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Brock Biology of Microorganisms

Eleventh Edition

Chapter 12:

Prokaryotic Diversity:
The *Bacteria*

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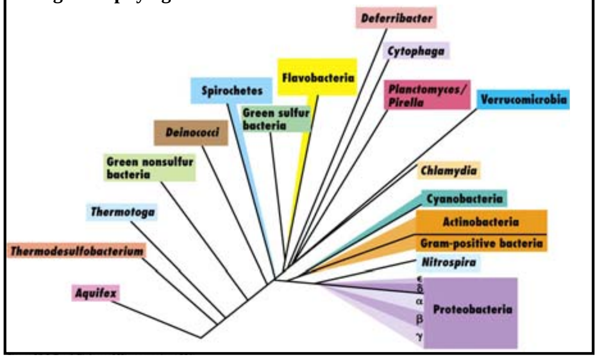
12.1 Phylogenetic Overview of *Bacteria*, p. 331

Nearly 7000 species of prokaryotes are known. Figure 12.1 gives a phylogenetic overview of *Bacteria*



PROTEOBACTERIA

- The **Proteobacteria** = five clusters.
- Proteobacteria include phototrophs, chemolithotrophs, and chemoorganotrophs
- Each cluster of several genera is designated by a Greek letter:
- alpha (α), beta (β), Gamma (γ), delta (δ), or epsilon (ε) (Table 12.1).

Table 12.1 Major General of Proteobacteria

Alpha: *Acetobacter, Agrobacterium, Alcaligenes, Azospirillum, Bradyrhizobium, Brucella, Caulobacter, Ehrlichia, Gluconobacter, Hyphomicrobium, Nitrobacter, Rhodobacter, Rhodopseudomonas, Rhodospirillum, Rhizobium, Rickettsia, Sphingomonas*

Beta: *Aquaspirillum, Bordatella, Burkholderia, Chromobacterium, Dechloromonas, Gallionella, Leptothrix, Methylophilus, Neisseria, Nitrosomonas, Polaromonas, Ralstonia, Sphaerotilus, Spirillum, Thiobacillus, Zoogloea*

Gamma: *Acinetobacter, Azotobacter, Chromatium, Escherichia, Ectothiorhodospira, Erwinia, Francisella, Halothiobacillus, Legionella, Leucothrix, Methylomonas, Oceanospirillum, Photobacterium, Pseudomonas, Nitrosococcus, Nitrococcus, Thiomicrospira, Thiospirillum* (purple S), *Salmonella, Vibrio, Xanthomonas*

Delta: *Aeromonas, Bdellovibrio, Desulfovibrio, Francisella, Geobacter, Moraxella, Myxococcus, Pelobacter, Syntrophobacter*

Epsilon: *Campylobacter, Helicobacter pylori, Thiovulum, Wolniella* (approx 70)

12.1 PHYLUM 1: PROTEOBACTERIA see Table 12.1
12.2 Purple Phototrophic *Bacteria*
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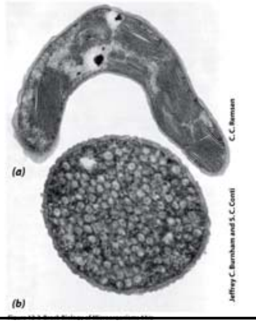
12.17 Gliding Myxobacteria - Fruiting **12.18 Sulfate- and Sulfur-Reducing Proteobacteria**

Purple Sulfur Bacteria
12.2 Purple Phototrophic Bacteria

Blue = carotenoidless mutant of *Rhodospirillum rubrum*

Figure 12.3 Membrane systems of phototrophic purple bacteria via electron microscope. (a) *Ectothiorhodospira mobilis* - photosynthetic membranes in flat sheets (lamellae). (b) *Allochromatium vinosum* - membranes as individual, spherical-shaped vesicles.



Phylum 1: **Proteobacteria, p. 332**

12.2 Purple Phototrophic *Bacteria*, p. 332

Purple Bacteria are anoxygenic phototrophs
They occur in α, β, and γ subdivisions of the Proteobacteria

Purple sulfur bacteria ► carbon from CO_2 + H_2S (electron donor) (Table 12.2) Yields S granules – inside (later [O] to sulfate)

Purple nonsulfur bacteria (Table 12.3) from organic compounds - most can grow as chemoorganotrophs in darkness

Major total input into salt marsh systems

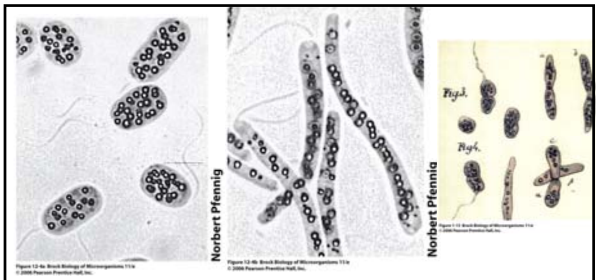


Figure 12.4a Bright-field purple sulfur bacteria (cf. Table 12.2).
(a) *Chromatium okenii*; cells are about 5 µm wide.
Note the globules of elemental sulfur inside the cells.
(b) *Thiospirillum jenense*, a very large, polarly flagellated spiral;
cells are about 30 µm long. Note the sulfur globules.
Figure 1.15 Hand-colored drawings Sergei Winogradsky about 1887
Hand-colored by his wife Hélène. *Chromatium*, such as *C. okenii*

Fig. 12.5a Blooms - purple sulfur bacteria. (a) *Thiopedia roseopersicina* -a sulfide spring in Madison, Wisconsin. The bacteria grow near the bottom of the spring pool and float via their gas vesicles, when disturbed (Sect 4.12 - gas vesicles). Note the green eukaryotic alga *Spirogyra*.

Purple Sulfur Phototrophic *Bacteria*

- Illuminated anoxic zones esp. with sulfur springs or oceanic water
- Can be under the salt marsh upper green layer
- Some lakes are stratified [meromictic], perhaps saline, and the layering effect produces dense blooms.

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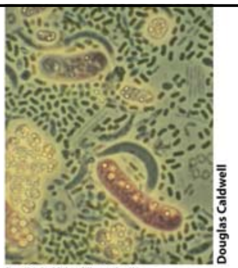

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(b) Sample of water from 7 m in Lake Mahoney, British Columbia. The major organism is *Amoebobacter purpureus*.

c) Phase-contrast photomicrograph of layers of purple sulfur bacteria from a small stratified lake in Michigan. The purple sulfur bacteria include *Chromatium* species (large rods) and *Thiocystis* (small cocci).

PURPLE NONSULFUR BACTERIA

Purple nonsulfur bacteria (Table 12.3) from organic compounds
- most can grow as chemoorganotrophs in darkness, fermentative respiration – represses photosynthetic machinery

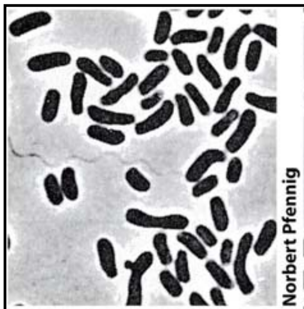
They can use sulfide but at much lower concentration than the Purple Sulfur Bacteria $CO_2 + H_2S$ (electron donor) or also $CO_2 + H_2$

As they can use organics and also light, this gives them a competitive advantage.

Nutrition: diverse substrates

Most fix nitrogen

Diverse group but all fall in the alpha or beta Proteobacteria



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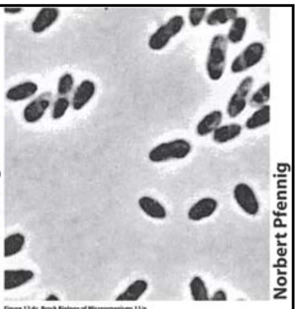

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Purple nonsulfur bacteria (see Table 12.3).
Rhodopseudomonas acidophila; cells are about 4 µm long.
Rhodobacter sphaeroides; cells are about 1.5 µm wide.

12.2 Concept Check

Purple bacteria are anoxygenic phototrophs that grow phototrophically, obtaining carbon from CO_2 + H_2S (purple sulfur bacteria) or organic compounds (purple nonsulfur bacteria). Purple nonsulfur bacteria are physiologically diverse and most can grow as chemoorganotrophs in darkness. The purple bacteria reside in the alpha, beta, and gamma subdivisions of the Proteobacteria.

- What is meant by the term *anoxygenic*?
- Give a major reason why photosynthesis in purple nonsulfur bacteria does not occur under aerobic conditions.
- Can purple bacteria grow in the absence of light?

12.3 THE NITRIFYING *BACTERIA* p. 335

Chemolithotrophs are prokaryotes that oxidize inorganic electron donors and in many cases use CO_2 as their sole carbon source.

NITROSIFYERS AND NITRIFYERS p.336

Nitrifying bacteria

•Several reactions occur in the oxidation of inorganic nitrogen
•compounds by chemolithotrophic nitrifying bacteria (Fig. 12.9).
Occur in alpha, beta, gamma and delta Proteobacteria

Sequential action. First:
Ammonia oxidizers or Nitrosifyers (*Nitroso* - genus)
ammonia ► hydroxylamine ► nitrite

Nitrite oxidizers – or Nitrifying bacteria (esp. *Nitrosomonas* &
Nitrosomonas Nitrite to nitrate

Most are obligate aerobes. Yet grow with high ammonia e.g. sewage.
A scourge to farmers – fertilizers ► soluble and leachable nitrates

Membrane associated nitrification enzymes

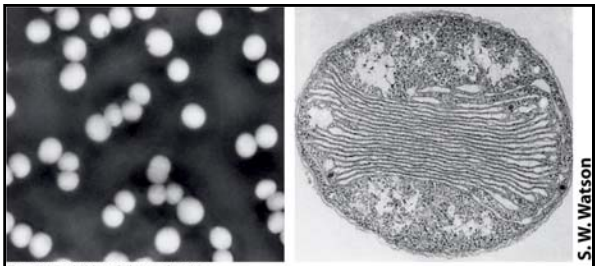

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Fig. 12.7 Phase-contrast photomicrograph (l) and electron micrograph (r) of the NITROSIFYING bacterium *Nitrosococcus oceani*.
A single cell is about 2 µm in diameter

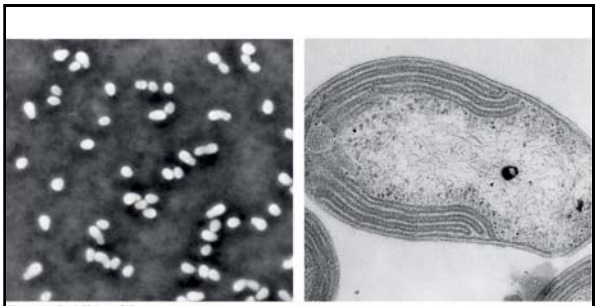

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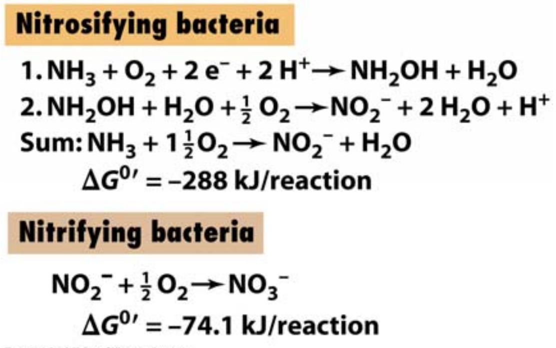
Figure 12.8 Phase-contrast photomicrograph (left) and electron micrograph (right) of the NITRIFYING BACTERIUM *Nitrobacter winogradskyi*. - A cell is about 0.7 µm in diameter.



