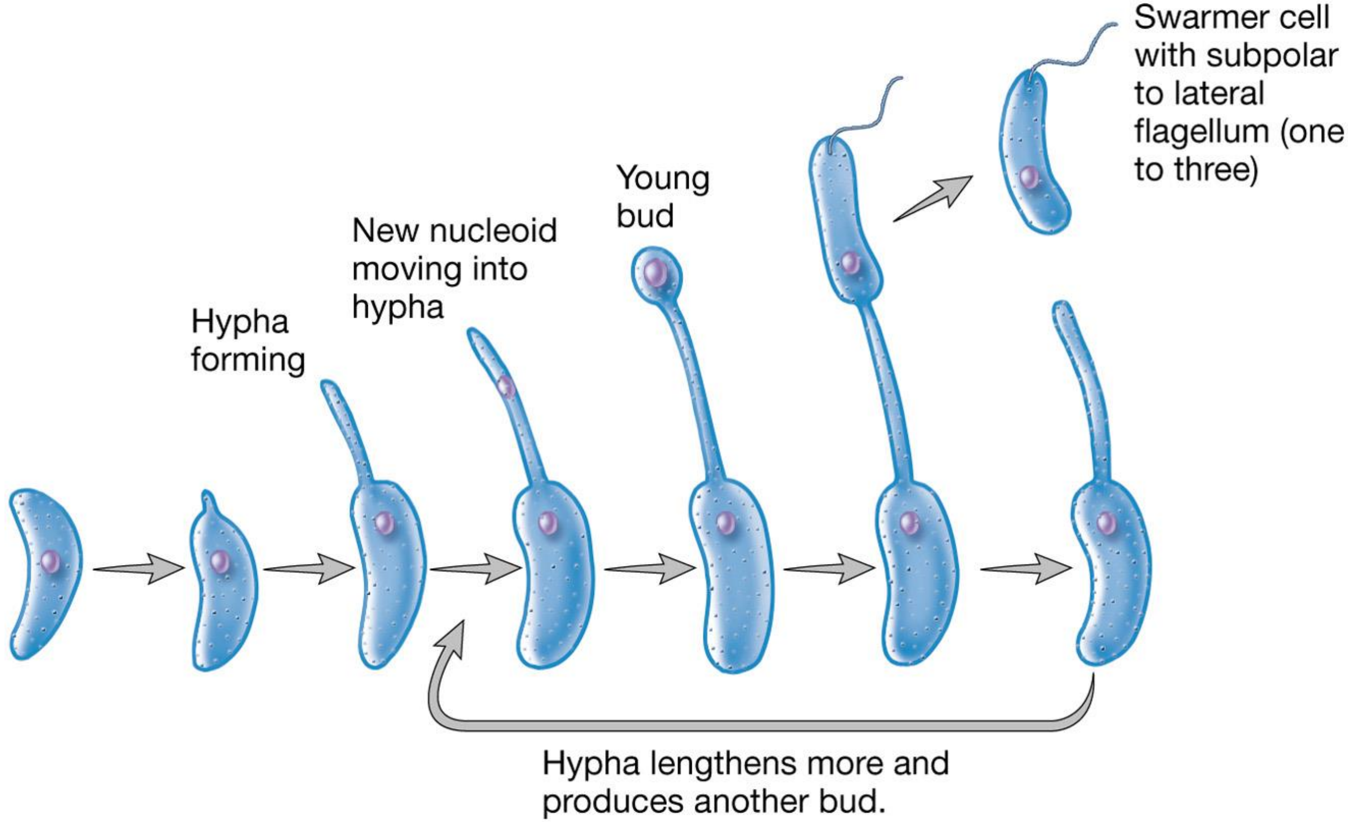
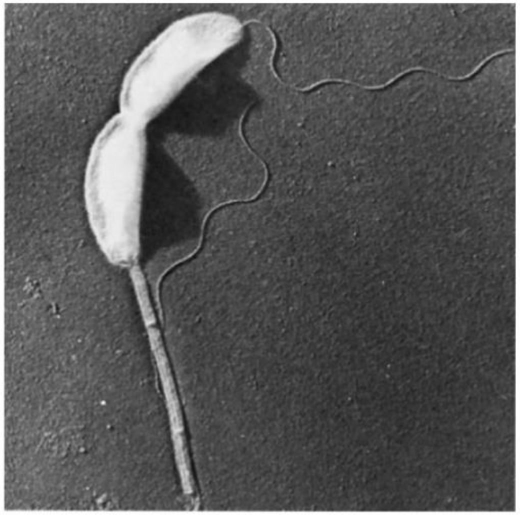


Genus *Caulobacter*

- may be polarly flagellated rods or may possess prostheca and holdfast
  - used to attach to solid substrata with what is known as the strongest biological adhesion molecule
  - prostheca lacks cytoplasmic components

Figure 20.9

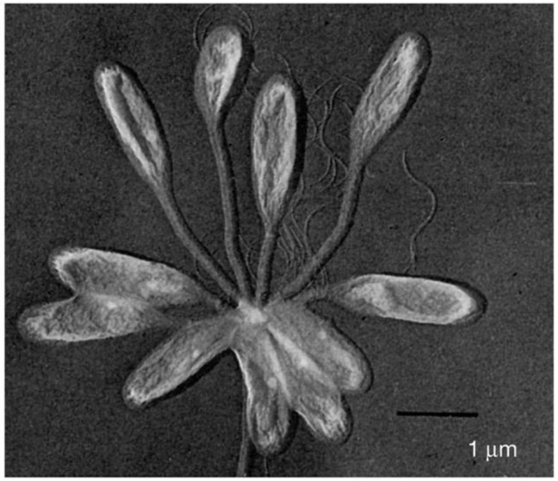


(a)

Courtesy of Jeanne S. Poindexter, Long Island Univ.

(b)

Courtesy of Jeanne S. Poindexter, Long Island Univ.



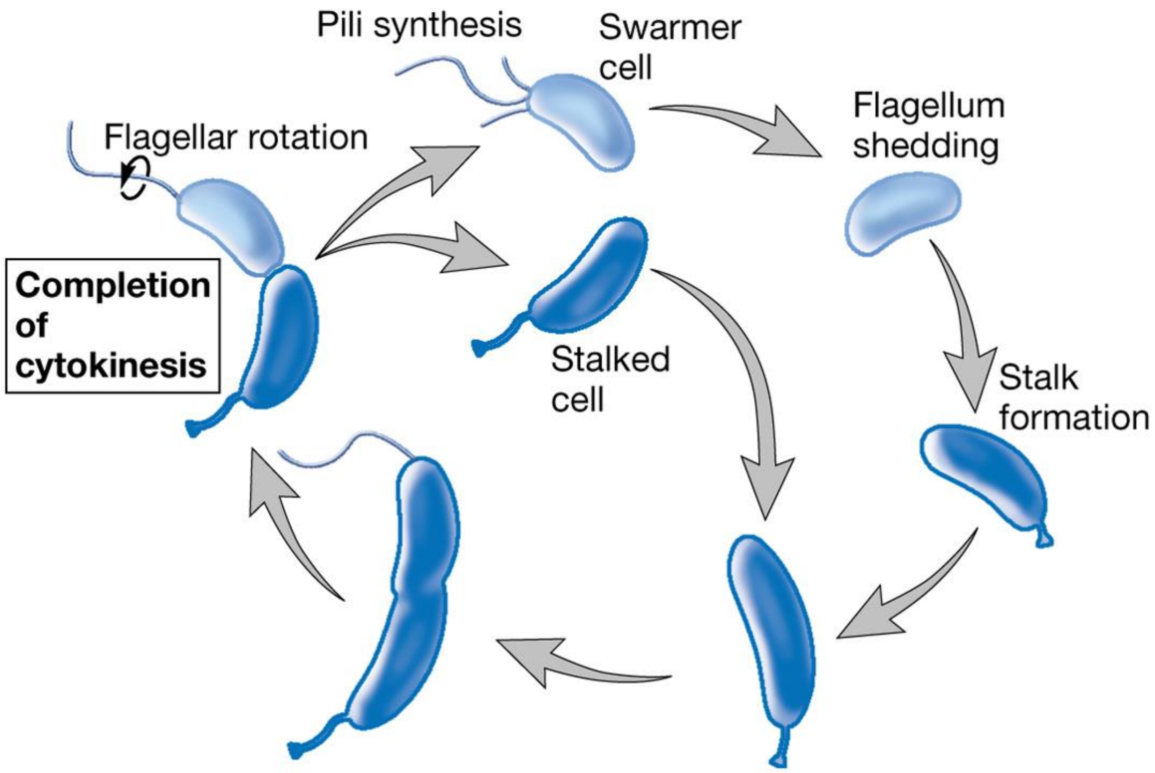
(c)

From J.T. Staley, M.P. Bryant, N. Pfenning and J.G. Holt (Eds), *Bergey's Manual of Systematic Bacteriology*, Vol. 3. © 1989 Williams and Wilkins Co., Baltimore

Genus *Caulobacter*

- usually found in oligotrophic aquatic and terrestrial habitats
  - may absorb nutrients released from hosts
  - long prosthecae may improve nutrient uptake
- reproduction
  - asymmetric transverse binary fission

Figure 20.10



Pili synthesis
Swarmer cell
Flagellum shedding
Flagellar rotation
Completion of cytokinesis
Stalked cell
Stalk formation

Genus *Rhizobium*

- **gram-negative, pleomorphic, motile rods**
  - **often contain poly-β-hydroxybutyrate granules**
- **grow symbiotically as nitrogen-fixing bacteroids within root nodule cells of legumes**
  - **most successful plant family on earth**

Figure 20.11

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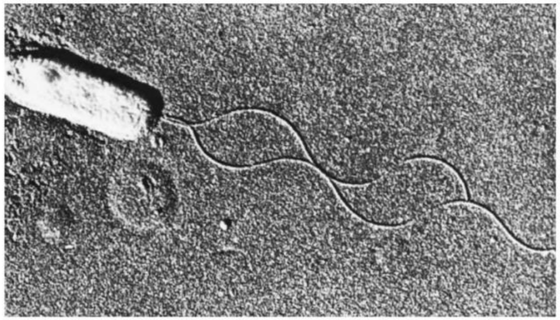

From N.R. Krieg and J.G. Holt (Eds), *Bergeys Manual of Systematic Bacteriology*, Vol. 1, 1984. Williams and Wilkins Co., Baltimore

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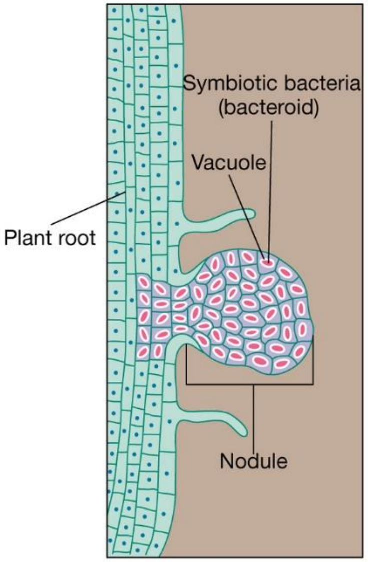

(b)

Genus *Agrobacterium*

- **do not stimulate nodule formation or fix nitrogen**
- **invade crown, roots, and stems of many plants**
  - **transform infected plant cells into autonomously proliferating tumors**
- **e.g., *Agrobacterium tumefaciens***
  - **causes crown gall disease by means of tumor-inducing (Ti) plasmid**

Figure 20.12

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Genus *Brucella*

- important human and animal pathogen
  - undulant fever – zoonosis
- tiny, faintly staining coccobacilli

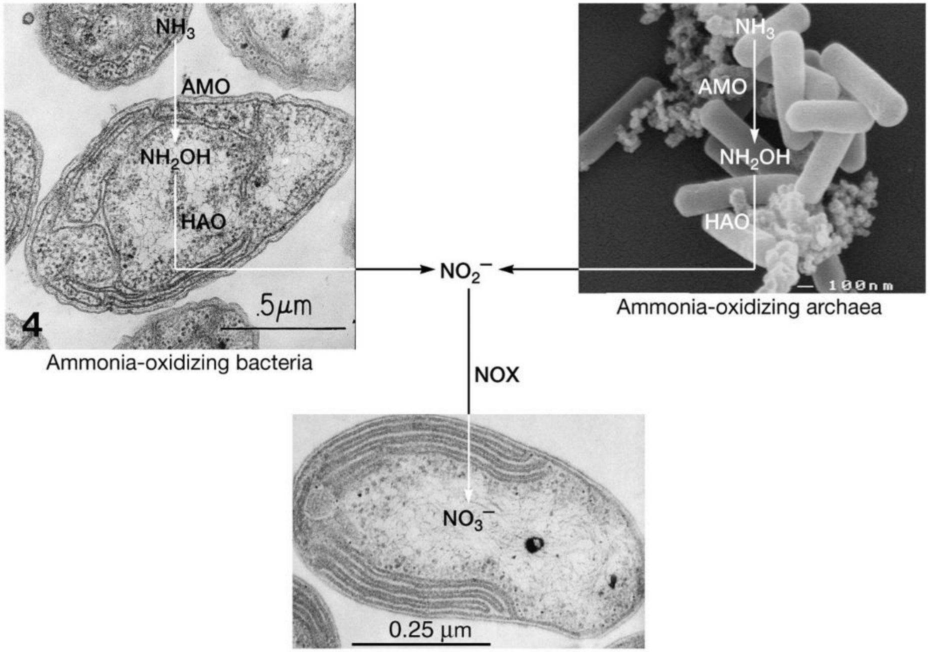
Nitrifying Bacteria

- **very diverse chemolithoautotrophs**
  - **nitrification – gain electrons from oxidation of**
    - **ammonium to nitrate or nitrite**
    - **nitrite further oxidized to nitrate**

Nitrification

- **ammonia → nitrite → nitrate**
- **conversion of ammonia to nitrate by action of two genera**
  - **e.g., *Nitrosomonas* – ammonia to nitrite**
  - **e.g., *Nitrobacter* – nitrite to nitrate**
- **fate of nitrate**
  - **easily used by plants**
  - **lost from soil through leaching or denitrification**