Nitrosifying bacteria

1. $NH_3 + O_2 + 2\,e^- + 2\,H^+ \rightarrow NH_2OH + H_2O$
2. $NH_2OH + H_2O + \frac{1}{2}\,O_2 \rightarrow NO_2^- + 2\,H_2O + H^+$

Sum: $NH_3 + 1\frac{1}{2}O_2 \rightarrow NO_2^- + H_2O$

$\Delta G^{0\prime} = -288$ kJ/reaction

Nitrifying bacteria

$NO_2^- + \frac{1}{2}\,O_2 \rightarrow NO_3^-$

$\Delta G^{0\prime} = -74.1$ kJ/reaction

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12.4 SULFUR- AND IRON-OXIDIZING *BACTERIA*   p. 337

A diverse group of Proteobacteria grow chemolithotrophically on reduced sulfur compounds (Table 12.5).

Some S chemolithotrophs are facultative chemolithotrophs, i.e. they grow chemolithotrophically (and thus are autotrophs) or chemoorganotrophically

One group grow at neutral pH and another at acidic pH. Some of the latter can also use Fe^{++} as an electron donor.

Some sulfur chemolithotrophs are obligate and must use inorganics as electron donors **Carboxysomes** are often present inside the cells of obligate chemolithotrophs (sites of Calvin cycle enzymes.

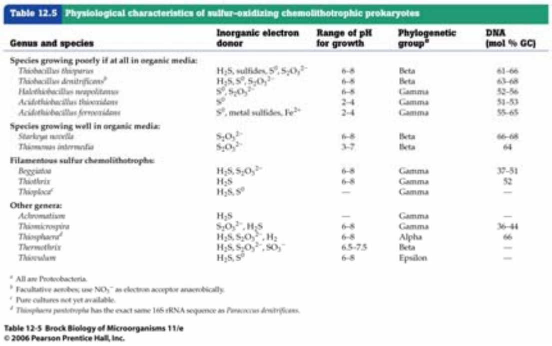

Table 12.5 Physiological characteristics of sulfur-oxidizing chemolithotrophic prokaryotes

Genus and species	Inorganic electron donor	Range of pH for growth	Phylogenetic group[a]	DNA (mol % GC)
Species growing poorly if at all in organic media:				
Thiobacillus thioparus	H_2S, sulfides, S^0, $S_2O_3^{2-}$	6–8	Beta	61–66
Thiobacillus denitrificans[b]	H_2S, S^0, $S_2O_3^{2-}$	6–8	Beta	63–68
Halothiobacillus neapolitanus	S^0, $S_2O_3^{2-}$	6–8	Gamma	52–56
Acidithiobacillus thiooxidans	S^0	2–4	Gamma	51–53
Acidithiobacillus ferrooxidans	S^0, metal sulfides, Fe^{2+}	2–4	Gamma	55–65
Species growing well in organic media:				
Starkeya novella	$S_2O_3^{2-}$	6–8	Beta	66–68
Thiomonas intermedia	$S_2O_3^{2-}$	3–7	Beta	64
Filamentous sulfur chemolithotrophs:				
Beggiatoa	H_2S, $S_2O_3^{2-}$	6–8	Gamma	37–51
Thiothrix	H_2S	6–8	Gamma	52
Thioploca[c]	H_2S, S^0	—	Gamma	—
Other genera:				
Achromatium	H_2S	—	Gamma	—
Thiomicrospira	$S_2O_3^{2-}$, H_2S	6–8	Gamma	36–44
Thiosphaera[d]	H_2S, $S_2O_3^{2-}$, H_2	6–8	Alpha	66
Thermothrix	H_2S, $S_2O_3^{2-}$, SO_3^-	6.5–7.5	Beta	—
Thiovulum	H_2S, S^0	6–8	Epsilon	—

[a] All are Proteobacteria.

[b] Facultative aerobes; use NO_3^- as electron acceptor anaerobically.

[c] Pure cultures not yet available.

[d] *Thiosphaera pantotropha* has the exact same 16S rRNA sequence as *Paracoccus denitrificans*.

Table 12-5 Brock Biology of Microorganisms 11/e

Thiobacillus and *Achromatium*

► *Thiobacillus oxidans* first isolated by Waksman & Joffe – Cook College

- Diverse group in α, β and γ groups.
- Chemolithotrophic growth yields sulfuric acid

►*Acidithiobacillus ferro-oxidans* [O] uses ferrous iron (FeS – pyrites) –
acid produced can aid ore leaching and be disastrous in acid mine waste

►*Achromatium* sulfidic freshwater. Cocci 10-100µm.
γ Proteobacteria. Sulfur appears internally and also large calcite –
$CaCO_3$ granules (storage?).

Thiobacillus and *Achromatium*

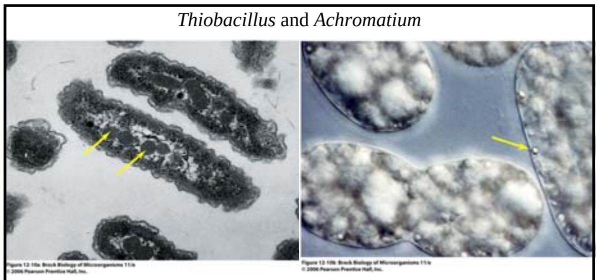
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Figure 12.10a Nonfilamentous sulfur chemolithotrophs.
(a) Transmission EM of sulfur oxidizer *Halothiobacillus neapolitanus*. A cell diam. about 0.5 µm. Polyhedral bodies (carboxysomes) distributed throughout the cell (arrows).
(b) *Achromatium*. From a small German lake (Nomarski microscopy.) Small globular peripheral structures (arrow) are elemental sulfur; large granules are of calcium carbonate. A cell is about 25 µm in diameter

BEGGIATOA

Filamentous, gliding, sulfur oxidizing bacteria

Winogradsky S ► S^0 ► SO_4^{2-} Energy obtained but it does need organic carbon (no Calvin cycle enzymes) . Termed a MIXOTROPH

Probably aids rice by detoxifying H_2S around the roots
One culprit of flocs and settling in sewage treatment waste lagoons

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Thioploca* and *Thiothrix

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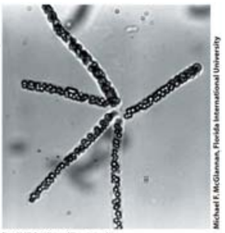

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12.5 Hydrogen-Oxidizing *Bacteria*

Some bacteria use hydrogen (electron donor) plus oxygen (e acceptor) for all energy production (Knall gas reaction)
Some grow autotrophically (Calvin enzymes)
Best studied *Ralstonia*, *Pseudomonas* & *Paracoccus*
(*also Aquifex* and *Mycobacterium gordonae)*

All hydrogen-oxidizing bacteria contain 1 or more hydrogenase enzymes that bind H_2 and use it either to produce ATP or as reducing power for autotrophic growth (Table 12.6). Nickel essential in the hydrogenases.

But many are facultative chemolithotrophs
And some use CO (carboxydobacteria – certain Pseudomonads) perhaps essential in keeping CO levels down

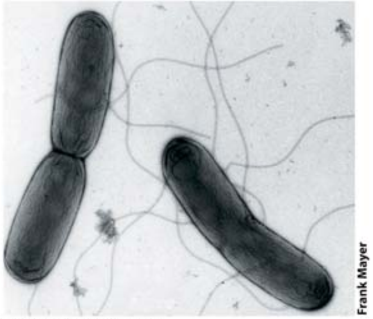
Frank Mayer

Figure 12-14 Brock Biology of Microorganisms 11/e

Figure 12.14 Hydrogen bacteria. Transmission EM negatively stained. Hydrogen-[O] chemolithotroph *Ralstonia eutropha*. Cell = 0.6 µm diam. “n” flagella.

12.3–12.5 Concept Check

Chemolithotrophs are prokaryotes that can oxidize inorganic electron donors and in many cases use CO_2 as sole carbon source.

- Compare and contrast the nitrifying bacteria with the sulfur, iron, and hydrogen bacteria in terms of inorganic electron donors used, carbon sources, E_0' of electron donors, and habitats.
- What major pathway is present for assimilation of CO_2 in many chemolithotrophs?

12.6 METHANOTROPHS AND METHYLOTROPHS

CH_4 is produced in anaerobic sites by methanogenic Archaea, e.g. muds, marshes, rumen, mammalian guts. CH_4 is very stable and yet methanotrophs use it readily as an electron donor for energy production.
Methanotrophs reside in water and soil and can also exist as symbionts of marine shellfish. Not maritime environments which have lesser methane (competition with sulfate reduction).
METHYLOTROPHS all grow on one-carbon organics !!! (Table 12.7), while some METHYLOTROPHS (Table 12.8) can use C-1 cmpds and also methane and as are termed such are METHANOTROPHS.
All are aerobic (have methane mono-oxygenase).
Methanotrophs cannot use C-C compounds, i.e. obligate C-1 users.
However, some non-methanogenic methylotrophs can use sugars, acids and ethanol.

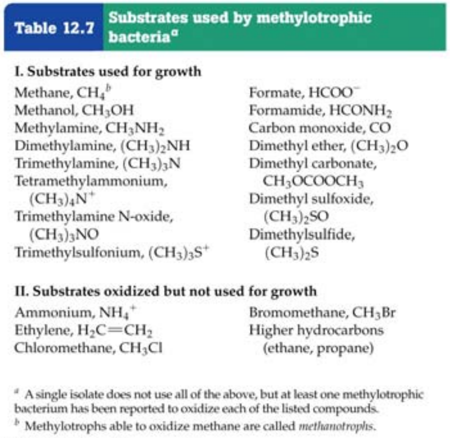

Table 12.7 Substrates used by methylotrophic bacteria[a]

I. Substrates used for growth

Methane, CH_4[b]
Methanol, CH_3OH
Methylamine, CH_3NH_2
Dimethylamine, $(CH_3)_2NH$
Trimethylamine, $(CH_3)_3N$
Tetramethylammonium, $(CH_3)_4N^+$
Trimethylamine N-oxide, $(CH_3)_3NO$
Trimethylsulfonium, $(CH_3)_3S^+$
Formate, $HCOO^-$
Formamide, $HCONH_2$
Carbon monoxide, CO
Dimethyl ether, $(CH_3)_2O$
Dimethyl carbonate, $CH_3OCOOCH_3$
Dimethyl sulfoxide, $(CH_3)_2SO$
Dimethylsulfide, $(CH_3)_2S$

II. Substrates oxidized but not used for growth

Ammonium, NH_4^+
Ethylene, $H_2C{=}CH_2$
Chloromethane, CH_3Cl
Bromomethane, CH_3Br
Higher hydrocarbons (ethane, propane)

[a] A single isolate does not use all of the above, but at least one methylotrophic bacterium has been reported to oxidize each of the listed compounds.
[b] Methylotrophs able to oxidize methane are called *methanotrophs*.

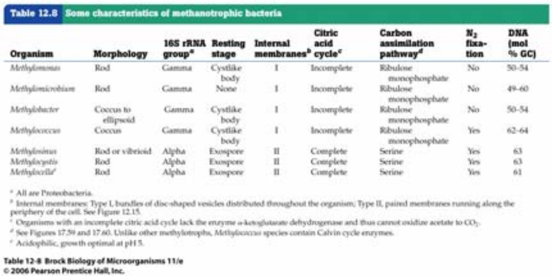

Table 12.8 Some characteristics of methanotrophic bacteria

Organism	Morphology	16S rRNA group[a]	Resting stage	Internal membranes[b]	Citric acid cycle[c]	Carbon assimilation pathway[d]	N_2 fixation	DNA (mol % GC)
Methylomonas	Rod	Gamma	Cystlike body	I	Incomplete	Ribulose monophosphate	No	50-54
Methylomicrobium	Rod	Gamma	None	I	Incomplete	Ribulose monophosphate	No	49-60
Methylobacter	Coccus to ellipsoid	Gamma	Cystlike body	I	Incomplete	Ribulose monophosphate	No	50-54
Methylococcus	Coccus	Gamma	Cystlike body	I	Incomplete	Ribulose monophosphate	Yes	62-64
Methylosinus	Rod or vibrioid	Alpha	Exospore	II	Complete	Serine	Yes	63
Methylocystis	Rod	Alpha	Exospore	II	Complete	Serine	Yes	63
Methylocella[e]	Rod	Alpha	Exospore	II	Complete	Serine	Yes	61

[a] All are Proteobacteria.
[b] Internal membranes: Type I, bundles of disc-shaped vesicles distributed throughout the organism; Type II, paired membranes running along the periphery of the cell. See Figure 12.15.
[c] Organisms with an incomplete citric acid cycle lack the enzyme α-ketoglutarate dehydrogenase and thus cannot oxidize acetate to CO_2.
[d] See Figures 17.59 and 17.60. Unlike other methylotrophs, *Methylococcus* species contain Calvin cycle enzymes.
[e] Acidophilic, growth optimal at pH 5.

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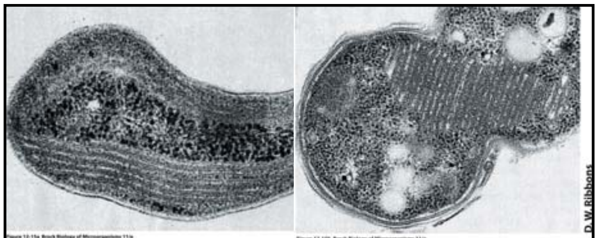
TWO PHYSIOLOGIES

- Two classes are known for uptake of C-1 are known. Type I use the ribulose monophosphate cycle (All gamma Proteobacteria), and have bundles of disc shaped vesicles, the site of MMO.
- Type II use the serine pathway to assimilate C-1 and are all Alpha Proteobacteria, and have paired peripheral membranes.
- Type I lack citric acid cycle enzymes – NADH does not regenerate, cannot use other compounds and hence are obligate methylotrophs.



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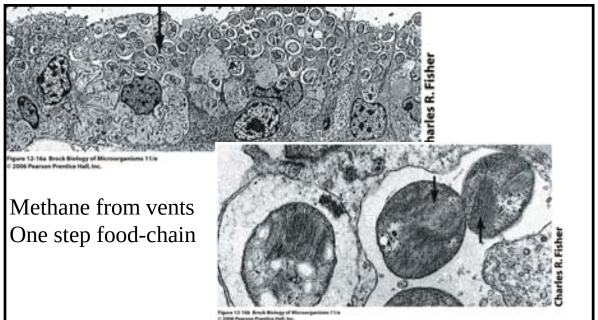
D. W. Ribbons

Figure 12.15a Electron micrographs of methanotrophs.
(a) Methylosinus species, illustrating a Type II membrane system. Cells about 0.6 µm diam.
(b) *Methylococcus capsulatus*, Type I membrane system. Cells about 1 µm diam.

METHANOTROPHS AND NITROSIFYING BACTERIA p.344.

Methanotrophs can [0] ammonia but cannot live on it chemolithotrophically. However, MMO can oxidize ammonia, leading to the speculation that there is some evolutionary relationship. However as the methane producing bacteria are Archaea, this gives speculation of lateral gene transf

Methanotrophic Symbionts of Animals



Methane from vents
One step food-chain

Figure 12.16a Methanotrophic symbionts of marine mussels.
(a) EM (low mag.) Marine mussel gill tissue - hydrocarbon seeps, Gulf of Mexico.
Symbiotic methanotrophs (arrows) in the tissues.
(b) Gill tissue with Type I methanotrophs. (High mag.)
Note membrane bundles (arrows). The methanotrophs are about 1 µm diam. Compare Figure 12.15b.

12.6 Concept Check

Methylotrophs are prokaryotes able to grow on carbon compounds that lack carbon-carbon bonds. Some methylotrophs are also methanotrophs, able to grow on CH_4. Two classes of methanotrophs are known, each having a number of structural and biochemical properties in common. Methanotrophs reside in water and soil and can also exist as symbionts of marine shellfish.

- What is the difference between a *methanotroph* and a *methylotroph*?
- What features differentiate Type I from Type II methanotrophs?

Characteristics of Pseudomonads p.345

Pseudomonads include many gram-negative chemo-organotrophic aerobic rods; many nitrogen-fixing species are phylogenetically closely related.

*Pseudomonas (*omnivorous*), Commamonas (testeroni), Ralstonia solanacearum* (plant pathogen), *Burkholderia pseudomallei* (melioidosis) see Tables 12.10 and 12.11.

Many pseudomonads, as well as a variety of other gram-negative *Bacteria*, metabolize glucose via the Entner-Doudoroff pathway (Figure 12.17c).

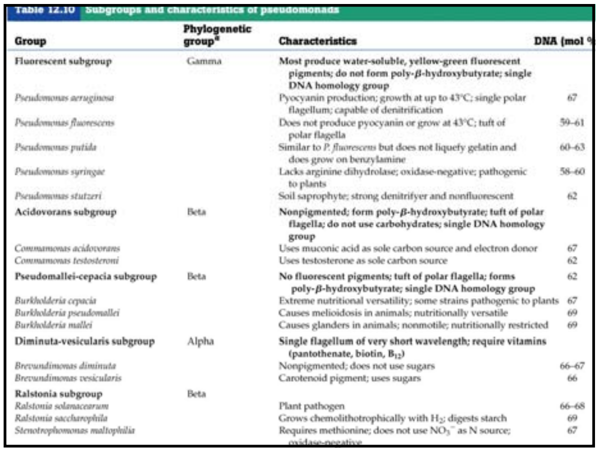


Table 12.10 Subgroups and characteristics of pseudomonads

Group	Phylogenetic group[a]	Characteristics	DNA (mol
Fluorescent subgroup	Gamma	**Most produce water-soluble, yellow-green fluorescent pigments; do not form poly-β-hydroxybutyrate; single DNA homology group**	
Pseudomonas aeruginosa		Pyocyanin production; growth at up to 43°C; single polar flagellum; capable of denitrification	67
Pseudomonas fluorescens		Does not produce pyocyanin or grow at 43°C; tuft of polar flagella	59–61
Pseudomonas putida		Similar to *P. fluorescens* but does not liquefy gelatin and does grow on benzylamine	60–63
Pseudomonas syringae		Lacks arginine dihydrolase; oxidase-negative; pathogenic to plants	58–60
Pseudomonas stutzeri		Soil saprophyte; strong denitrifyer and nonfluorescent	62
Acidovorans subgroup	Beta	**Nonpigmented; form poly-β-hydroxybutyrate; tuft of polar flagella; do not use carbohydrates; single DNA homology group**	
Commamonas acidovorans		Uses muconic acid as sole carbon source and electron donor	67
Commamonas testosteroni		Uses testosterone as sole carbon source	62
Pseudomallei-cepacia subgroup	Beta	**No fluorescent pigments; tuft of polar flagella; forms poly-β-hydroxybutyrate; single DNA homology group**	62
Burkholderia cepacia		Extreme nutritional versatility; some strains pathogenic to plants	67
Burkholderia pseudomallei		Causes melioidosis in animals; nutritionally versatile	69
Burkholderia mallei		Causes glanders in animals; nonmotile; nutritionally restricted	69
Diminuta-vesicularis subgroup	Alpha	**Single flagellum of very short wavelength; require vitamins (pantothenate, biotin, B_{12})**	
Brevundimonas diminuta		Nonpigmented; does not use sugars	66–67
Brevundimonas vesicularis		Carotenoid pigment; uses sugars	66
Ralstonia subgroup	Beta		
Ralstonia solanacearum		Plant pathogen	66–68
Ralstonia saccharophila		Grows chemolithotrophically with H_2; digests starch	69
Stenotrophomonas maltophilia		Requires methionine; does not use NO_3^- as N source; oxidase-negative	67