Figure 20.13



Ammonia-oxidizing bacteria

Ammonia-oxidizing archaea

Nitrite-oxidizing bacteria

(Ammonia- Oxidizing Bacteria): Dr. John B. Waterbury, Wood Hole Oceanographic Inst.;
(Ammonia- Oxidizing Archaea): Dr. Martin Könneke;
(Nitrite-Oxidizing Bacteria): © Woods Hole Oceanographic Institution

Nitrifying Bacteria

- **divided into several taxa**
  - **class *Alphaproteobacteria***
    - **e.g., genus *Nitrobacter***
  - **class *Betaproteobacteria***
    - **e.g., genera *Nitrosomonas* and *Nitrosospira***
  - **class *Gammaproteobacteria***
    - **family *Ectothiorhodospiraceae***
      - **e.g., genus *Nitrococcus***
    - **family *Chromatiaceae***
      - **e.g., genus *Nitrosococcus***

Table 20.2

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Table 20.2 Selected Characteristics of Representative Nitrifying Bacteria

Species	*Cell Morphology and Size (μm)*	*Reproduction*	*Motility*	*Cytomembranes*	*G + C Content (mol%)*	*Habitat*
Ammonia-Oxidizing Bacteria						
Nitrosomonas europaea (β-proteobacteria)	Rod; 0.8–1.1 × 1.0–1.7	Binary fission	–	Peripheral, lamellar	50.6–51.4	Soil, sewage, freshwater, marine
Nitrosococcus oceani (γ-proteobacteria)	Coccoid; 1.8–2.2 in diameter	Binary fission	+; 1 or more subpolar flagella	Centrally located parallel bundle, lamellar	50.5	Obligately marine
Nitrosospira briensis (β-proteobacteria)	Spiral; 0.3–0.4 in diameter	Binary fission	+ or –; 1 to 6 peritrichous flagella	Rare	53.8–54.1	Soil
Nitrite-Oxidizing Bacteria						
Nitrobacter winogradskyi (α-proteobacteria)	Rod, often pear-shaped; 0.5–0.9 × 1.0–2.0	Budding	+ or –; 1 polar flagellum	Polar cap of flattened vesicles in peripheral region of the cell	61.7	Soil, freshwater, marine
Nitrococcus mobilis (γ-proteobacteria)	Coccoid; 1.5–1.8 in diameter	Binary fission	+; 1 or 2 subpolar flagella	Tubular cytomembranes randomly arranged in cytoplasm	61.3 (1 strain)	Marine

From Brenner, D. J., et al., eds. 2005. Bergey's Manual to Systemic Bacteriology, *2d ed. Vol. 2:* The Proteobacteria. *Garrity, G. M. Ed-in-Chief. New York: Springer.*

Class *Betaproteobacteria*

- **seven orders, 12 families**
- **considerable metabolic diversity**
  - **overlap α-proteobacteria metabolically but generally use decomposed organic matter anoxically**
  - **some use hydrogen, methane, ammonia, volatile fatty acids**

Figure 20.14

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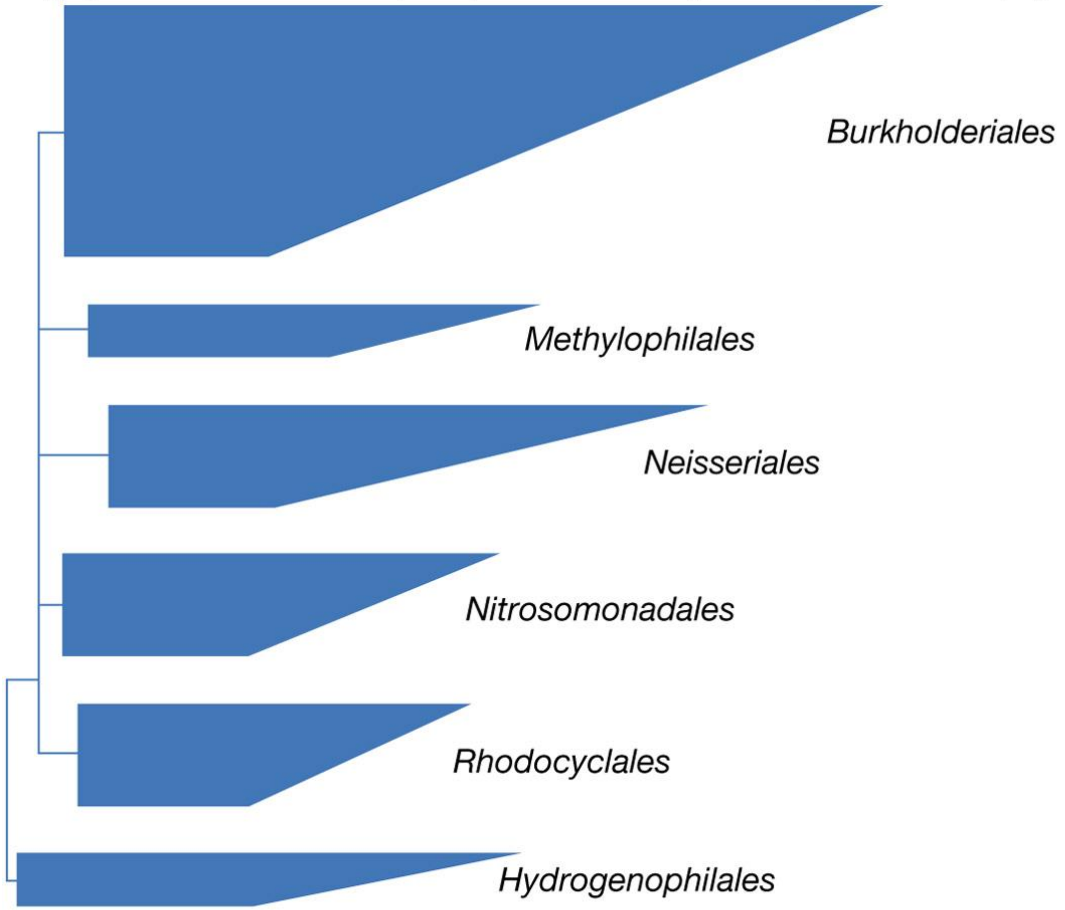


Order *Neisseriales*

- **one family, *Neisseriaceae* and 15 genera**
- **Genus *Neisseria***
  - **nonmotile, gram-negative cocci**
    - **most often occur in pairs with adjacent sides flattened**
    - **may have capsules and fimbriae**
  - **aerobic chemoorganotrophs**
    - **oxidase positive and usually catalase positive**

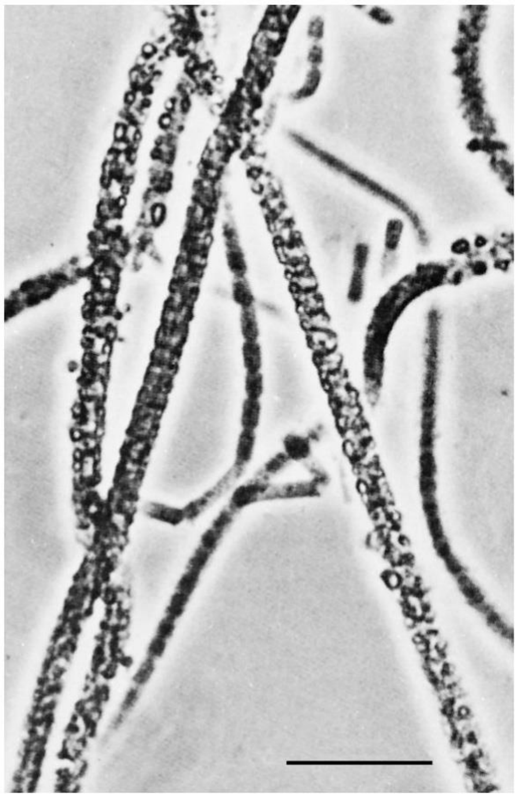
Genus *Neisseria*…

- **may have capsules and fimbriae**
- **inhabitants of mucous membranes of mammals**
  - **some human pathogens**
    - ***Neisseria gonorrhoeae* – gonorrhea**
    - ***Neisseria meningitidis* – meningitis**

Order *Burkholderiales*

- well-known genera
  - *Burkholderia, Bordetella, Sphaerotilus,* and *Leptothrix*
- some members have a sheath
  - hollow tubelike structure surrounding chain of cells
  - may contain ferric or manganic oxides
  - functions
    - attachment to surfaces
    - obtaining nutrients from slowly running water
    - protection against predators

Figure 20.15



Mulder, E.G. & van Veen, W.L., Investigations on the Sphaeerotilus-Leptothrix group, Antonie von Leeuwenhoek *Journal of Microbiology and Serology* 29: 121–153. Kluwer Publishers

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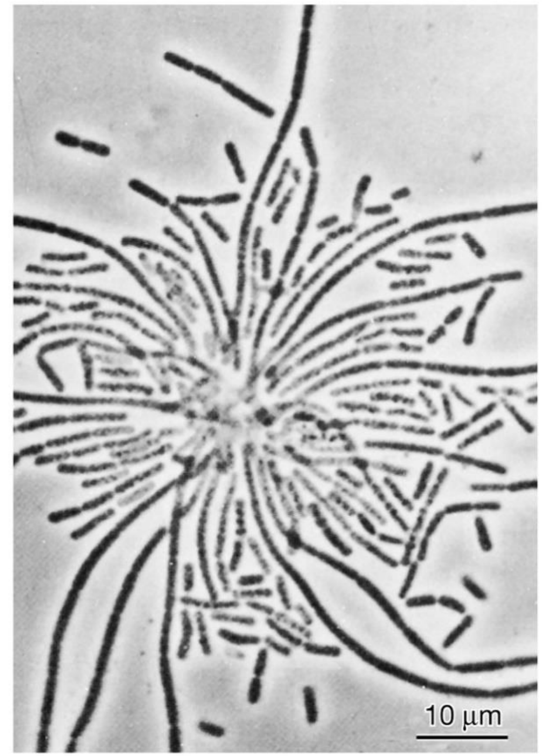
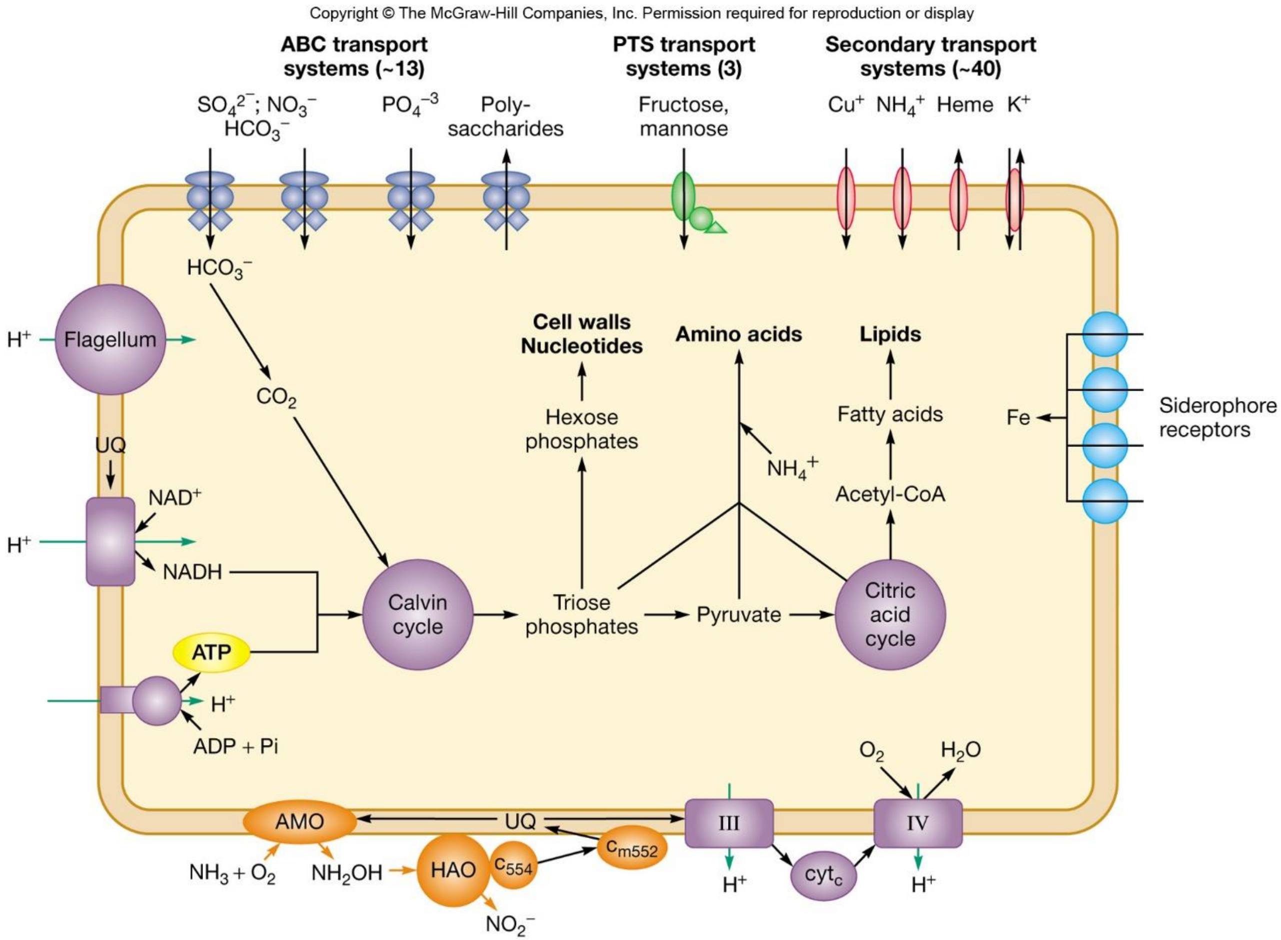


W L van Veen, E G Mulder, and M H Deinema Th e Sphaerotilus-L eptothrix group of bacteria, *Microbiol. Mol. Biol. Rev.* 1978 42: 329–356, fig. 6, p. 334. American Society of Microbiology