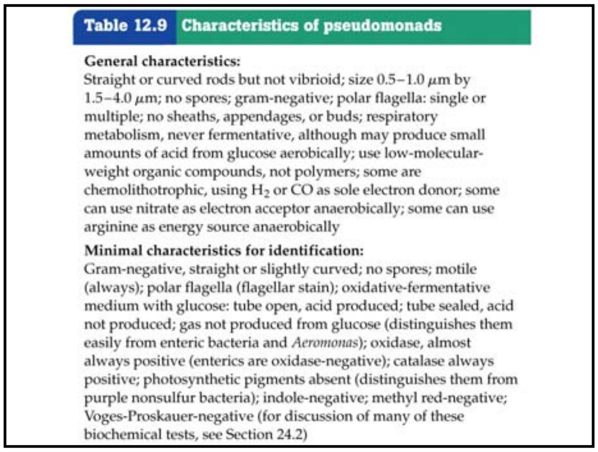


Table 12.9 Characteristics of pseudomonads

General characteristics:
Straight or curved rods but not vibrioid; size 0.5–1.0 μm by 1.5–4.0 μm; no spores; gram-negative; polar flagella: single or multiple; no sheaths, appendages, or buds; respiratory metabolism, never fermentative, although may produce small amounts of acid from glucose aerobically; use low-molecular-weight organic compounds, not polymers; some are chemolithotrophic, using H_2 or CO as sole electron donor; some can use nitrate as electron acceptor anaerobically; some can use arginine as energy source anaerobically

Minimal characteristics for identification:
Gram-negative, straight or slightly curved; no spores; motile (always); polar flagella (flagellar stain); oxidative-fermentative medium with glucose: tube open, acid produced; tube sealed, acid not produced; gas not produced from glucose (distinguishes them easily from enteric bacteria and *Aeromonas*); oxidase, almost always positive (enterics are oxidase-negative); catalase always positive; photosynthetic pigments absent (distinguishes them from purple nonsulfur bacteria); indole-negative; methyl red-negative; Voges-Proskauer-negative (for discussion of many of these biochemical tests, see Section 24.2)

Entner-Doudoroff biochemical pathway common in pseudomonads.

Many pseudomonads, as well as a variety of other gram-negative *Bacteria*, metabolize glucose via the Entner-Doudoroff pathway (Figure 12.17c).

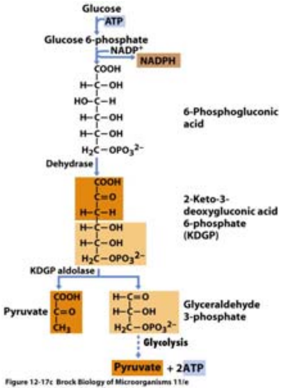


Figure 12-17c Brock Biology of Microorganisms 11/e

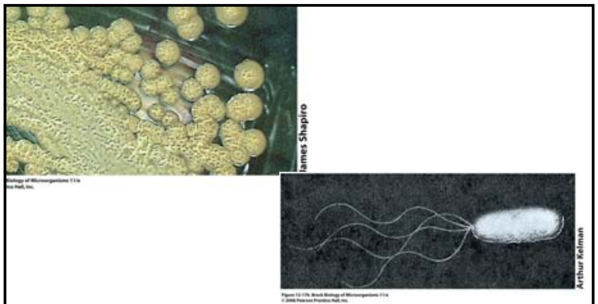


Figure 12.17a Typical pseudomonad colonies and cell morphology (a) *Burkholderia cepacia* on agar
(b) Shadow-cast TEM preparation of *Pseudomonas* sp. The cell = about 1 µm diam.

Pathogenic Pseudomonads

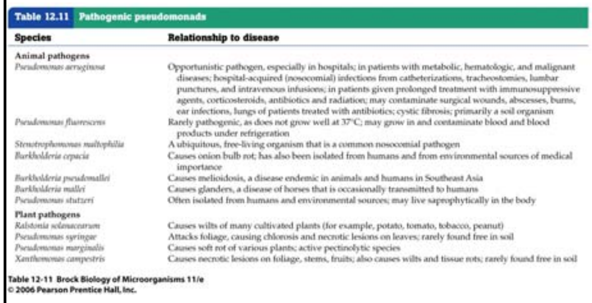


Table 12.11 Pathogenic pseudomonads

Species	Relationship to disease
Animal pathogens	
Pseudomonas aeruginosa	Opportunistic pathogen, especially in hospitals; in patients with metabolic, hematologic, and malignant diseases; hospital-acquired (nosocomial) infections from catheterizations, tracheostomies, lumbar punctures, and intravenous infusions; in patients given prolonged treatment with immunosuppressive agents, corticosteroids, antibiotics and radiation; may contaminate surgical wounds, abscesses, burns, ear infections, lungs of patients treated with antibiotics; cystic fibrosis; primarily a soil organism
Pseudomonas fluorescens	Rarely pathogenic, as does not grow well at 37°C; may grow in and contaminate blood and blood products under refrigeration
Stenotrophomonas maltophilia	A ubiquitous, free-living organism that is a common nosocomial pathogen
Burkholderia cepacia	Causes onion bulb rot; has also been isolated from humans and from environmental sources of medical importance
Burkholderia pseudomallei	Causes melioidosis, a disease endemic in animals and humans in Southeast Asia
Burkholderia mallei	Causes glanders, a disease of horses that is occasionally transmitted to humans
Pseudomonas stutzeri	Often isolated from humans and environmental sources; may live saprophytically in the body
Plant pathogens	
Ralstonia solanacearum	Causes wilts of many cultivated plants (for example, potato, tomato, tobacco, peanut)
Pseudomonas syringae	Attacks foliage, causing chlorosis and necrotic lesions on leaves; rarely found free in soil
Pseudomonas marginalis	Causes soft rot of various plants; active pectinolytic species
Xanthomonas campestris	Causes necrotic lesions on foliage, stems, fruits; also causes wilts and tissue rots; rarely found free in soil

Table 12-11 Brock Biology of Microorganisms 11/e

Zymomonas p. 347

Sugar fermentation to ethanol (cf. yeast)

Common on plant saps and also poorly processed beer (side reaction to produce hydrogen sulfide)

In Mexico, *Agave* plant sap for PULQUE

Fermentative, anaerobic physiology (cf. *Pseudomonas*)

12.8 Acetic Acid *Bacteria* p. 348

.

Oxidize ethanol to acetate aerobically.
Phylogenetically related to pseudomonads
A. *Gluconobacter* – polar flagellation
no citric acid cycle ► stops – yields HAc
Industrial – vinegar
Under oxidation Sorbitol ► sorbose [Vit C]

B *Acetobacter* – peritrichous flagellation
full citric acid cycle ► to carbon dioxide
Also cellulose synthesis – pure (as pellicle)

12.9 Free-Living Aerobic Nitrogen-Fixing *Bacteria* p. 348

- Various soil bacteria can fix N_2 aerobically **(Tab 12.12)**

- **Gamma Proteobacteria**
  - ***Azotobacter chroococcum* – Beijerinck 1901**
    - ***Azotobacter vinelandii* - Lipman 1903 cysts**
- **Alpha Proteobacteria**
    - ***Azospirillum* microaerophilic – plant roots**
    - ***Beijerinckia*** slimy – in acid soils
- **Beta Proteobacteria**
  - ***Azoarcus* small curved cells**

- **NITROGEN FIXATION:**
- **Conceptually and practically**
- **Mo enzymes**
- **but *A. chroococcum* also V (plus Fe)**

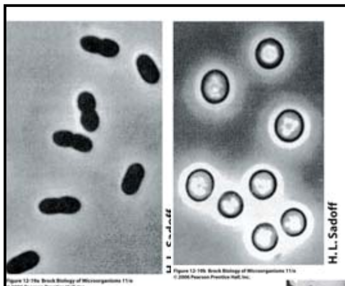
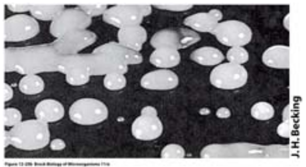


Fig. 12.19
Azotobacter vinelandii
vegetative cells and cysts

Slimy *Beijerinckia*



12.7–12.9 Concept Check

Pseudomonads include many gram-negative chemoorganotrophic aerobic rods; many N_2-fixing species are phylogenetically closely related. The acetic acid bacteria are also phylogenetically related to pseudomonads and are characterized by an ability to oxidize ethanol to acetate aerobically.

- Compare and contrast the pseudomonads, *Azotobacter*, and the acetic acid bacteria in terms of O_2 and nitrogen requirements, electron donors, pathogenicity, and habitats.
- Compare and contrast the organisms *Acetobacter* and *Gluconobacter* in as many ways as you can think of.

12.10 *NEISSERIA, CHROMOBACTERIUM* & relatives

•This group of beta and gamma Proteobacteria comprises a diverse, related phylogenetically as well as by Gram stain, morphology, lack of motility, and aerobic metabolism.
The genera *Neisseria, Moraxella, Branhamella, Kingella*, and *Acinetobacter* - Table 12.13.
Neisseria – obligate aerobes. Coccoid through Culture. *N. meningitidis and N. gonorrhea*
Acinetobacter soil but occasionally nosocomial.
Acinetobacter & Moraxella twitch via pili
Chromobacterium common in soil – rod - violacein

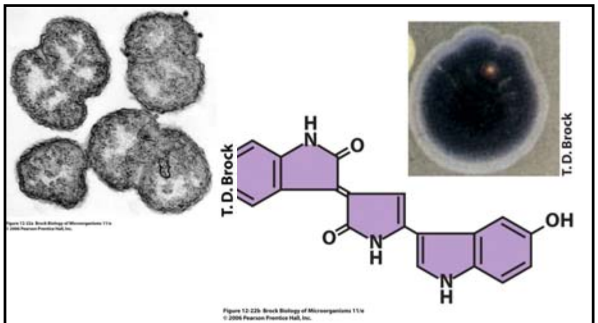


Figure 12.22 *Neisseria* and *Chromobacterium*.
(a) TM electron micrograph of *Neisseria gonorrhoeae*
- typical diplococcus cell arrangements
(b) A large colony of *Chromobacterium violaceum*.
The purple pigment - aromatic compound called *violacein*.

12.11 ENTERIC *BACTERIA* p. 351

The **enteric bacteria** are a large group of facultative aerobic rods of medical and molecular biological significance.

The phenotypic characteristics used to separate the enteric bacteria from similar bacteria are focused on in the Lab class (Table 12.14)

Escherichia O157:H7 vs lab strains (Delhi belly)
Enterobacter common soil bacteria *vs. E. coli* in water
Shigella – 70% DNA homology to *E. coli* but ►bacillary dysentery
Salmonella Typhoid fever with > 1,000 serotypes (LPS)
Klebsiella Pneumonia – common in soil – fix nitrogen
Yersinia Plague – rat flea vector. Rats die but also a persistent reservoir

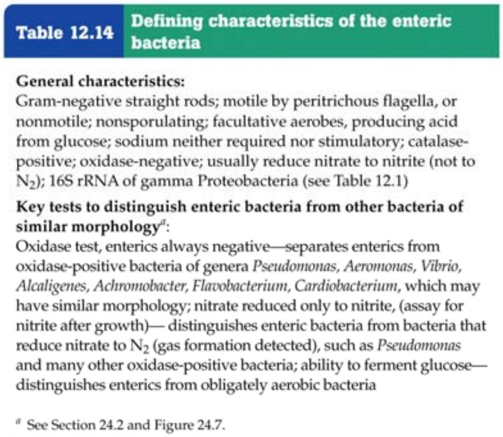
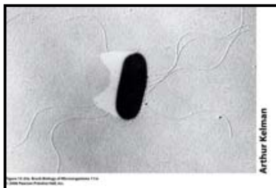


Table 12.14 Defining characteristics of the enteric bacteria

General characteristics:
Gram-negative straight rods; motile by peritrichous flagella, or nonmotile; nonsporulating; facultative aerobes, producing acid from glucose; sodium neither required nor stimulatory; catalase-positive; oxidase-negative; usually reduce nitrate to nitrite (not to N_2); 16S rRNA of gamma Proteobacteria (see Table 12.1)

Key tests to distinguish enteric bacteria from other bacteria of similar morphology[a]:
Oxidase test, enterics always negative—separates enterics from oxidase-positive bacteria of genera *Pseudomonas, Aeromonas, Vibrio, Alcaligenes, Achromobacter, Flavobacterium, Cardiobacterium*, which may have similar morphology; nitrate reduced only to nitrite, (assay for nitrite after growth)— distinguishes enteric bacteria from bacteria that reduce nitrate to N_2 (gas formation detected), such as *Pseudomonas* and many other oxidase-positive bacteria; ability to ferment glucose—distinguishes enterics from obligately aerobic bacteria

[a] See Section 24.2 and Figure 24.7.



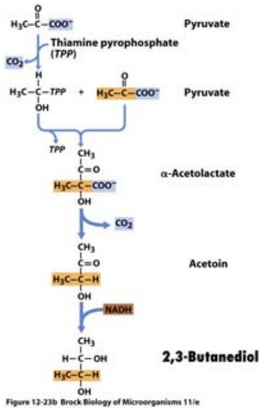


Figure 12-23b Brock Biology of Microorganisms 11/e
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Butanediol:

(a) Shadow-cast EM of the butanediol producing enteric bacterium *Erwinia carotovora*. Cells about 0.8 µm wide.

Peritrichous flagella (see Section 4.14).

(b) Biochemical pathway for formation of butanediol from two molecules of pyruvate by butanediol fermenters.

(c) Overall stoichometry. N.b. Only *one* NADH but *two* pyruvate are required to make butanediol.

Fermentation Patterns

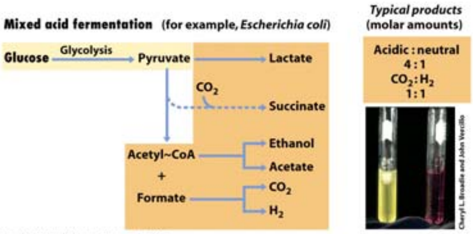

Figure 12-24a Brock Biology of Microorganisms 11/e
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Distinction between (a) mixed acid & (b) butanediol fermentation in enteric bacteria. Bold arrows = reactions leading to major products. Dashed arrows = minor products.

(a) Shows the production of acid (yellow color) and gas (in the inverted Durham tube) in a culture of *E. coli*. Purple tube was uninoculated.

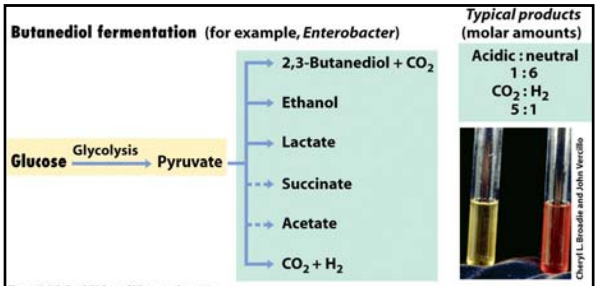

Figure 12-24b Brock Biology of Microorganisms 11/e
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(b) the pink-red color in the Voges-Proskauer (VP) test, which indicates butanediol production - *Enterobacter aerogenes*. Left (yellow) tube was uninoculated. N.B. the major difference in CO_2 production in the two pathways, butanediol production leading to substantially greater CO_2 yields.

Because the production of one molecule of butanediol from two pyruvates consumes only one NADH (pathway Figure 12.23 b, c), 0.5 molecules of ethanol must be made for each butanediol produced to consume the second NADH generated in glycolysis.

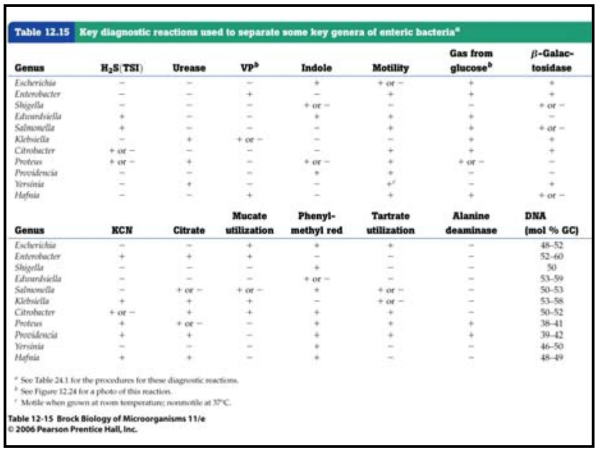

Table 12.15 Key diagnostic reactions used to separate some key genera of enteric bacteria[a]

Genus	H_2S(TSI)	Urease	VP[b]	Indole	Motility	Gas from glucose[b]	β-Galactosidase
Escherichia	–	–	–	+	+ or –	+	+
Enterobacter	–	–	+	–	+	+	+
Shigella	–	–	–	+ or –	–	–	+ or –
Edwardsiella	+	–	–	+	+	+	–
Salmonella	+	–	–	–	+	+	+ or –
Klebsiella	–	+	+ or –	–	–	+	+
Citrobacter	+ or –	–	–	–	+	+	+
Proteus	+ or –	+	–	+ or –	+	+ or –	–
Providencia	–	–	–	+	+	–	–
Yersinia	–	+	–	–	+[c]	–	+
Hafnia	–	–	+	–	+	+	+ or –

Genus	KCN	Citrate	Mucate utilization	Phenyl-methyl red	Tartrate utilization	Alanine deaminase	DNA (mol % GC)
Escherichia	–	–	+	+	+	–	48–52
Enterobacter	+	+	+	–	–	–	52–60
Shigella	–	–	–	+	–	–	50
Edwardsiella	–	–	–	+ or –	–	–	53–59
Salmonella	–	+ or –	+ or –	+	+ or –	–	50–53
Klebsiella	+	+	+	–	+ or –	–	53–58
Citrobacter	+ or –	+	+	+	+	–	50–52
Proteus	+	+ or –	–	+	+	+	38–41
Providencia	+	+	–	+	+	+	39–42
Yersinia	–	–	–	+	–	–	46–50
Hafnia	+	+	–	+	–	–	48–49

[a] See Table 24.1 for the procedures for these diagnostic reactions.
[b] See Figure 12.24 for a photo of this reaction.
[c] Motile when grown at room temperature; nonmotile at 37°C.

Table 12-15 Brock Biology of Microorganisms 11/e
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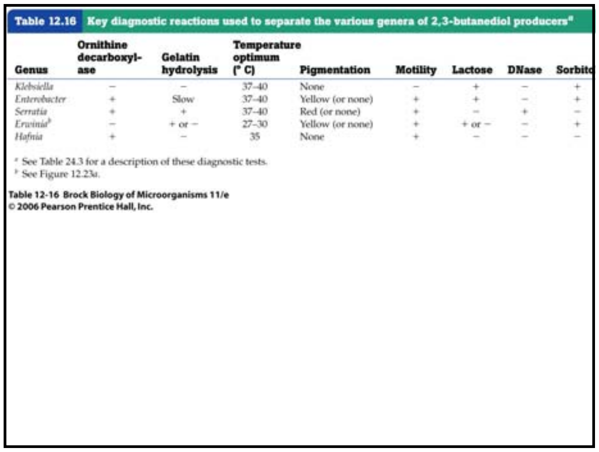

Table 12.16 Key diagnostic reactions used to separate the various genera of 2,3-butanediol producers[a]

Genus	Ornithine decarboxylase	Gelatin hydrolysis	Temperature optimum (° C)	Pigmentation	Motility	Lactose	DNase	Sorbit
Klebsiella	–	–	37–40	None	–	+	–	+
Enterobacter	+	Slow	37–40	Yellow (or none)	+	+	–	+
Serratia	+	+	37–40	Red (or none)	+	–	+	–
Erwinia[b]	–	+ or –	27–30	Yellow (or none)	+	+ or –	–	+
Hafnia	+	–	35	None	+	–	–	–

[a] See Table 24.3 for a description of these diagnostic tests.
[b] See Figure 12.23a.