Figure 20.16



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ABC transport systems (~13)
PTS transport systems (3)
Secondary transport systems (~40)
SO_4^{2-}; NO_3^- HCO_3^-
PO_4^{-3}
Poly-saccharides
Fructose, mannose
Cu^+ NH_4^+ Heme K^+
HCO_3^-
H^+
Flagellum
CO_2
Cell walls Nucleotides
Amino acids
Lipids
Hexose phosphates
Fatty acids
Fe
Siderophore receptors
UQ
NH_4^+
NAD^+
Acetyl-CoA
H^+
NADH
Calvin cycle
Triose phosphates
Pyruvate
Citric acid cycle
ATP
H^+
ADP + Pi
O_2
H_2O
AMO
UQ
III
IV
c_{m552}
$NH_3 + O_2$
NH_2OH
HAO
c_{554}
H^+
cyt_c
H^+
NO_2^-

Genus *Burkholderia*

- gram-negative, non–spore-forming, straight rods
  - most motile with single flagellum or tuft of polar flagella
- aerobic and mesophilic
- nonfermentative chemoorganotrophs
  - catalase positive; often oxidase positive
  - most use poly-β-hydroxybutyrate as carbon reserve

e.g., *Burkholderia Cepacia*

- degrades >100 organic molecules
  - very active in recycling organic material
- plant pathogen
- has become a major nosocomial pathogen
  - particular problem for cystic fibrosis patients

Nitrogen Fixation by *Burkholderia* and *Ralstonia*

- **form symbiotic associations with legumes similar to that formed by rhizobia**
- **have nodulation genes (*nod*) similar to rhizobia suggesting a common genetic origin**
  - **genetic information may have been obtained through lateral gene transfer**

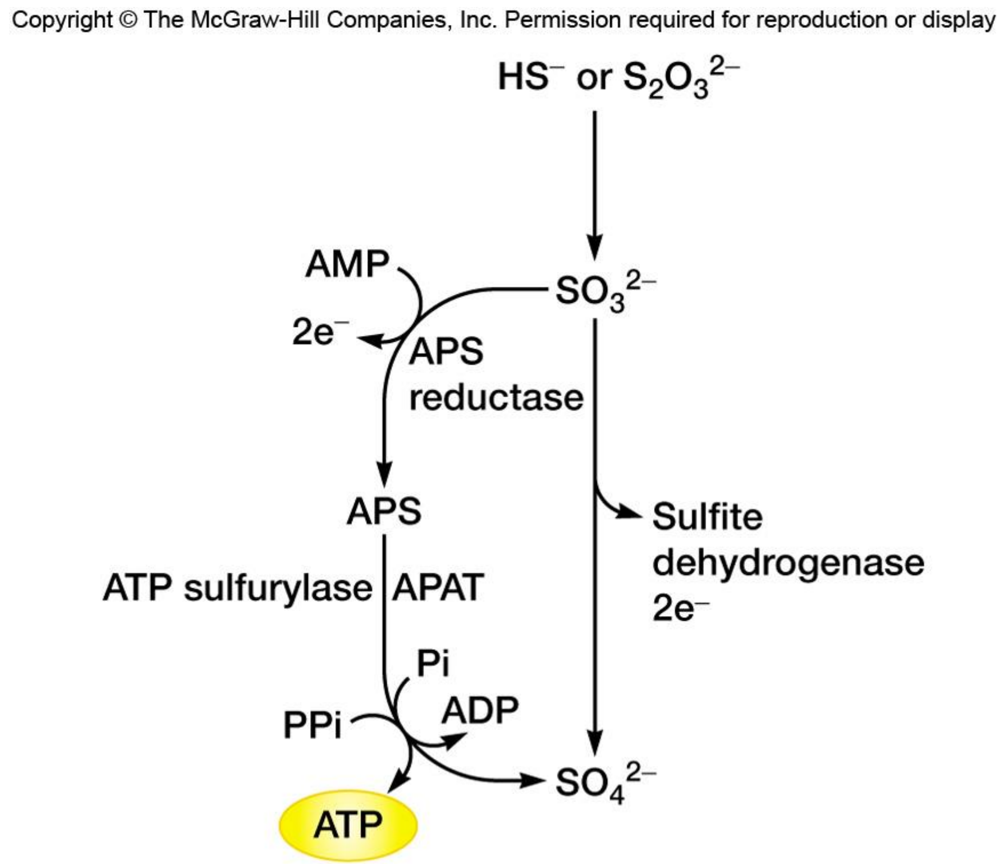
Genus *Bordetella*

- **gram-negative coccobacilli**
  - **some have capsules**
- **aerobic chemoorganotrophs**
  - **respiratory metabolism**
  - **require organic sulfur and amino acids for growth**
- **mammalian parasites that multiply in respiratory epithelial cells**
    - **nonmotile, encapsulated species**
    - **whooping cough and kennel cough**

Order *Nitrosomonadales*

- **number of chemolithotrophs**
  - **e.g., two genera of nitrifying bacteria**
    - ***Nitrosomonas* and *Nitrosospira***
  - **oxidize ammonia to nitrite**
    - **enzyme ammonia monooxygenase (AMO)**
    - **enzyme hydroxylamine oxidoreductase**
  - **also auxotrophic metabolism**
    - **fixes CO_2 in Calvin cycle**

Figure 20.17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HS⁻ or $S_2O_3^{2-}$
AMP
SO_3^{2-}
2e⁻
APS
reductase
APS
Sulfite
dehydrogenase
2e⁻
ATP sulfurylase
APAT
Pi
ADP
PPi
SO_4^{2-}
ATP

Order *Hydrogenophilales*

- **contains genus *Thiobacillus***
  - **Well-studied chemolithotroph**
  - **prominent member of colorless sulfur bacteria**
    - **chemolithotrophs that oxidize sulfur compounds**
    - **other colorless sulfur bacteria are in class *Gamma proteobacteria***

Table 20.4

Table 20.4 Colorless Sulfur-Oxidizing Genera

Genus	*Cell Shape*	*Motility; Location of Flagella*	*G + C Content (mol%)*	*Sulfur Deposit*[a]	*Nutritional Type*
Thiobacillus	Rods	+; polar	62–67	Extracellular	Obligate or facultative chemolithotroph
Thiomicrospira	Spirals, comma, or rod shaped	− or +; polar	39.6–49.9	Extracellular	Obligate chemolithotroph
Thiobacterium	Rods embedded in gelatinous masses	−	N.A.[b]	Intracellular[c]	Probably chemoorgano-heterotroph
Thiospira	Spiral rods, usually with pointed ends	+; polar (single or in tufts)	N.A.	Intracellular	Unknown
Macromonas	Rods, cylindrical or bean shaped	+; polar tuft	67	Intracellular[c]	Probably chemoorgano-heterotroph

[a] When hydrogen sulfide is oxidized to elemental sulfur.
[b] N.A., data not available.
[c] May use sulfur oxidation to detoxify H_2O_2.

Genus *Thiobacillus*

- **found in soil and aquatic habitats**
  - **production of sulfuric acid can cause corrosion of concrete and metal structures**
  - **may increase soil fertility by releasing sulfate**
  - **used in leaching metals from low grade metal ores**

Figure 20.18

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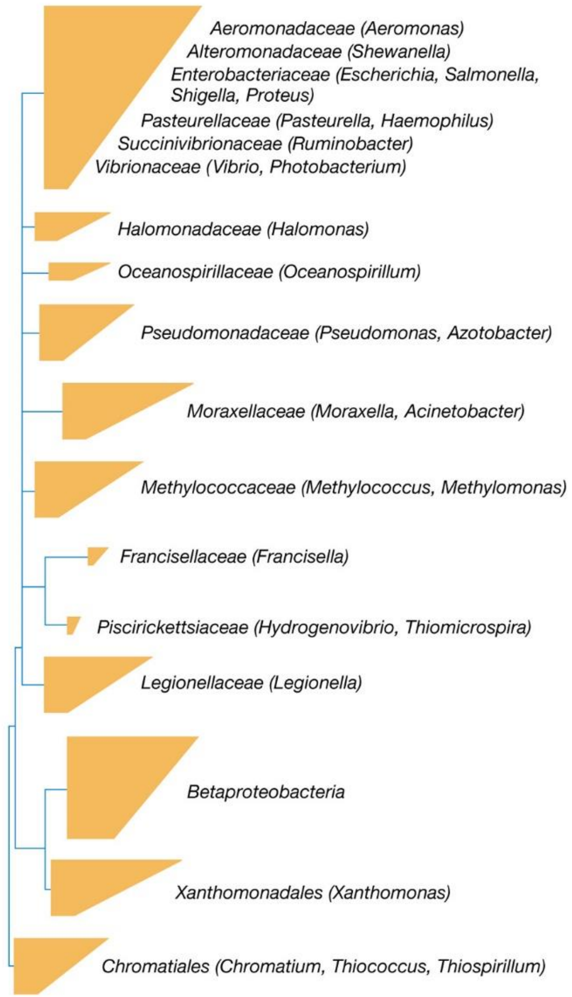
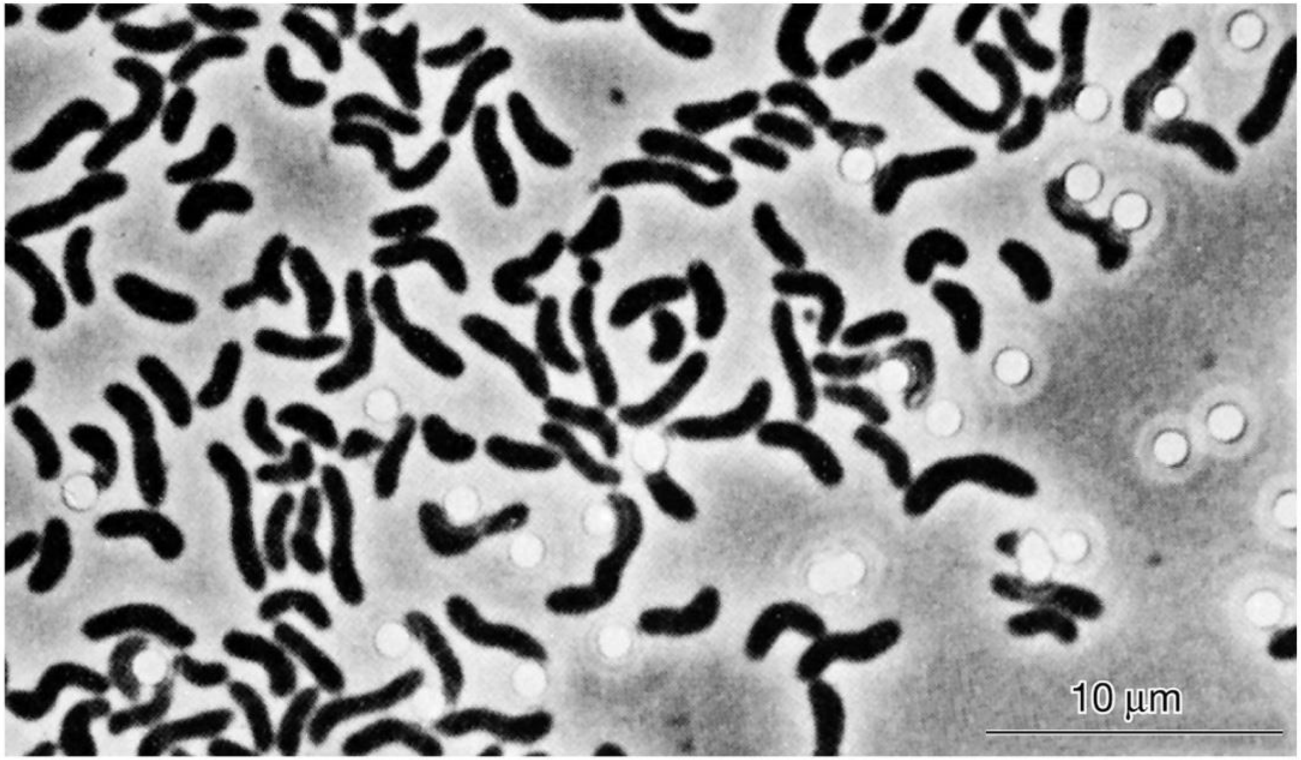


Class *Gammaproteobacteria*

- largest subgroup of proteobacteria
  - contains 14 orders and 28 families
- very diverse physiological types
  - chemoorganotrophs, photolithotrophs, chemolithotrophs, methylotrophs
  - aerobic and anaerobic
- many deeply branching groups

Figure 20.19



From M.P. Starr, et al. (Eds), *The Prokaryotes*, Springer- Verlag

Table 20.5

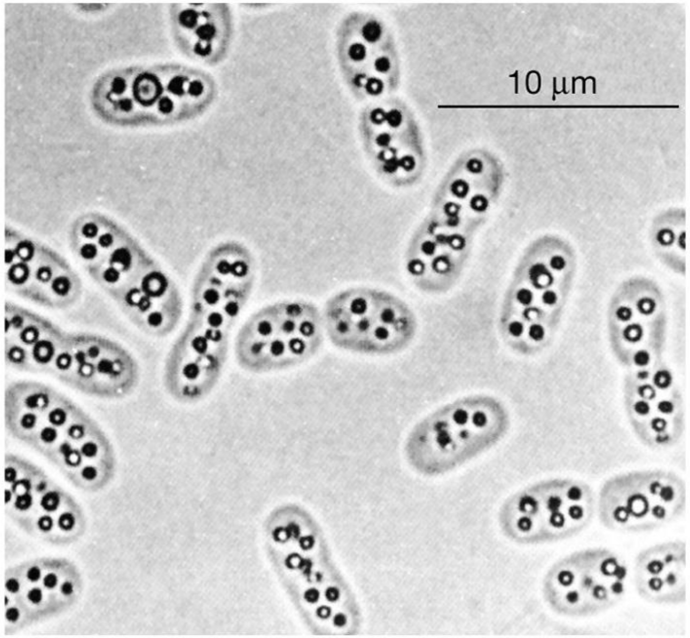
Table 20.5 Characteristics of Selected γ-Proteobacteria