Table 12-16 Brock Biology of Microorganisms 11/e
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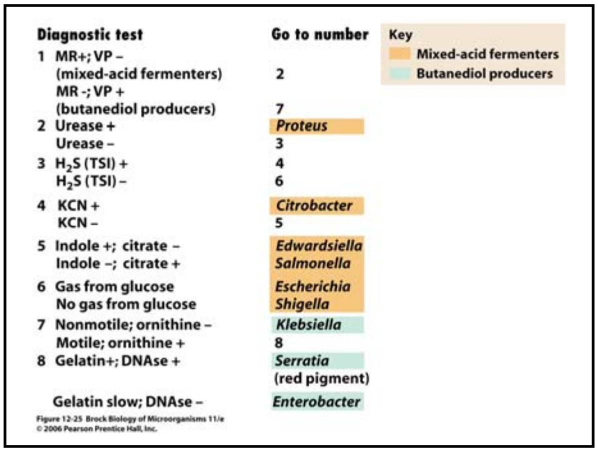

	Diagnostic test	Go to number
1	MR+; VP – (mixed-acid fermenters)	2
	MR –; VP + (butanediol producers)	7
2	Urease +	*Proteus*
	Urease –	3
3	H_2S (TSI) +	4
	H_2S (TSI) –	6
4	KCN +	*Citrobacter*
	KCN –	5
5	Indole +; citrate –	*Edwardsiella*
	Indole –; citrate +	*Salmonella*
6	Gas from glucose	*Escherichia*
	No gas from glucose	*Shigella*
7	Nonmotile; ornithine –	*Klebsiella*
	Motile; ornithine +	8
8	Gelatin+; DNAse +	*Serratia* (red pigment)
	Gelatin slow; DNAse –	*Enterobacter*

Key
🟧 Mixed-acid fermenters
🟩 Butanediol producers

Figure 12-25 Brock Biology of Microorganisms 11/e
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James Shapiro

Figure 12-26b Brock Biology of Microorganisms 11/e
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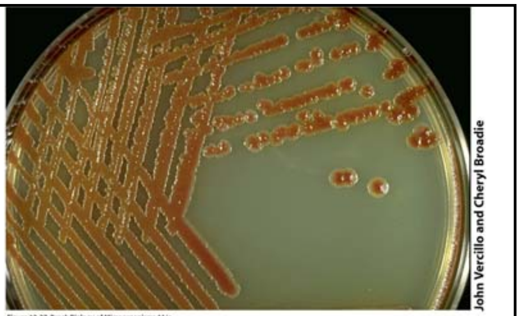
Proteus mirabilis – swarms in concentric circles

Infections of the urinary tract (urea positive)



John Vercillo and Cheryl Broadie

Figure 12-27 Brock Biology of Microorganisms 11/e
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***Serratia* – soil, water, gut. Red prodigiosin as an Easy marker (San Francisco)**

12.12 *VIBRIO* AND *PHOTOBACTERIUM*

Vibrio – Gram negative “commas”.
Vibrios are oxidase positive (cf. enterics)

Robert Koch *V. cholerae* 1884 – water distribution systems – John Snow, London, UK

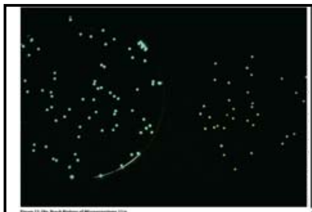
V. parahaemolyticus – marine – shell fish,

Photobacterium and Bioluminescence - regulation

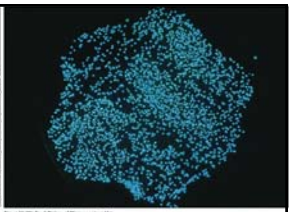
Bioluminescence – mainly *Photobacterium* and sometimes *Vibrio* spp.

Facultative aerobes and only give off light in the presence of oxygen. Saprophytic on fish but sometimes in a special organ.

The light enzyme, luciferase, is controlled by autoinduction. The auto inducer in *V. fischeri* is N-β-ketocaproyl homoserine lactone.
When cells reach high density, the inducer is at high concentration and the system turns on. = **quorum sensing**

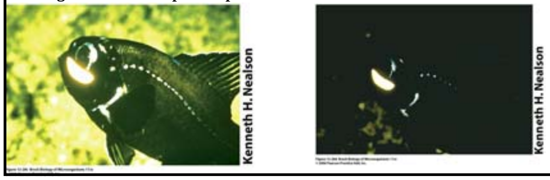


Vibrio fischeri **blue and** ***V. fischeri*** **green strains**



Photobacterium phosphoreum

Flashlight fish ***Photoblepharon palbebratus***



12.11–12.12 Concept Check

The enteric bacteria are a large group of facultative aerobic rods of medical and molecular biological significance. *Vibrio* and *Photobacterium* species are marine organisms; some species are pathogenic while others are bioluminescent.

- How is *Escherichia coli* distinguished from *Enterobacter aerogenes* based on physiology?
- Describe two major properties of *Proteus* species that distinguish them from other enteric bacteria.
- What is necessary for an organism like *Photobacterium* to give off visible light?

12.13 RICKETTSIAS p.347

•The rickettsias are obligate intracellular parasites, many of which cause disease (Table 12.7). Rickettsias are deficient in many metabolic functions and obtain key metabolites from their hosts.

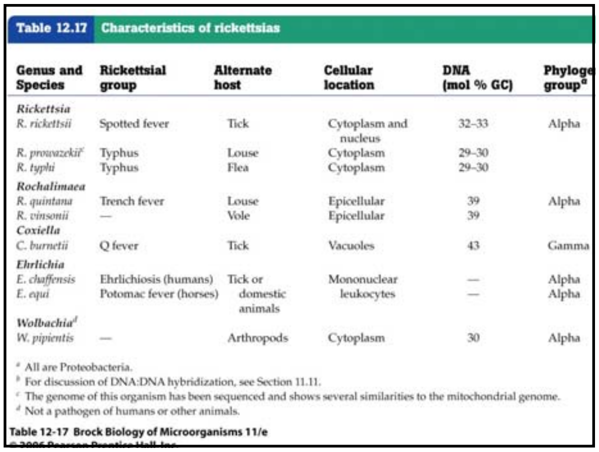


Table 12.17 Characteristics of rickettsias

Genus and Species	Rickettsial group	Alternate host	Cellular location	DNA (mol % GC)	Phyloge group[a]
Rickettsia					
R. rickettsii	Spotted fever	Tick	Cytoplasm and nucleus	32–33	Alpha
R. prowazekii[c]	Typhus	Louse	Cytoplasm	29–30	
R. typhi	Typhus	Flea	Cytoplasm	29–30	
Rochalimaea					
R. quintana	Trench fever	Louse	Epicellular	39	Alpha
R. vinsonii	—	Vole	Epicellular	39	
Coxiella					
C. burnetii	Q fever	Tick	Vacuoles	43	Gamma
Ehrlichia					
E. chaffensis	Ehrlichiosis (humans)	Tick or domestic animals	Mononuclear leukocytes	—	Alpha
E. equi	Potomac fever (horses)			—	Alpha
Wolbachia[d]					
W. pipientis	—	Arthropods	Cytoplasm	30	Alpha

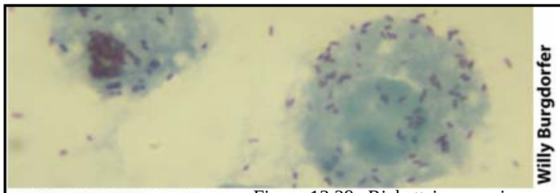
[a] All are Proteobacteria.

[b] For discussion of DNA:DNA hybridization, see Section 11.11.

[c] The genome of this organism has been sequenced and shows several similarities to the mitochondrial genome.

[d] Not a pathogen of humans or other animals.

Table 12-17 Brock Biology of Microorganisms 11/e



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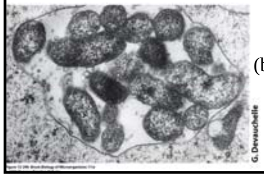

Figure 12.29a Rickettsias growing within host cells.
(a) Rickettsia rickettsii in tunica vaginalis cells of *Microtus pennsylvanicus (*vole). Cells are about 0.3 µm in diameter.

(b) EMicrograph of *Rickettsiella popilliae* within a blood cell of its host, the beetle *Melolontha melolontha*. Notice that the bacteria are growing in a vacuole within the host cell.

Richard Stouthamer and Merijn Salverda

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Intracellular parasite of arthro-♀pod insects. Can promote parthenogenesis (development of unfertilized eggs, killing ♂s. And feminization of males. Feed antibiotics and parthenogenesis ceases.

Wolbachia can be essential. River blindness (worms) and elephantiasis – antibiotics kill Wolbachia and the worms die.

Pill bugs ♂s ► female

Genome small 1.5 Mbp

Figure 12.30 *Wolbachia*.
Micrograph of a DAPI (4′,6-diamidine-2′ phenylindole dihydrochloride) stained (see Section 18.3) egg of parasitoid wasp, *Trichogramma kaykai* infected with *Wolbachia pipientis*, which induces parthenogenesis.
The *W. pipientis* cells are primarily in the egg’s narrow end (arrows).

12.13 Concept Check

The rickettsias are obligate intracellular parasites, many of which cause disease. Rickettsias are deficient in many metabolic functions and obtain key metabolites from their hosts.

- Name a disease caused by a *Rickettsia* species.
- What is meant by the phrase “obligate intracellular parasite”?