Genus	*Dimensions (μm) and Morphology*	*G + C Content (mol%)*	*Oxygen Requirement*	*Other Distinctive Characteristics*
Azotobacter	1.5–2.0; ovoid cells, pleomorphic, peritrichous flagella or nonmotile	63.2–67.5	Aerobic	Can form cysts, fix nitrogen nonsymbiotically
Beggiatoa	1–200 × 2–10; colorless cells form filaments, either single or in colonies	35–39	Aerobic or microaerophilic	Gliding motility; can form sulfur inclusions with hydrogen sulfide present
Chromatium	1–6 × 1.5–16; rod-shaped or ovoid, straight or slightly curved, polar flagella	48–50	Anaerobic	Anoxygenic photolithoautotroph that can use sulfide; sulfur stored within the cell
Ectothiorhodospira	0.7–1.5 in diameter; vibrioid- or rod-shaped, polar flagella	61.4–68.4	Anaerobic, some aerobic or microaerophilic	Internal lamellar stacks of membranes; deposits sulfur granules outside cells
Escherichia	1.1–1.5 × 2–6; straight rods, peritrichous flagella or nonmotile	48–59	Facultatively anaerobic	Mixed acid fermenter; formic acid converted to H_2 and CO_2, lactose fermented, citrate not used
Haemophilus	<1.0 in width, variable lengths; coccobacilli or rods, nonmotile	37–44	Aerobic or facultatively anaerobic	Fermentative; requires growth factors present in blood; parasites on mucous membranes
Leucothrix	Long filaments of short cylindrical cells, usually holdfast is present	46–51	Aerobic	Dispersal by gonidia, filaments don't glide; rosettes formed; heterotrophic
Methylococcus	0.8–1.5 × 1.0–1.5; cocci with capsules, nonmotile	59–65	Aerobic	Can form cysts; uses methane, methanol, and formaldehyde as sole carbon and energy sources
Photobacterium	0.8–1.3 × 1.8–2.4; straight, plump rods with polar flagella	39–44	Facultatively anaerobic	Two species can emit blue-green light; Na^+ needed for growth
Pseudomonas	0.5–1.0 × 1.5–5.0; straight or slightly curved rods, polar flagella	58–69	Aerobic or facultatively anaerobic	Respiratory metabolism with oxygen or nitrate as acceptor; some use H_2 or CO as energy source
Vibrio	0.5–0.8 × 1.4–2.6; straight or curved rods with sheathed polar flagella	38–51	Facultatively anaerobic	Fermentative or respiratory metabolism; sodium ions stimulate or are needed for growth; oxidase positive

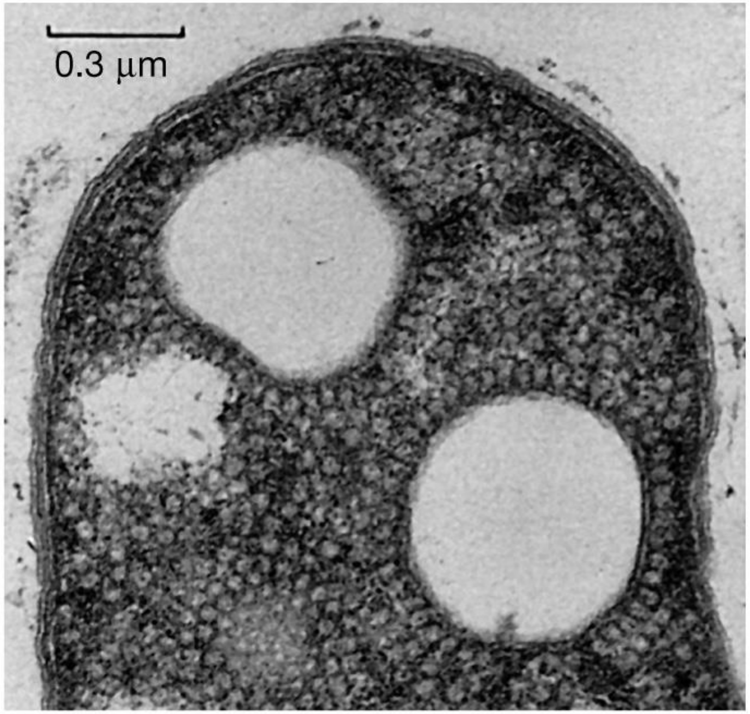
The Purple Sulfur Bacteria

- **placed in order *Chromatiales***
  - **divided into two families, *Chromatiaceae* and *Ectothiorhodospiraceae***
  - **Family *Ectothiorhodospiraceae* contains eight genera**

Figure 20.20



From M.P. Starr, et al. (Eds), *The Prokaryotes*, Springer-Verlag



From J.T. Staley, M.P. Bryant, N. Pfenning and J.G. Holt (Eds),
Bergey's Manual of Systematic Bacteriology, Vol. 3.
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Family *Chromatiaceae*

- **strict anaerobes**
- **usually photoautolithotrophs**
  - **use H_2S as electron donor**
    - **deposit sulfur granules internally**
    - **often eventually oxidize sulfur to sulfate**
  - **may also use hydrogen as electron donor**
- **usually found in anaerobic, sulfide-rich zones of lakes**
  - **can cause large blooms in bogs and lagoons**

Figure 20.21

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From ASM News 53(2): cover, 187, American Society for Microbiology. Photo by H. Kaltwasser

Figure 20.22

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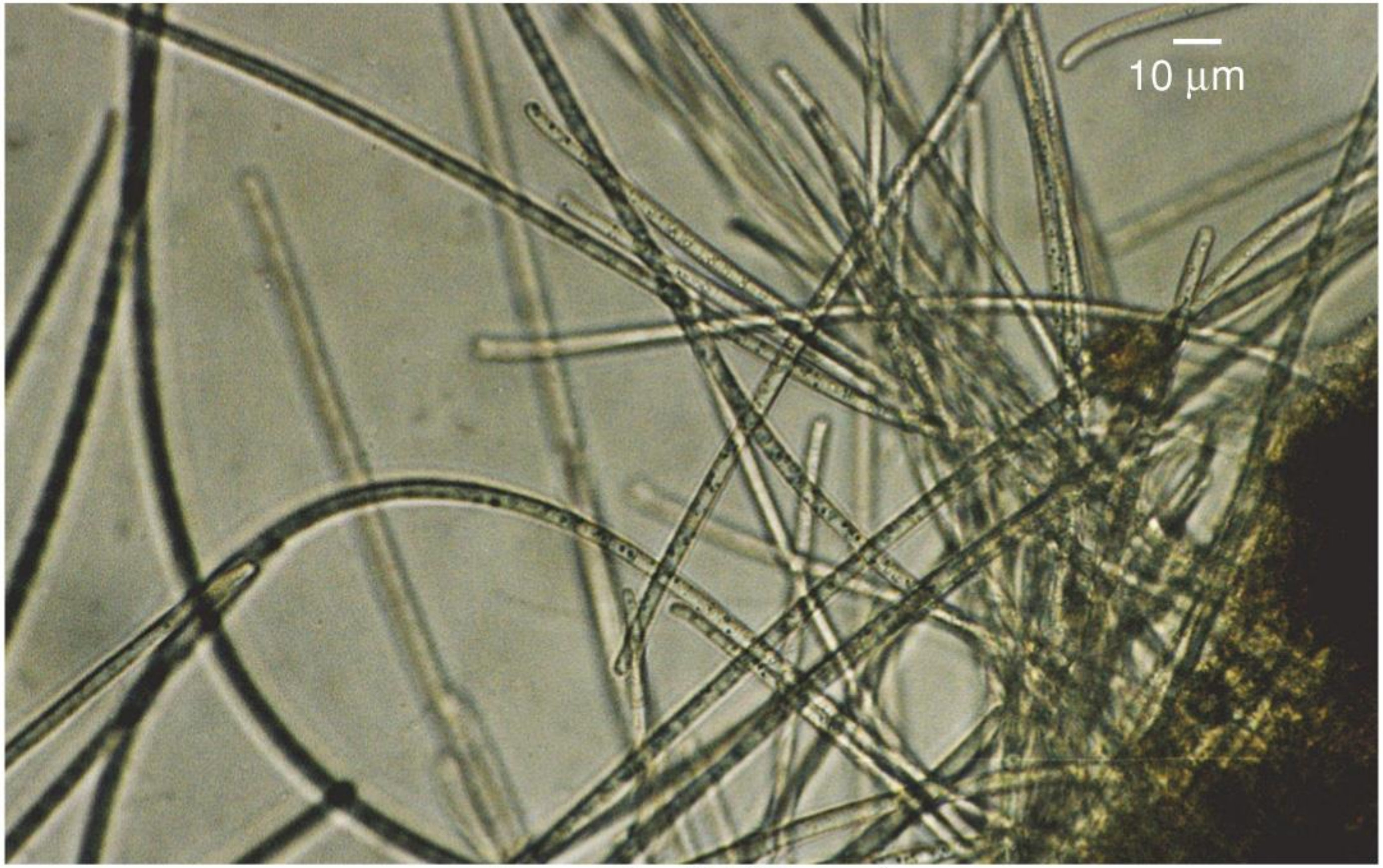

Image courtesy Mark Schneegurt

Order *Thiotrichales*

- **contains three families**
  - **largest is *Thiotrichaceae***
    - **contains several genera of that oxidize sulfur**
    - **rods and filamentous forms**
    - **best studied genera are *Beggiatoa, Leucothrix,* and *Thiothrix***

Figure 20.23

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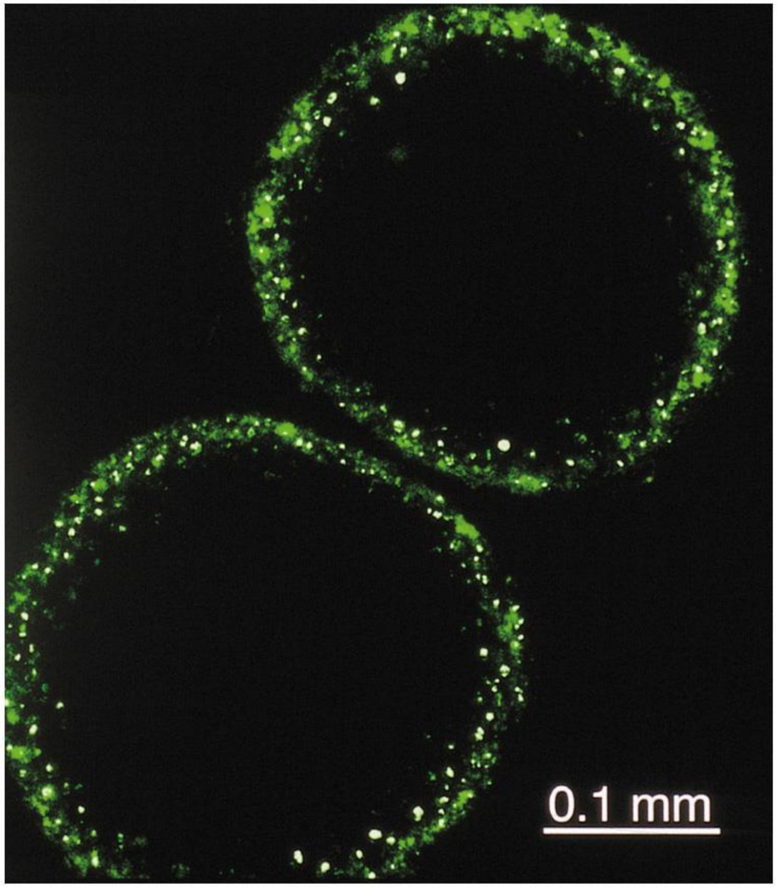

Reprinted with permission from Schulz; H.N., Brinkhoff , T., Ferdelman, T.G., Hernandez Marine, M., Teske, A., and Jorgensen, B.B. 1999. Dense Populations of a Giant Sulfur Bacterium in Namibian Shelf Sediments, *Science* 284, 493–495, fig 1.
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Genus *Beggiatoa*

- **filaments lack sheath**
- **metabolically versatile**
  - **can oxidize H_2S to sulfur**
    - **deposited internally in pockets formed by invaginations of plasma membrane**
  - **can grow heterotrophically with acetate as a carbon source**
  - **some may incorporate CO_2 autotrophically**
  - **grow in sulfide-rich habitats**

Genus *Thiomargarita*

- **among largest bacteria**
- **over 100 microns in diameter and hundreds of centimeters long**
- ***Beggiatoa, Thioploca, Thiomargarita*** **grow in bundles, appear hollow**