12.14 SPIRILLA p. 359

•Spirilla are spiral-shaped, chemoorganotrophic prokaryotes, widespread in the aquatic environment. Shape, size, polar flagella (single vs multiple) Broad physiology. Halophiles, thermophiles, *Azospirillum lipoferum* a plant root symbiont
•The genera *Helicobacter* (ulcers) and *Campylobacter* (commensal and cattle abortion) are pathogenic. *Bdellovibrio* pathogenic to *E. coli*
Spirilla are distributed among all five subdivisions of the Proteobacteria. [Ant v Leewenhoek]

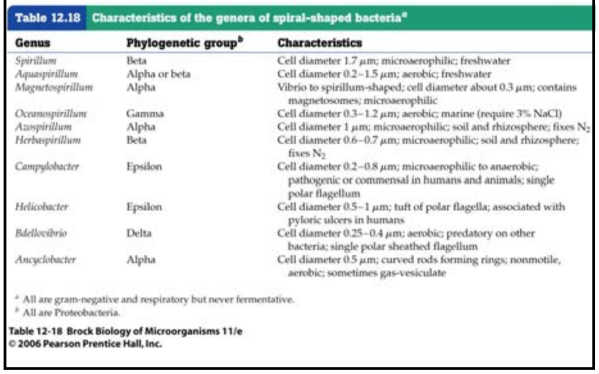


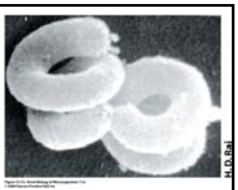
Table 12.18 Characteristics of the genera of spiral-shaped bacteria[a]

Genus	Phylogenetic group[b]	Characteristics
Spirillum	Beta	Cell diameter 1.7 µm; microaerophilic; freshwater
Aquaspirillum	Alpha or beta	Cell diameter 0.2–1.5 µm; aerobic; freshwater
Magnetospirillum	Alpha	Vibrio to spirillum-shaped; cell diameter about 0.3 µm; contains magnetosomes; microaerophilic
Oceanospirillum	Gamma	Cell diameter 0.3–1.2 µm; aerobic; marine (require 3% NaCl)
Azospirillum	Alpha	Cell diameter 1 µm; microaerophilic; soil and rhizosphere; fixes N_2
Herbaspirillum	Beta	Cell diameter 0.6–0.7 µm; microaerophilic; soil and rhizosphere; fixes N_2
Campylobacter	Epsilon	Cell diameter 0.2–0.8 µm; microaerophilic to anaerobic; pathogenic or commensal in humans and animals; single polar flagellum
Helicobacter	Epsilon	Cell diameter 0.5–1 µm; tuft of polar flagella; associated with pyloric ulcers in humans
Bdellovibrio	Delta	Cell diameter 0.25–0.4 µm; aerobic; predatory on other bacteria; single polar sheathed flagellum
Ancyclobacter	Alpha	Cell diameter 0.5 µm; curved rods forming rings; nonmotile, aerobic; sometimes gas-vesiculate

[a] All are gram-negative and respiratory but never fermentative.

[b] All are Proteobacteria.

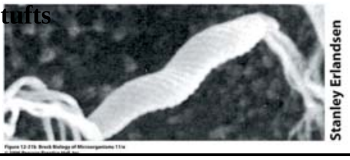
Table 12-18 Brock Biology of Microorganisms 11/e



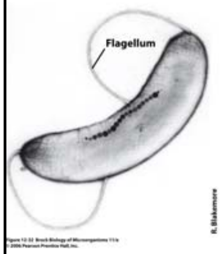
Spirillum volutans
dark field (volutin)

***Ancyclobacter aquaticus* (0.5 µm)**

Intestinal Spirillum – flagella in tufts



MAGNETOTACTIC SPIRILLA



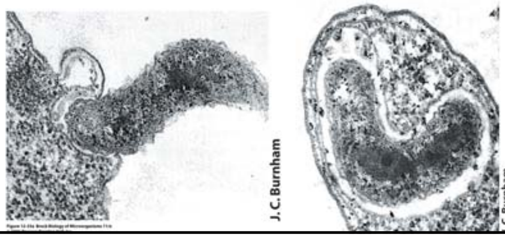
Magnetospirillum magnetotacticum

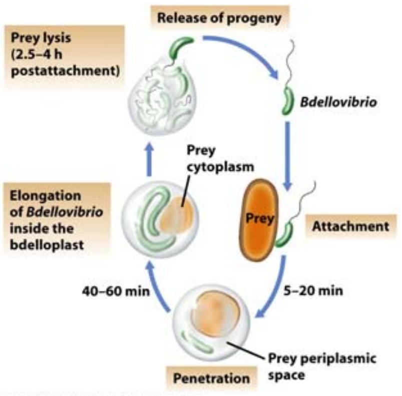
40-45 magnetosomes
- Magnetite (Fe_3O_4),and greigite (Fe_3S_4)

Microaerophilic – orient in mud and down a little

BDELLOVIBRIO

Bdellovibrio **(0.3 µm) attacking *E. coli* –**
Inter-periplasmic predator!!
Note others such as *Vampirococcus*
Bdv, - aerobic; delta; forms plaques on agar





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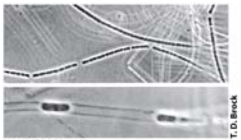
12.14 Concept Check

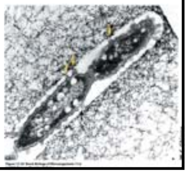
Spirilla are spiral-shaped, chemoorganotrophic prokaryotes widespread in the aquatic environment. The genera *Helicobacter* and *Campylobacter* are pathogenic spirilla. Spirilla are distributed among all five subdivisions of the Proteobacteria.

- What is a *volutin granule*?
- What is unique about the spirilla *Bdellovibrio* and *Magnetospirillum*?

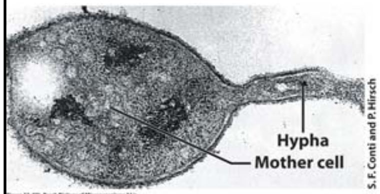
12.15 Sheathed Proteobacteria: *Sphaerotilus* and *Leptothrix*
(Sewage fungus)
Flagellated swarmer cells formed in a sheath
Occur in rich (polluted) aquatic systems –
Sewage outflow, paper mills??

Sheaths coated with Ferric hydroxide
Sphaerotilus (chemical rxn)
Manganese oxide on *Leptothrix* sheaths
(physiological rxn).





12.16 BUDDING AND PROSTHECATE (APPENDAGED) AND STALKED *BACTERIA*



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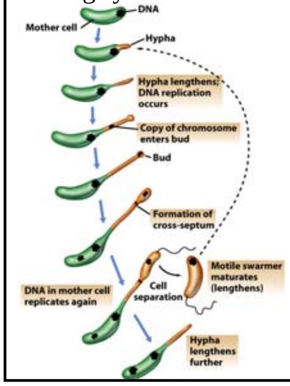
Hyphomicrobium

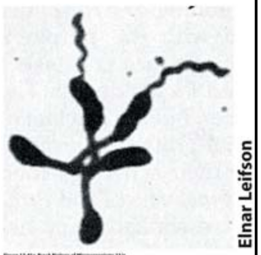
Dilute culture media

Hyphomicrobium is chemoorganotrophic, & *Rhodomicrobium*, is phototrophic. These organisms release buds from the ends of long, thin hyphae.

Hyphomicrobium
budding system



Caulobacter
rosette



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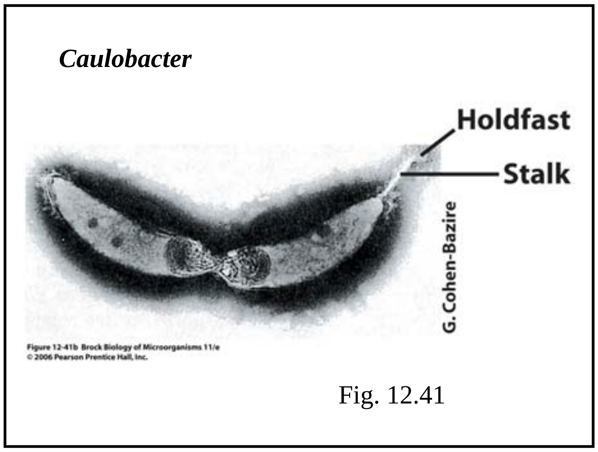

Caulobacter

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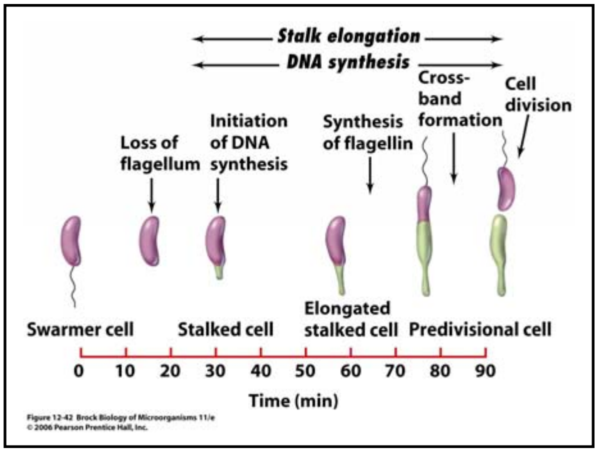
Fig. 12.41



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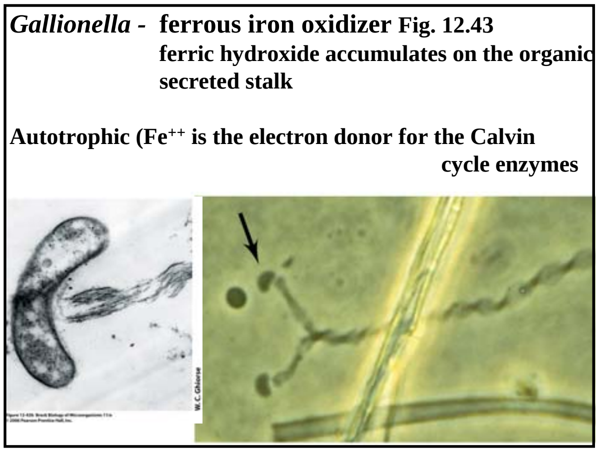


***Gallionella* -** **ferrous iron oxidizer Fig. 12.43**

ferric hydroxide accumulates on the organic secreted stalk

Autotrophic (Fe^{++} is the electron donor for the Calvin cycle enzymes

12.15–12.16 Concept Check

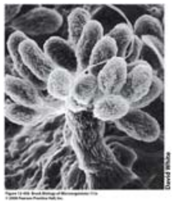
Sheathed bacteria are filamentous Proteobacteria in which individual cells form chains within an outer layer called the sheath. Budding and prosthecate bacteria are appendaged cells that form stalks or prosthecae used for attachment or nutrient absorption and are primarily aquatic.

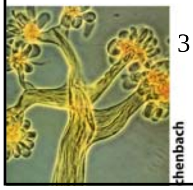
- Physiologically, what is unique about the sheathed bacterium *Leptothrix*?
- How does *budding* division differ from *binary* fission? How does binary fission differ from the division process in *Caulobacter*?
- What advantage might a prosthecate organism have in a very nutrient-poor environment?