Figure 20.24

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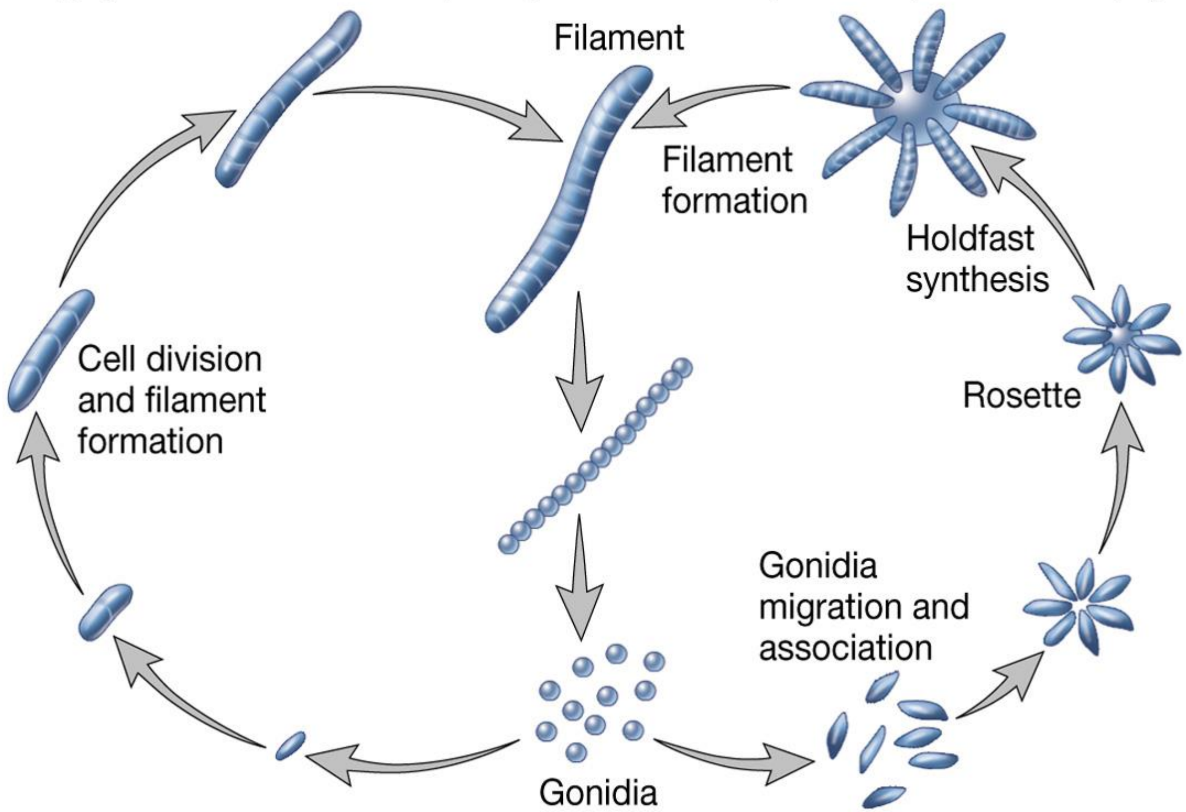
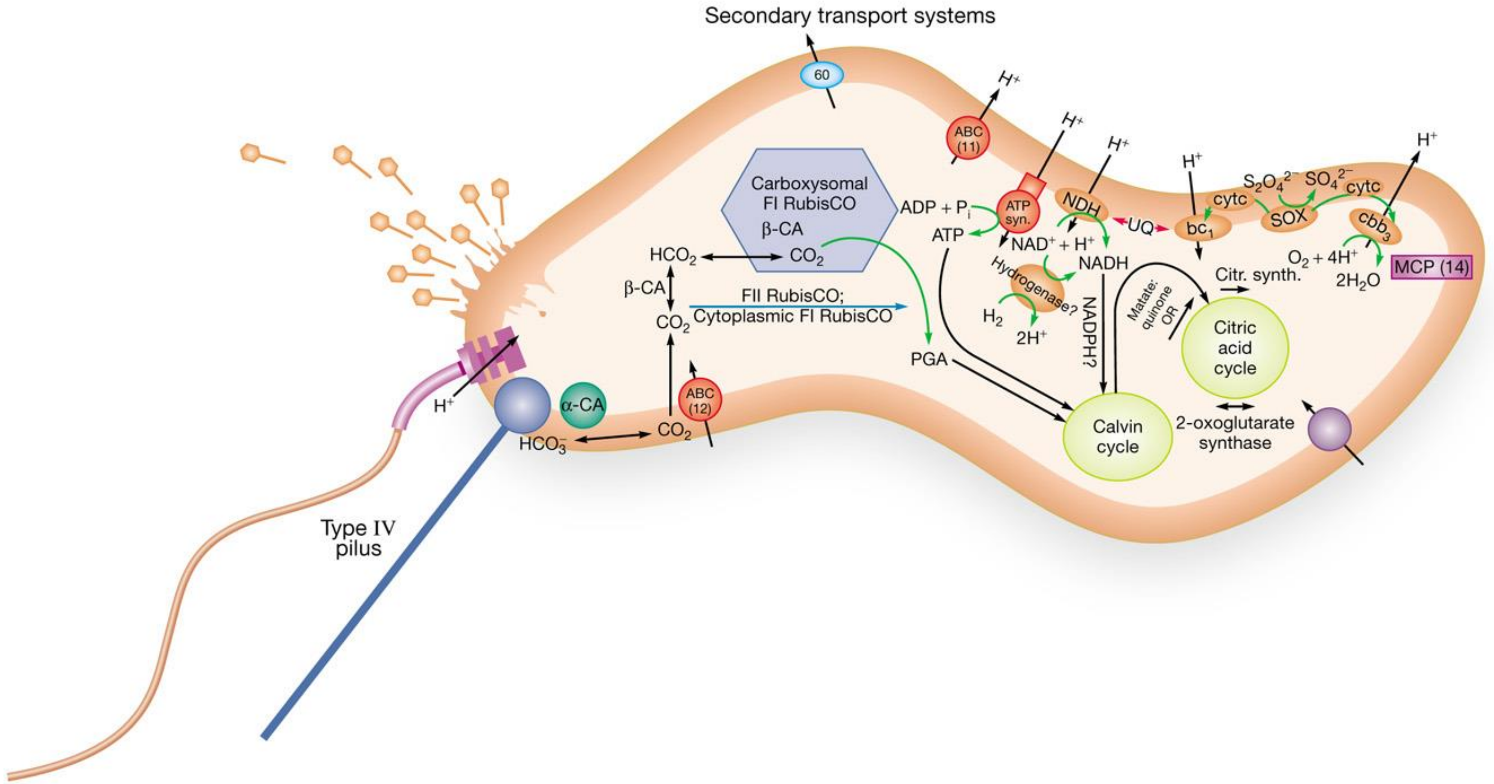


Genus *Leucothrix*

- aerobic chemoorganotrophs
- forms filaments or trichomes up to 400 microns long
- marine, complex lifestyle in which dispersal is by formation of gonidia

Figure 20.25



Secondary transport systems
60
H+
ABC (11)
H+
H+
H+
H+
Carboxysomal FI RubisCO
β-CA
CO2
ADP + Pi
ATP
ATP syn.
NDH
UQ
bc1
cytc
S2O4 2− SO4 2−
cytc
SOX
cbb3
HCO2
β-CA
CO2
FII RubisCO; Cytoplasmic FI RubisCO
NAD+ + H+
NADH
Hydrogenase?
H2
2H+
NADPH?
Malate: quinone OR
Citr. synth.
O2 + 4H+
2H2O
MCP (14)
PGA
Citric acid cycle
Calvin cycle
2-oxoglutarate synthase
H+
α-CA
ABC (12)
HCO3−
CO2
Type IV pilus

Genus *Thiothrix*

- **related to *Leucothrix* with gonidia**
- **chemolithotrophic**
  - **oxidize hydrogen sulfide**
  - **deposit sulfur granules internally**
  - **mixotrophic**
    - **use inorganic energy source and organic carbon source**
- **found in sulfide-rich flowing water and activated sludge sewage systems**

Genus *Thiomcrospira*

- **polyphyletic – γ- Ɛ-proteobacteria**
- **unique environment**
  - **hydrothermal vent deep sea microbe**
  - **can utilize differences in dissolved CO_2**
  - **multienzyme complex (SOX) for sulfur oxidation**
  - **aerobic – oxygen is electron acceptor**
  - **prophage in chromosome**

Figure 20.26

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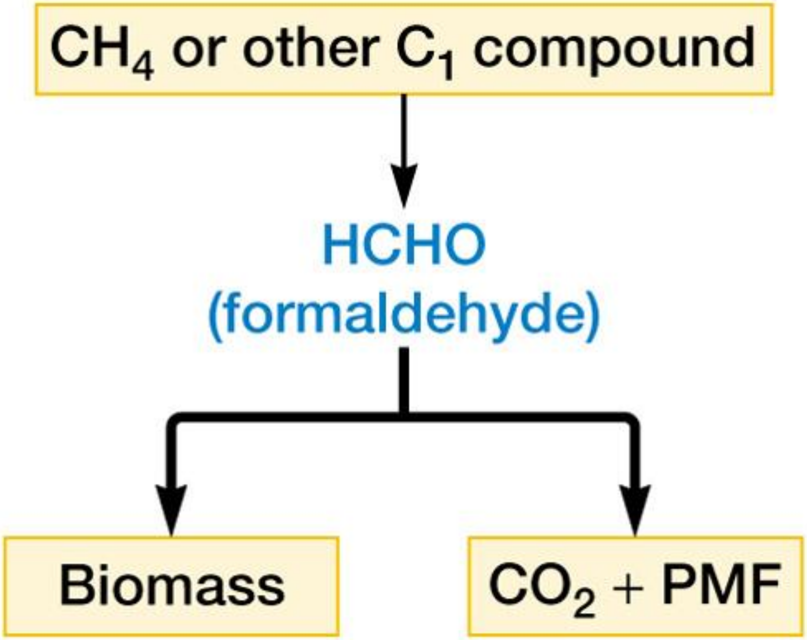

Order *Methylococcales*

- **contains family *Methylococcaceae*; seven genera**
- **morphologically diverse**
  - **e.g., genus *Methylococcus* – spherical, nonmotile**
  - **e.g., genus *Methylomonas* – straight, curved, or branched rods with single polar flagella**
  - **almost all form resting stage (cystlike structure)**
- **methylotrophs**
  - **use reduced one-carbon compounds as sole carbon and energy source**

Methane Oxidation

- occurs in complex arrays of intracellular membranes
- oxidized to methanol and then to formaldehyde
  - electrons donated to electron transport chain for ATP synthesis
  - formaldehyde can be assimilated into cell material

Figure 20.27

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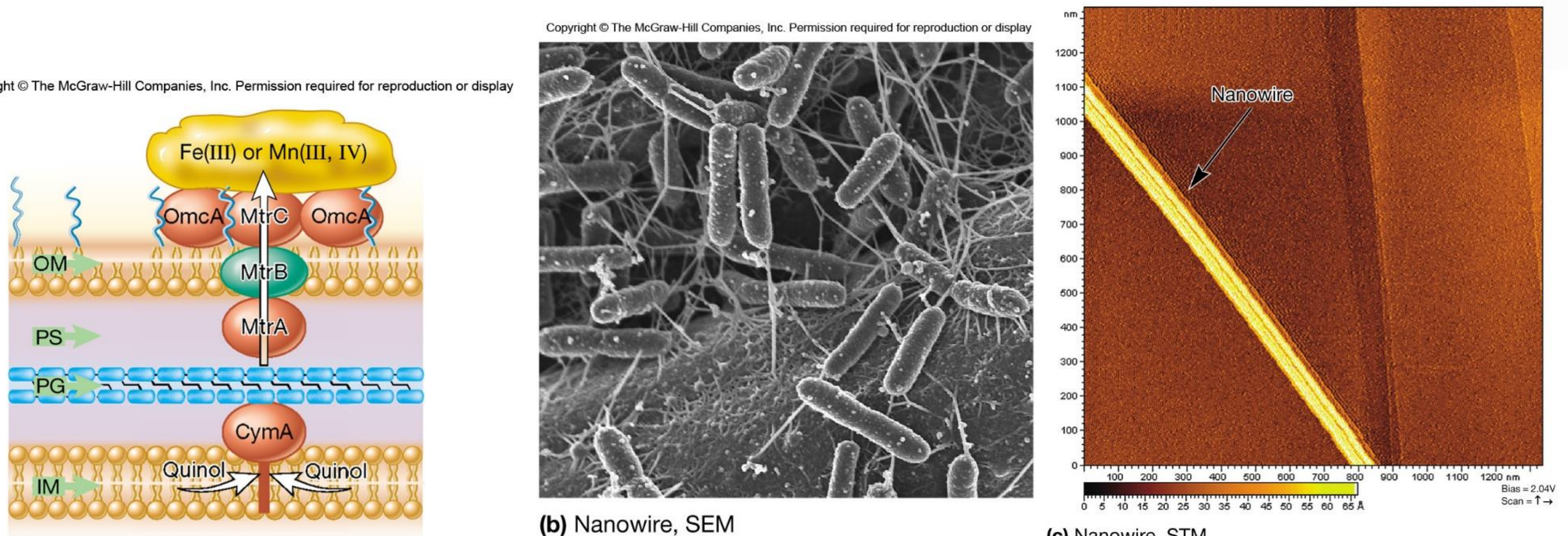


(a)

(b) Nanowire, SEM

Bruce Arey and Yuri Gorby

(c) Nanowire, STM

Photo courtesy of PNNL

Order *Legionellaceae*

- **family *Legionellacaea***
  - **genus *Legionella***
- **family *Coxiellaceae***
  - **genera *Coxiella* and *Rickettsiella***
- **all are intracellular pathogens**
  - **dimorphic lifestyle (two forms)**

Genus *Legionella*

- ***L. pneumophilia*** **intensely studied**
  - **causative agent Legionnaire's disease**
  - **transmission through aerosols**
  - **intracellular pathogen of protozoa**
    - **invade cooling towers, air conditioning, hot tubs**
  - **gram-negative rods that replicates by binary fission**

Genus *Legionella*

- Life cycle in Protist
  - replicative forms (RFs) reside in host vacuole (replicative endosome)
  - RFs differentiate into mature intracellular forms (MIFs) which are the infectious form
    - MIF are metabolically dormant, heat tolerant, and resistant to antibiotics
    - Hsp60 is invasin used to invade host cell

Genus *Coxiella*

- **host range**
  - **birds, insects, fish, rodents, sheep, goats, humans**
- **transmitted through aerosol**
- **life cycle similar to *L. pneumophilia***
  - **small cell variant (SCV) enters cell by phagocytosis**
  - **phagosome low pH triggers SCV to become metabolically active**
  - **SCV differentiates into large cell variant (LCV)**
  - **replicates by binary fission, are infectious**
  - **long-term survival outside the host**

Order *Pseudomonadales*

- **contains family *Pseudomonadaceae***
  - ***Pseudomonas* is the most important genus in the order Pseudomonadales**
    - **heterogenous - 60 species**
    - **gram-negative straight or slightly curved rods**
    - **0.5 to 1.0 μm by 1.5 to 5.0 μm in length**
    - **motile by one or several polar flagella**
    - **lack prosthecae or sheaths**

Pseudomonas

- chemoheterotrophs with respiratory metabolism
  - usually use oxygen as electron acceptor
  - sometimes use nitrate as electron acceptor
  - have functional TCA cycle
  - most hexoses are degraded by Entner-Duodoroff pathway

Practical Importance of Pseudomonads

- degrade wide variety of organic molecules
  - mineralization - microbial breakdown of organic materials to inorganic substrates
- important experimental subjects
- some are major animal and plant pathogens
- some cause spoilage of refrigerated food
  - can grow at 4°C

Genus *Azotobacter*

- often pleomorphic, motile rods
- aerobic, catalase positive
- chemoorganotrophs
- widespread in soil and water

Order *Alteromonadales*

- **Genus *Altermonas***
  - **strictly aerobic, nonspore-forming, straight or curved rods, motile with single polar flagella**
  - **mesophilic, require sodium ions for growth**

Genus *Shewanella*

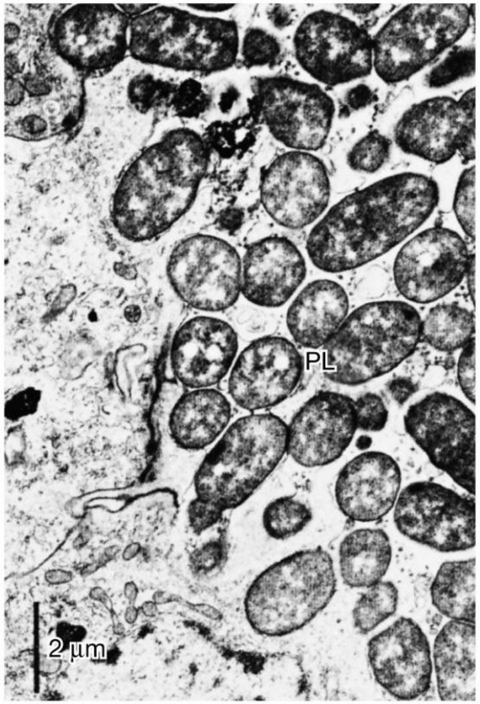
- found in seawater, lake sediments, salted foods
- facultatively anaerobic
- diverse electron acceptors used, e.g.,
  - uranium, chromium, neptunium, plutonium, selnite, vanadate, tellurite
  - excellent candidate for bioremediation of contaminated radionuclides

Genus *Shewanella*…

- **dissimilatory metal reduction**
  - **no assimilation of metals**
  - **evolved strategies for enabling use of insoluble metals such as Fe(III) or Mn(IV) as electron acceptors**
    - **localize cytochromes in outer membrane**
    - **electron shuttles transfer electrons to mineral surface**

Figure 20.28

© Kenneth Lucas, Steinhart Aquarium/ Biological Photo Service



Courtesy of James G. Morin, University of California Los Angeles

Order *Vibrionales*

- **contains one family, *Vibrionaceae*; eight genera**
- **most are aquatic, most free-living**
  - **straight or curved rods, oxidase positive, flagellated**
  - **some important pathogens**
  - **some symbiotic in luminous organs of fish**
- **closely related to two other orders**
  - ***Enterobacteriales* and *Pasteurellales***

Vibrio Cholerae

- **pathogen that causes cholera**
- **genome has been sequenced**
  - **has two circular chromosomes**
  - **copies of some genes present on both chromosomes**
  - **cholera toxin gene is integrated phage on chromosome 1**

Table 20.6

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Table 20.6 Characteristics of Families of Facultatively Anaerobic Gram-Negative Rods

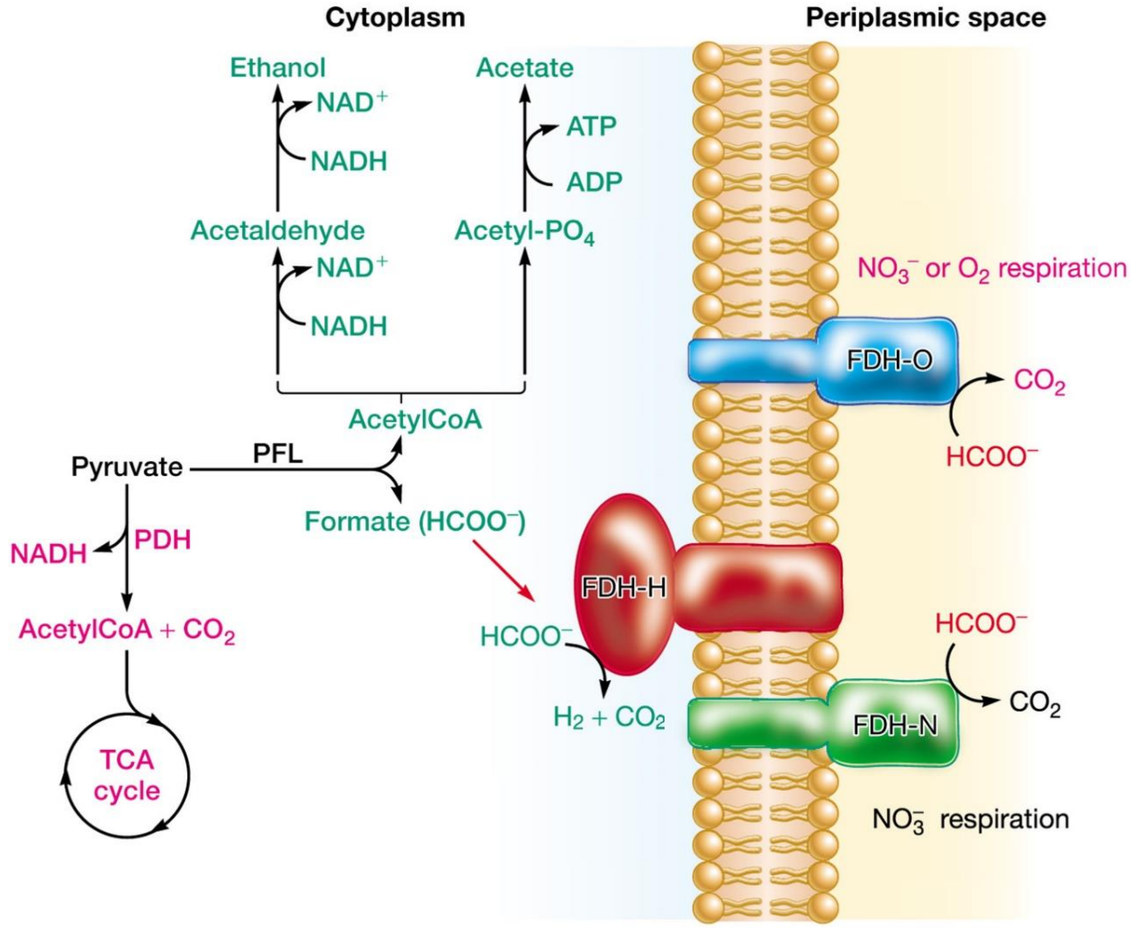
Characteristics	*Enterobacteriaceae*	*Vibrionaceae*	*Pasteurellaceae*
Cell dimensions	0.3–1.0 × 1.0–6.0 μm	0.3–1.3 × 1.0–3.5 μm	0.2–0.4 × 0.4–2.0 μm
Morphology	Straight rods; peritrichous flagella or nonmotile	Straight or curved rods; polar flagella; lateral flagella may be produced on solid media	Coccoid to rod-shaped cells, sometimes pleomorphic; nonmotile
Physiology	Oxidase negative	Oxidase positive; all can use D-glucose as sole or principal carbon source	Oxidase positive; heme and/or NAD^+ often required for growth; organic nitrogen source required
G + C content	38–60%	38–51%	38–47%
Symbiotic relationships	Some parasitic on mammals and birds; some species are plant pathogens	Most not pathogens; several inhabit light organs of marine organisms	Parasites of mammals and birds
Representative genera	*Escherichia, Shigella, Salmonella, Citrobacter, Klebsiella, Enterobacter, Erwinia, Serratia, Proteus, Yersinia*	*Vibrio, Photobacterium*	*Pasteurella, Haemophilus*

From Garrity, G. M., editor-in-chief. Bergey's Manual of Systematic Bacteriology, *vol. 2. Copyright © 2005 New York: Springer. Reprinted by permission.*

V. fischeri, V. harveyi

- **free-living**
- **capable of bioluminescence**
  - **emission of light catalyzed by luciferase**
  - **symbiotic relationship with fish organs**
  - **also observed in at least two species of *Photobacterium***

Figure 20.29


Cytoplasm
Periplasmic space
Ethanol
NAD+
NADH
Acetate
ATP
ADP
Acetaldehyde
NAD+
NADH
Acetyl-PO4
AcetylCoA
PFL
Pyruvate
Formate (HCOO−)
PDH
NADH
AcetylCoA + CO2
TCA cycle
HCOO−
FDH-H
H2 + CO2
NO3− or O2 respiration
FDH-O
CO2
HCOO−
HCOO−
CO2
FDH-N
NO3− respiration

Order *Enterobacteriales*

- **one family, *Enterobacteriaceae*; 44 genera**
  - **enteric bacteria or enterobacteria**
- **facultative anaerobes**
- **chemoorganotrophs that degrade sugars by glycolytic pathway**
  - **can cleave pyruvate to yield formic acid (formic acid fermentation)**

Family *Enterobacteriaceae*…

- **two groups based on fermentation products**
  - **majority are mixed acid fermenters**
    - **produce lactate, acetate, succinate, formate, and ethanol**
  - **others are butanediol fermenters**
    - **butanediol, ethanol, and carbon dioxide**

Figure 20.30

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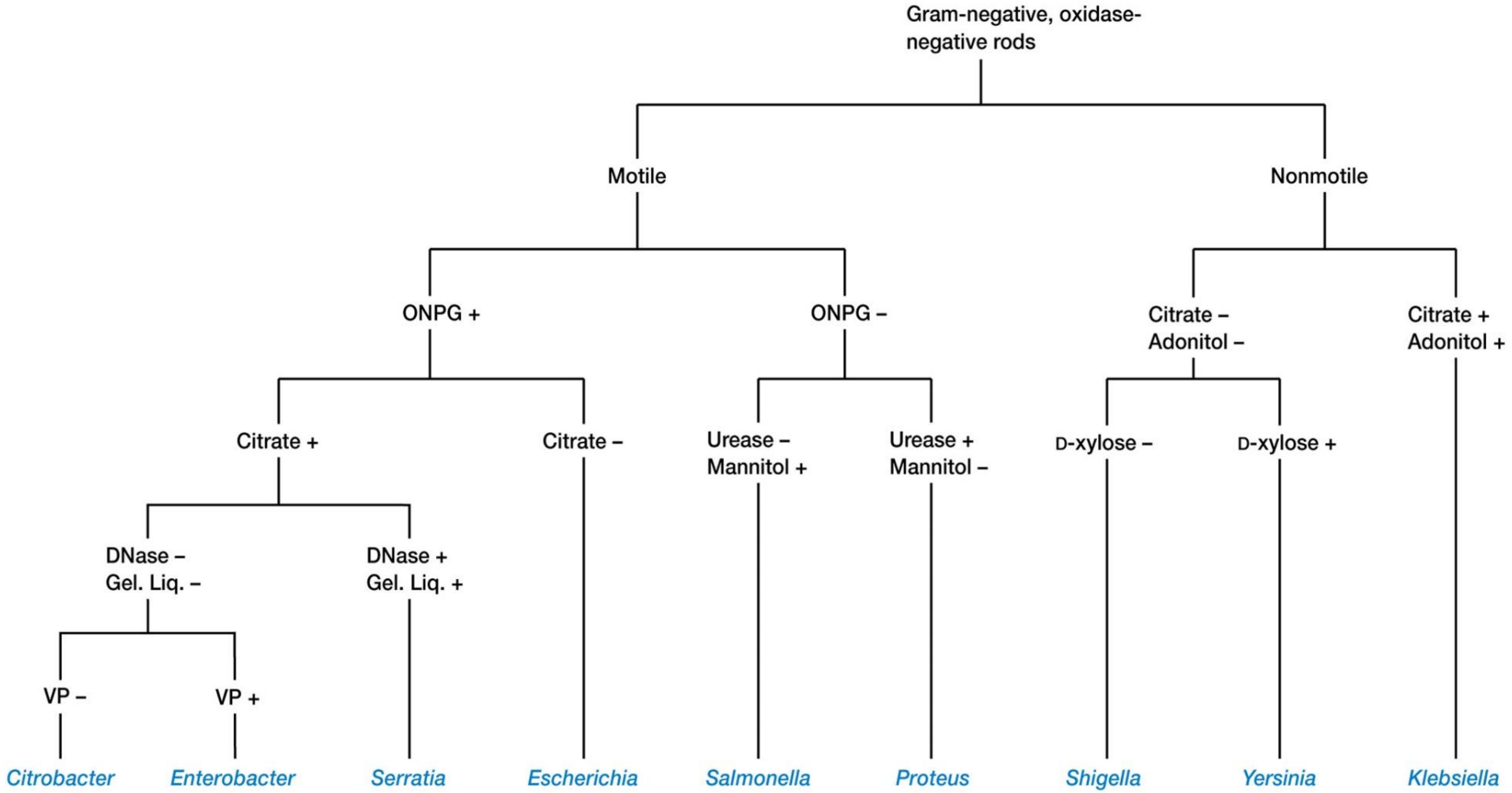

Family *Enterobacteriaceae*…

- **biochemical tests used to distinguish genera in addition to morphology, motility, growth responses**
- **very common, widespread, and important**