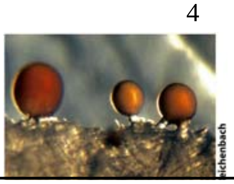
FRUITING BODIES – GLIDING MYXOBACTERS

Fruit bodies

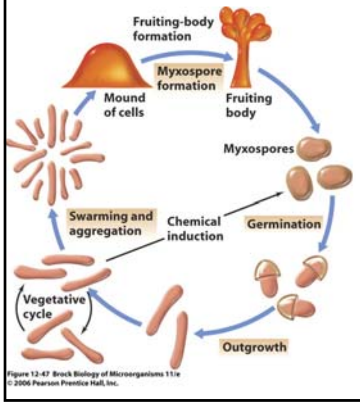
1 – 2. *Stigmatella aurantica*
3. *Chondromyces crocatus*
4. *Myxococcus fulvus*
5 *Myxococcus. stipatus*







LIFE CYCLE OF A FRUITING *MYXOBACTERIUM*



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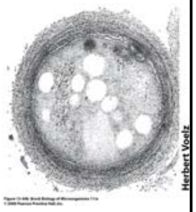

Myxospore of
Myxococcus xanthus
Wall layers
On decaying matter
- rabbit pellets

12.17 Concept Check

The fruiting myxobacteria are rod-shaped, gliding bacteria that aggregate to form complex masses of cells called *fruiting bodies*. Myxobacteria are chemoorganotrophic soil bacteria that live by consuming dead organic matter or other bacterial cells.

- What environmental conditions trigger fruiting body formation in myxobacteria?
- What is a *myxospore* and how does it compare with an *endospore*?
- To what specific phylogenetic group do the myxobacteria belong?

12.18 SULFATE- & SULFUR-REDUCING PROTEOBACTERIA

Sulfate- and sulfur-reducing bacteria are a large group of delta Proteobacteria unified by their physiological process of reducing either SO_4^{2-} or S^0 to H_2S under anoxic conditions.

Two physiological subgroups of **sulfate-reducing bacteria** are known: group I, which is incapable of oxidizing acetate to CO_2, and group II, which is capable of doing so. Table 12.21

Major importance – Ankor Wat temples, Venice Gondolas, pristine beaches

Isolation – anoxic.

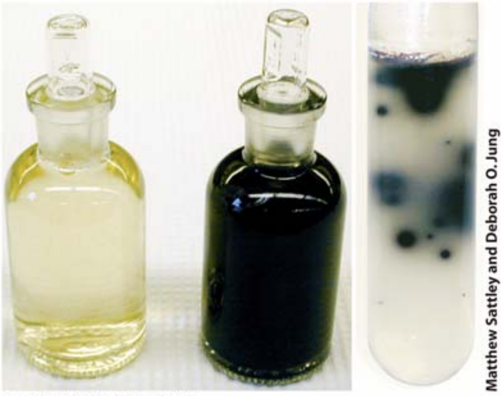

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Figure 12-50g Brock Biology of Microorganisms 11/e

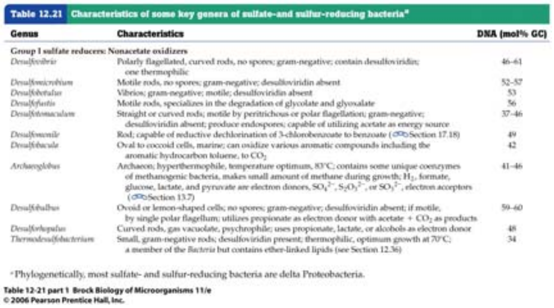

Table 12.21 Characteristics of some key genera of sulfate-and sulfur-reducing bacteria[a]

Genus	Characteristics	DNA (mol% GC)
Group I sulfate reducers: Nonacetate oxidizers		
Desulfovibrio	Polarly flagellated, curved rods, no spores; gram-negative; contain desulfoviridin; one thermophilic	46–61
Desulfomicrobium	Motile rods, no spores; gram-negative; desulfoviridin absent	52–57
Desulfobotulus	Vibrios; gram-negative; motile; desulfoviridin absent	53
Desulfofustis	Motile rods, specializes in the degradation of glycolate and glyoxalate	56
Desulfotomaculum	Straight or curved rods; motile by peritrichous or polar flagellation; gram-negative; desulfoviridin absent; produce endospores; capable of utilizing acetate as energy source	37–46
Desulfomonile	Rod; capable of reductive dechlorination of 3-chlorobenzoate to benzoate (Section 17.18)	49
Desulfobacula	Oval to coccoid cells, marine; can oxidize various aromatic compounds including the aromatic hydrocarbon toluene, to CO_2	42
Archaeoglobus	Archaeon; hyperthermophile, temperature optimum, 83°C; contains some unique coenzymes of methanogenic bacteria, makes small amount of methane during growth; H_2, formate, glucose, lactate, and pyruvate are electron donors, SO_4^{2-}, $S_2O_3^{2-}$, or SO_3^{2-}, electron acceptors (Section 13.7)	41–46
Desulfobulbus	Ovoid or lemon-shaped cells; no spores; gram-negative; desulfoviridin absent; if motile, by single polar flagellum; utilizes propionate as electron donor with acetate + CO_2 as products	59–60
Desulforhopalus	Curved rods, gas vacuolate, psychrophile; uses propionate, lactate, or alcohols as electron donor	48
Thermodesulfobacterium	Small, gram-negative rods; desulfoviridin present; thermophilic, optimum growth at 70°C; a member of the *Bacteria* but contains ether-linked lipids (see Section 12.36)	34

[a] Phylogenetically, most sulfate- and sulfur-reducing bacteria are delta Proteobacteria.

Table 12-21 part 1 Brock Biology of Microorganisms 11/e

Table 12.21 Characteristics of some key genera of sulfate-and sulfur-reducing bacteria[a]

Genus	Characteristics	DNA (mol% GC)
Group II sulfate reducers: Acetate oxidizers		
Desulfobacter	Rods; no spores, gram-negative; desulfoviridin absent; if motile, by single polar flagellum; utilizes only acetate as electron donor and oxidizes it to CO_2 via the citric acid cycle	45–46
Desulfobacterium	Rods, some with gas vesicles, marine; capable of autotrophic growth via the acetyl-CoA pathway	41–59
Desulfococcus	Spherical cells; nonmotile; gram-negative; desulfoviridin present, no spores; utilizes C_1 to C_{14} fatty acids as electron donor with complete oxidation to CO_2; capable of autotrophic growth via the acetyl-CoA pathway	57
Desulfonema	Large, filamentous gliding bacteria; gram-positive, no spores; desulfoviridin present or absent; utilizes C_2 to C_{12} fatty acids as electron donor with complete oxidation to CO_2; capable of autotrophic growth via the acetyl-CoA pathway (H_2 as electron donor)	35–42
Desulfosarcina	Cells in packets (sarcina arrangement); gram-negative; no spores; desulfoviridin absent; utilizes C_2 to C_{14} fatty acids as electron donor with complete oxidation to CO_2; capable of autotrophic growth via the acetyl-CoA pathway (H_2 as electron donor)	51
Desulfarculus	Vibrios; gram-negative; motile; desulfoviridin absent; utilizes only C_1 to C_{18} fatty acids as electron donor	66
Desulfacinum	Cocci to oval-shaped cells; gram-negative; utilizes C_1 to C_{18} fatty acids, very nutritionally diverse, capable of autotrophic growth; thermophilic	64
Desulforhabdus	Rods; no spores; gram-negative; nonmotile; utilizes fatty acids with complete oxidation to CO_2	52
Thermodesulforhabdus	Gram-negative motile rods; thermophilic; uses fatty acids up to C_{18}	51
Dissimilative sulfur reducers		
Desulfuromonas	Straight rods, single lateral flagellum; no spores; gram-negative; does not reduce sulfate; acetate, succinate, ethanol, or propanol used as electron donor; obligate anaerobe; one species is capable of the reductive dechlorination of trichloroethylene (Section 17.18)	50–63
Desulfurella	Motile short rods; gram-negative; requires acetate; thermophilic	31
Sulfurospirillum	Small vibrios, reduces S^0 with H_2 or formate as electron donors	—
Campylobacter	Curved, vibrio-shaped rods; polar flagella; gram-negative; no spores; unable to reduce sulfate but can reduce sulfur, sulfite, thiosulfate, nitrate, or fumarate anaerobically with acetate or a variety of other carbon or electron donor sources; facultative aerobe	40–42

[a] Phylogenetically, most sulfate- and sulfur-reducing bacteria are delta Proteobacteria.

Table 12-21 part 2 Brock Biology of Microorganisms 11/e

12.18 Concept Check

Sulfate- and sulfur-reducing bacteria are a large group of delta Proteobacteria unified by their physiological process of reducing either SO_4^{2-} or S^0 to H_2S under anoxic conditions. Two physiological subgroups of sulfate-reducing bacteria are known: group I, which is incapable of oxidizing acetate to CO_2, and group II, which is capable of doing so.

- What organic substrate would you use to enrich and isolate a *group II* sulfate reducer from nature?
- For sulfate-reducing bacteria capable of chemolithotrophic and autotrophic growth: (1) What is the electron donor? (2) What is the electron acceptor? (3) What is the source of cell carbon?
- Physiologically, how does *Desulfuromonas* differ from *Desulfovibrio*?

12.1 Phylogenetic Overview of *Bacteria* ***REVIEW***
PHYLUM 1: PROTEOBACTERIA
12.2 Purple Phototrophic *Bacteria*
12.3 The Nitrifying *Bacteria* Nitrosifyers Nitrifyers
12.4 Sulfur- and Iron-Oxidizing *Bacteria*
12.5 Hydrogen-Oxidizing *Bacteria*
12.6 Methanotrophs and Methylotrophs
12.7 *Pseudomonas* and the Pseudomonads
12.8 Acetic Acid *Bacteria*
12.9 Free-Living Aerobic Nitrogen-Fixing Bacteria
12.10 *Neisseria*, *Chromobacterium*, and Relatives
12.11 Enteric *Bacteria*
Escherichia, Salmonella and *Shigella*
12.12 *Vibrio* and *Photobacterium*
12.13 Rickettsias
12.14 Spirilla
12.15 Sheathed Proteobacteria: *Sphaerotilus* & *Leptothrix*
12.16 Budding and Prosthecate/Stalked *Bacteria*
Hyphomicrobium, and *Gallionella*
12.17 Gliding Myxobacteria - Fruiting
12.18 Sulfate- and Sulfur-Reducing Proteobacteria