Figure 20.31

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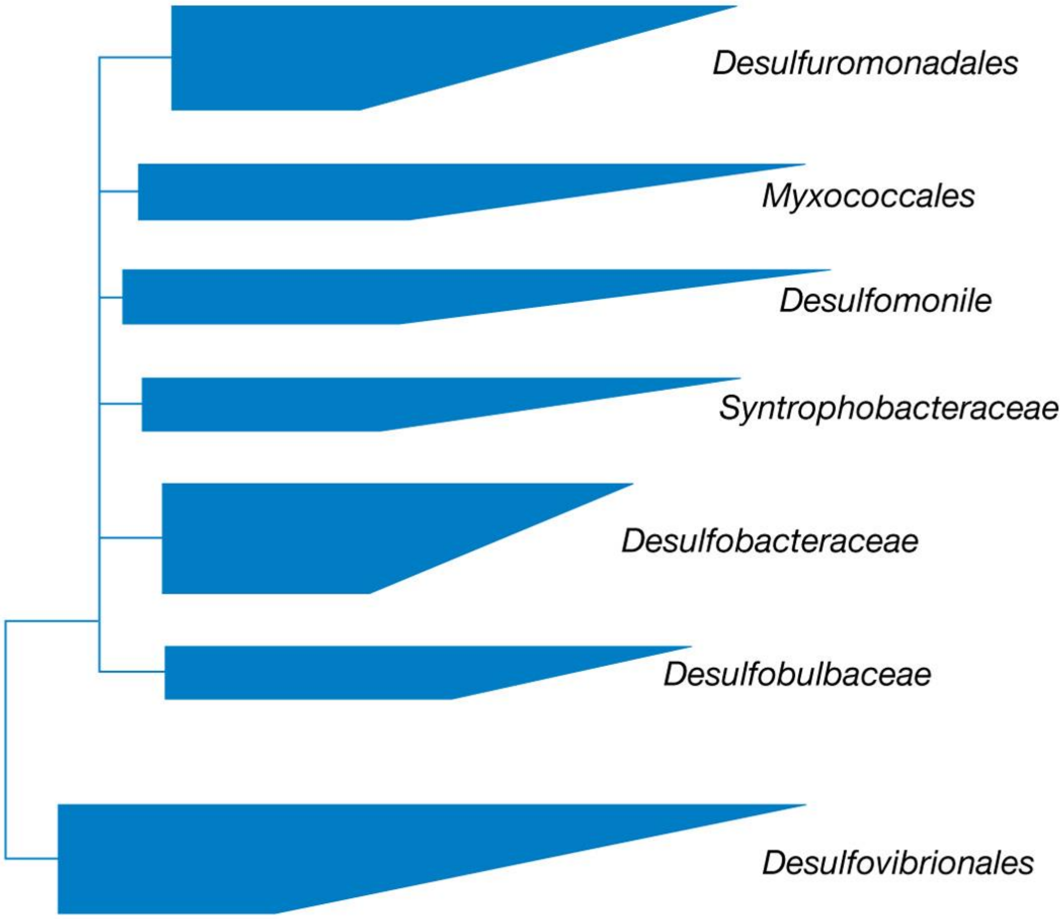

Table 20.7

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Table 20.7 Some Characteristics of Selected Genera in the *Enterobacteriaceae*

Characteristics	*Escherichia*	*Shigella*	*Salmonella*	*Citrobacter*	*Proteus*	*Yersinia*	*Klebsiella*	*Enterobacter*	*Erwinia*	*Serratia*
Methyl red	+	+	+	+	+	+	(+)[a]	(−)[b]	+	d[c]
Voges-Proskauer	−	−	−	−	d	− (37°C)	(+)	+	(+)	+
Indole production	(+)	d	−	d	d	d	d	−	(−)	(−)
Citrate use	−	−	(+)	+	d	(−)	(+)	+	(+)	+
H_2S production	−	−	(+)	d	(+)	−	−	−	(+)	−
Urease	−	−	−	(+)	+	d	(+)	(−)	−	−
β-galactosidase	(+)	d	d	+	−	+	(+)	+	+	+
Gas from glucose	+	−	(+)	+	+	(−)	(+)	(+)	(−)	d
Acid from lactose	+	−	(−)	d	−	(−)	(+)	(+)	d	d
Phenylalanine deaminase	−	−	−	−	+	−	−	(−)	(−)	−
Lysine decarboxylase	(+)	−	(+)	−	−	(−)	(+)	d	−	d
Ornithine decarboxylase	(+)	d	(+)	(+)	d	d	−	(+)	−	d
Motility	d	−	(+)	+	+	− (37°C)	−	+	+	+
Gelatin liquifaction (22°C)	−	−	−	−	+	(−)	−	d	d	(+)
% G + C	48–59	49–53	50–53	50–52	38–41	46–50	53–58	52–60	50–54	52–60
Genome size (Mb)	4.6–5.5	4.6	4.5–4.9	Nd[d]	Nd	4.6	Nd	Nd	5.1	5.1
Other characteristics	1.1–1.5 × 2.0–6.0 μm; peritrichous flagella when motile	No gas from sugars	0.7–1.5 × 2–5 μm; peritrichous flagella	1.0 × 2.0–6.0 μm; peritrichous flagella	0.4–0.8 × 1.0–3.0 μm; peritrichous flagella	0.5–0.8 × 1.0–3.0 μm; peritrichous flagella when motile	0.3–1.0 × 0.6–6.0 μm; capsulated	0.6–1.0 × 1.2–3.0 μm; peritrichous flagella	0.5–1.0 × 1.0–3.0 μm; peritrichous flagella; plant pathogens and saprophytes	0.5–0.8 × 0.9–2.0 μm; peritrichous flagella; colonies often pigmented

[a] (+) usually present
[b] (−) usually absent
[c] d, strains or species vary in possession of characteristic
[d] Nd: Not determined; genome not yet sequenced

Escherichia coli

- **probably best studied bacterium**
- **inhabitant of intestinal tracts of many animals**
- **used as indicator organisms for testing water for fecal contamination**
- **some strains are pathogenic**
  - **gastroenteritis**
  - **urinary tract infections**

Important Pathogenic Enteric Bacteria

- ***Salmonella* – typhoid fever and gastroenteritis**
- ***Shigella* – bacillary dysentery**
- ***Klebsiella* – pneumonia**
- ***Yersinia* – plague**
- ***Erwinia* – blights, wilts, etc., of crop plants**

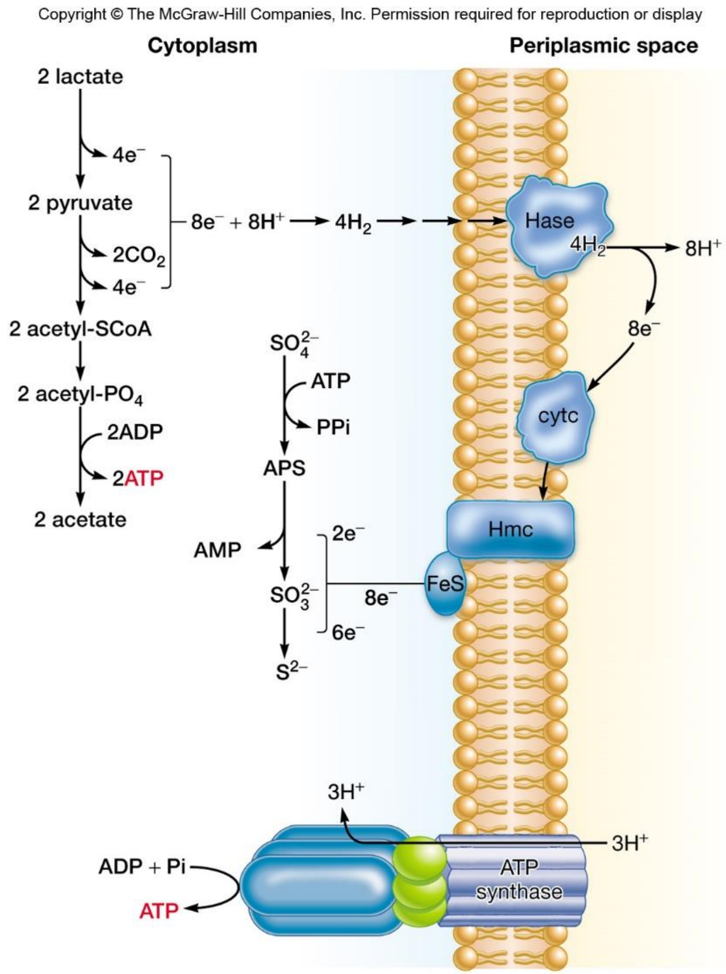
Order *Pasteurellales*

- **one family, *Pasteurellaceae*; six genera**
- **small, nonmotile, oxidase positive**
- **important pathogens**
  - ***Pasteurella multiocida* – fowl cholera**
  - ***Pasteurella haemolytica* – pneumonia in cattle, sheep, and goats**
  - ***Haemophilus influenzae* – variety of diseases, including meningitis in children; vaccine available**

Class *Deltaproteobacteria*

- **contains eight orders and 20 families**
  - **divided into two general groups**
    - **aerobic, chemoorganotrophic predators**
    - **anaerobic, chemoorganotrophic sulfur- and sulfate-reducers**

Figure 20.32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Cytoplasm
Periplasmic space
2 lactate
4e⁻
2 pyruvate
2CO2
4e⁻
2 acetyl-SCoA
2 acetyl-PO4
2ADP
2ATP
2 acetate
8e⁻ + 8H⁺
4H2
Hase
4H2
8H⁺
8e⁻
cytc
Hmc
FeS
SO4 2−
ATP
PPi
APS
AMP
2e⁻
SO3 2−
8e⁻
6e⁻
S2−
3H⁺
3H⁺
ADP + Pi
ATP
ATP synthase

Table 20.8

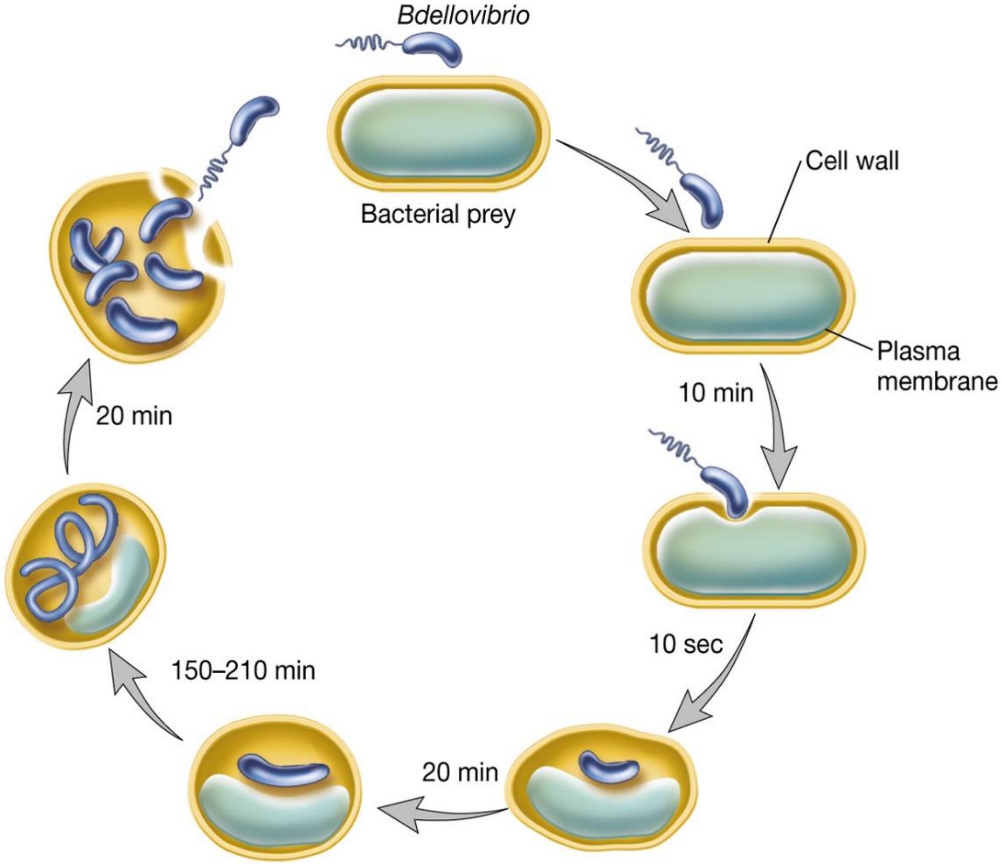
Table 20.8 Characteristics of Selected δ- and ε-Proteobacteria

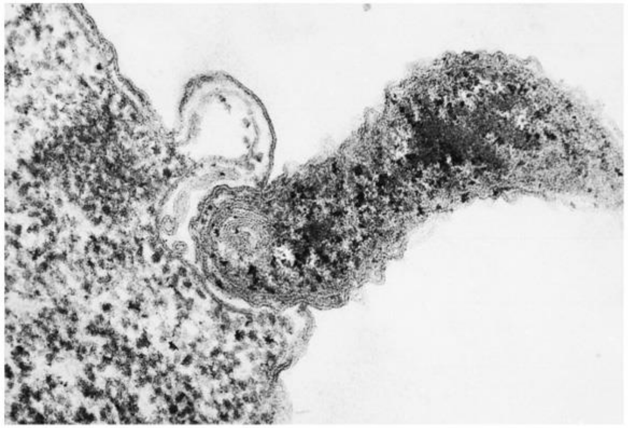
Class Genus	*Dimensions (μm) and Morphology*	*G + C Content (mol%)*	*Oxygen Requirement*	*Other Distinctive Characteristics*
δ-Proteobacteria				
Bdellovibrio	0.2–0.5 × 0.5–1.4; comma-shaped rods with a sheathed polar flagellum	49.5–51	Aerobic	Preys on other gram-negative bacteria where it grows in the periplasm; alternates between predatory and intracellular reproductive phases
Desulfovibrio	0.5–1.5 × 2.5–10; curved or sometimes straight rods, motile by polar flagella	46.1–61.2	Anaerobic	Oxidizes organic compounds to acetate and reduces sulfate or sulfur to H_2S
Desulfuromonas	0.4–0.9 × 1.0–4.0; straight or slightly curved or ovoid rods, lateral or subpolar flagella	54–62	Anaerobic	Reduces sulfur to H_2S, oxidizes acetate to CO_2; forms pink or peach-colored colonies
Myxococcus	0.4–0.7 × 2–8; slender rods with tapering ends, gliding motility	68–71	Aerobic	Forms fruiting bodies with microcysts not enclosed in a sporangium
Stigmatella	0.7–0.8 × 4–8; straight rods with tapered ends, gliding motility	67–68	Aerobic	Stalked fruiting bodies with sporangioles containing myxospores (0.9–1.2 × 2–4 μm)
ε-Proteobacteria				
Campylobacter	0.2–0.8 × 0.5–5; spirally curved cells with a single polar flagellum at one or both ends	29–47	Microaerophilic	Carbohydrates not fermented or oxidized; oxidase positive and urease negative; found in intestinal tract, reproductive organs, and oral cavity of animals
Helicobacter	0.2–1.2 × 1.5–10; helical, curved, or straight cells with rounded ends; multiple, sheathed flagella	24–48	Microaerophilic	Catalase and oxidase positive; urea rapidly hydrolyzed; found in the gastric mucosa of humans and other animals

Orders *Desulfovibrionales, Desulfobacterales,* and *Desulfuromonadales*

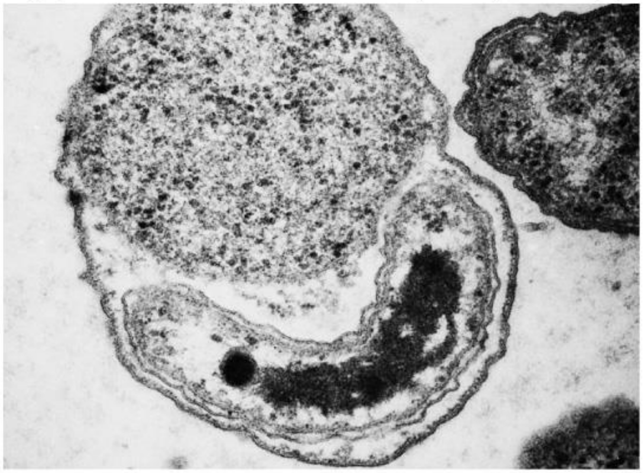
- **strict anaerobes**
- **sulfur- or sulfate-reducing bacteria**
  - **use sulfur and sulfate as electron acceptors during anaerobic respiration**
  - **electron transport chain used to generate ATP**
- **widespread in muds and sediments of aquatic environments, including sewage treatment systems**
  - **important in sulfur cycling in ecosystems**

Figure 20.33





Courtesy Dr. Jeffrey C. Burnham



Courtesy Dr. Jeffrey C. Burnham

Order *Desulfuromonales*

- **all strictly anaerobic with respiratory or fermentative metabolism**
  - **chemolithotrophs, chemoorganotrophs**
  - **mesophilic, marine, and fresh water**
- **environmentally important**
  - **conserve energy from dissimilatory metal reduction including toxic and radioactive metals**
  - **synthesize nanowires**
  - **electricity generated by microbial fuel cells**

Order *Bdellovibrionales*

- **one family, *Bdellovibrionaceae*; four genera**
  - **best studied is *Bdellovibrio***
    - **aerobic, gram-negative, motile curved rods**
    - **predatory bacteria life cycle that resembles bacteriophages in many ways**
      - **collides with prey, bores hole through cell wall, disrupts plasma membrane**

Figure 20.34

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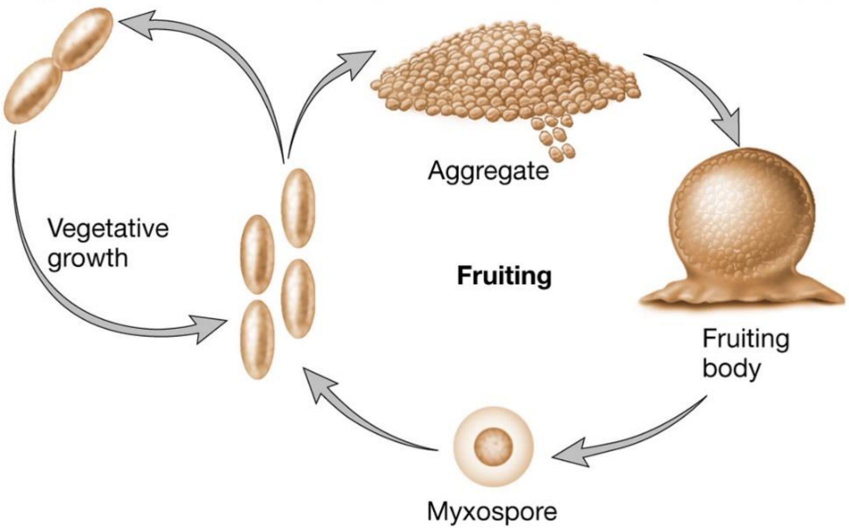

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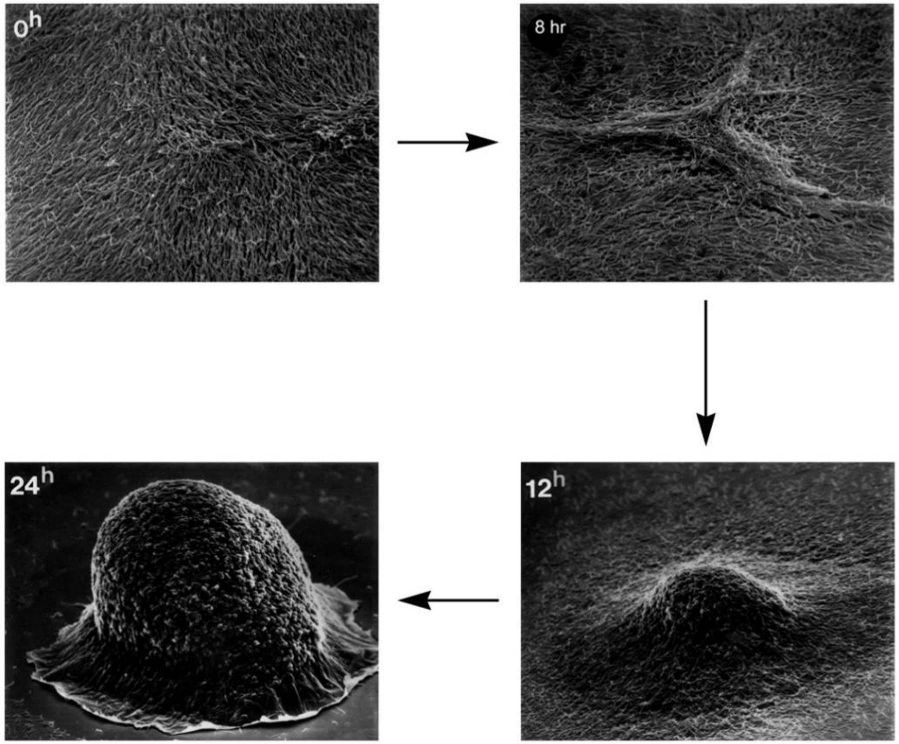

Jerry M. Kuner and Dale Kaiser, Fruiting body morphogenesis in submerged cultures of Myxococeus xauthus, *J. Bacteriol.* 151, 458–461, 1982

Order *Myxococcales*

- contains five families distinguished based on shape of vegetative cells, myxospores, and sporangia
- gram-negative, rod-shaped gliding bacteria
- aerobic chemoorganotrophs with respiratory metabolism
  - most are micropredators or scavengers that lyse bacteria and yeasts by secretion of digestive enzymes
    - most use amino acids as major source of C, N, and energy

Myxobacteria

- distinctive life cycle which resembles that of cellular slime molds
- in presence of food form a swarm and migrate on solid surfaces
- form a fruiting body when nutrients are exhausted
  - involves at least 5 extracellular signaling molecules which allow cells to communicate with each other

Figure 20.35

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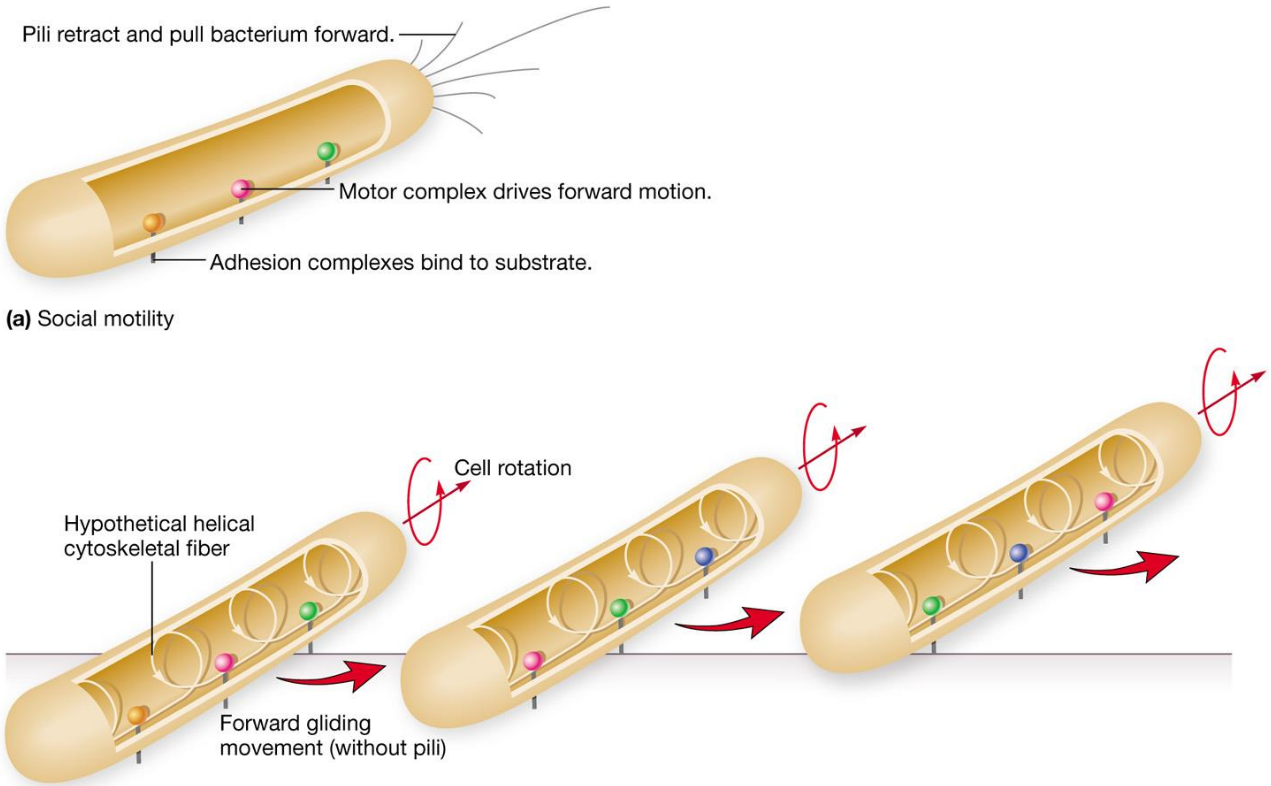
Fruiting Bodies

- **formation requires gliding motility and involves at least 5 extracellular signaling molecules which allow cells to communicate with each other**
- **range in height from 50 to 500 μm**
- **colored by carotenoid pigments**
- **vary in complexity**
- **some cells develop into myxospores**

Figure 20.36



(a) Social motility

(b) Adventurous motility

Myxospores

- **frequently enclosed in walled structures called sporangioles (sporangia)**
- **dormant and desiccation-resistant**
  - **may survive up to 10 years**

M. xanthus Gliding Motility

- **social (S) motility – twitching motility**
  - **governed by production of retractable type IV pili**
  - **when pili retract, cell creeps forward**
  - **requires cell to cell contact for pili**
- **adventurous (A) motility**
  - **single cells that leave the group**
  - **involved in slime secretion and clusters of motor proteins in contact with substrate**

Figure 20.37

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Annette Summers Engel, Ph.D

Class *Epsilonproteobacteria*

- **smallest of proteobacterial classes**
- **probably two one orders, *Campylobacteriales* and *Nautiliales*; three families**
- **slender gram-negative rods**

Genus *Campylobacter*

- ***Campylobacter fetus***
  - **reproductive disease and abortions in cattle and sheep**
  - **septicemia and enteritis in humans**
    - **septicemia – pathogens or their toxins in blood**
    - **enteritis – inflammation of intestinal tract**
  - **Guillain-Barre syndrome triggered in molecular mimicry**
- ***Campylobacter jejuni***
  - **abortions in sheep**
  - **enteritis diarrhea in humans**

Genus *Helicobacter*

- at least 23 species isolated from stomachs and upper intestines of mammals
- e.g., *Helicobacter pylori*
  - causes gastritis and peptic ulcer disease
  - motility important for colonization
  - does not grow below pH 4.5
    - urease converts urea to ammonia and CO_2
  - urea hydrolysis appears to be associated with virulence

Epsilonproteobacteria…

- **newly discovered are thermophilic, chemolithoautotrophic, and others**
- **found in marine hydrothermal vents, terrestrial springs, ground water, oil-field brines, limestone caves, sulphidic springs**
- **found in filamentous microbial mats in anoxic, sulfide-rich cave springs**

Table 20.9

Table 20.9 Some Recently Isolated ε-Proteobacteria

Species	*Isolation Site*	*Optimum Growth Temperature*	*Carbon Metabolism*	*Electron Donor*	*Electron Acceptor*	*Sulfur/Nitrogen Reduction Product*
Nautilia lithotrophica	Hydrothermal vent	52°C	Heterotroph	H_2, formate	SO_3^{2-}, S^0	H_2S
Caminibacter hydrogeniphilus	Hydrothermal vent	60°C	Heterotroph	H_2, complex organic compounds	NO_3^-, S^0	H_2S, NH_3
Nitratiruptor tergarcus	Hydrothermal vent	55°C	Autotroph	H_2	O_2, (microaerobic), NO_3^-, S^0	H_2S, N_2
Sulfurospirillum sp. str. Am-N	Hydrothermal vent	41°C	Heterotroph	Formate, fumarate	S^0	H_2S
Arcobacter sp. str. FWKO B	Oil-field production water	30°C	Autotroph	H_2, formate, HS^-	O_2, (microaerobic), NO_3^-, S^0	H_2S, N_2O^-
Sulfuricurvum kujiense	Oil-field production water	25°C	Autotroph	H_2, HS^-, $S_2O_3^{2-}$, S^0	O_2, (microaerobic), NO_3^-	NO_2^-

From Campbell, B. J., et al. 2006. The versatile ε-proteobacteria: Key players in sulphidic habitats. Nature Rev. Microbiol. *4:458–67.*