CHAPTER 05: STUDY of the MAJOR BACTERIAL GROUPS

5.1. PHOTOSYNTHETIC BACTERIA

5.1.2. ANOXYGENIC PHOTOSYNTHETIC BACTERIA

1. Introduction

Plants, algae and cyanobacteria which carry out *oxygenic photosynthesis* use water as the source of electrons and produce oxygen as a product (dominate the aerated upper layers of freshwater and marine microbial communities). The earliest photosynthesizing organisms were likely anoxygenic phototrophs. These bacteria named *anoxygenic photosynthetic bacteria* (inhabit the deeper anoxic zones) use hydrogen sulfide, sulfur, hydrogen or organic compounds rather than water as a source of electrons when making reducing power in the form of NADPH, and therefore they do not generate O_2. They produce an oxidized organic compound or an oxidized form of sulphur, usually elemental sulphur (S) as an end product.

$$2\,H_2S + CO_2 \xrightarrow{h\nu} (CH_2O) + H_2O + 2S^0$$

The photosynthetic systems of the anoxygenic phototrophs are fundamentally different from those of plants, algae, and cyanobacteria. They have a unique type of chlorophyll called **bacteriochlorophyll**. This pigment absorbs wave lengths of light that penetrate to greater depths (far-red spectrum) and are not used by other photosynthetic organisms. These bacteria are deeply colored- red, orange, purple and bright green, because of the chlorophyll and accessory photosynthetic pigments they contain (water samples with these organisms are intensely colored).

Physiologically, these bacteria carry out **photosynthesis anaerobically**. The anaerobic photosynthetic bacteria typically occur in aquatic habitats, often growing at the sediment-water interface of shallow lakes where there is sufficient light penetration to permit photosynthetic activity, anaerobic conditions are sufficient to permit the existence of these organisms, and there is a source of reduced sulphur or organic compounds to act as electron donors for the generation of reduced coenzymes.

The anoxygenic phototrophic bacteria include the *Rhodospirillaceae* (purple nonsulphur bacteria), *Chromatiaceae* (purple sulphur bacteria), *Chlorobiaceae* (green sulphur bacteria), and *Cloroflexaceae*

(green nonsulphur bacteria) (Tab. 01). Thus, purple sulfur bacteria and green sulfur bacteria use reduced sulfur compounds [hydrogen sulfide (H_2S)] instead of water, and they produce granules of sulfur (S^0) rather than oxygen (anoxygenic process). Whereas, purple non-sulfur bacteria and green non-sulfur bacteria (also photoautotrophic) reduce carbon dioxide through photosynthesis using organic compounds such as acids and carbohydrates.

2. Taxonomy and characteristics

2.1. Green sulfur bacteria (Phylum *Chlorobi*)

The phylum *Chlorobi*, also named **green sulfur bacteria**, has only one class (*Chlorobia*), order (*Chlorobiales*), and family (*Chlorobiaceae*). It's a small group of **obligately anaerobic photolithoautotrophs** that use hydrogen sulfide, elemental sulfur, and hydrogen gas as electron sources to reduce carbon dioxide and form organic compounds. These are some characteristics:

- The elemental sulfur produced by sulfide oxidation is deposited *outside the cell*.
- Their photosynthetic pigments are located in ellipsoidal vesicles called **chlorosomes** or **chlorobium vesicles**, which are attached to the plasma membrane but are not continuous with it (membrane is not a normal lipid bilayer). Chlorosomes contain accessory bacteriochlorophyll pigments, but the reaction center bacteriochlorophyll is located in the plasma membrane where it obtains energy from chlorosome pigments.
- These bacteria flourish in the anoxic, sulfide-rich zones of lakes.
- Although they lack flagella and are nonmotile, some species have gas vesicles to adjust their depth for optimal light and hydrogen sulfide. Those forms without vesicles are found in sulfide-rich muds at the bottom of lakes and ponds.
- They are very diverse morphologically, may be rods, cocci, or vibrios; some grow singly, and others form chains and clusters.
- They are either grass-green or chocolate-brown in color.
- Representative genera are *Chlorobium, Prosthecochloris,* and *Pelodictyon.*

Example:

Phylum: Chlorobiota (historically *Chlorobi*)

Class: Chlorobiia (historically *Chlorobia*)

Order: Chlorobiales

Family: *Chlorobiaceae*

Genus: *Chlorobium*

2.2. Green nonsulfur bacteria (Phylum *Chloroflexi*)

The phylum *Chloroflexi* has both photosynthetic and nonphotosynthetic members. *Chloroflexus* is the major representative of the photosynthetic **green nonsulfur bacteria**, these are some characteristics:

- *Chloroflexus* is a filamentous, gliding, thermophilic bacterium that often is isolated from neutral to alkaline hot springs where it grows in the form of orange-reddish mats, usually in association with *Cyanobacteria*.
- It resembles the green sulfur bacteria with small chlorosomes and accessory bacteriochlorophyll *c*.
- *Chloroflexus* can carry out anoxygenic photosynthesis with organic compounds as carbon sources or grow aerobically as a chemoheterotroph.
- It doesn't appear closely related to any other bacterial group based on 16S rRNA studies and is a deep and ancient branch of the bacterial tree.

Example:

Phylum: Chloroflexota (formerly *Chloroflexi*)

Class: Chloroflexi

Order: Chloroflexales

Family: Chloroflexaceae

Genus: Chloroflexus,

Species: *Chloroflexus aurantiacus*

2.3. Purple nonsulfur bacteria

The purple nonsulfur bacteria grow **anaerobically** as photoorganoheterotrophs (Tab. 01). These are some characteristics:

- One important characteristic that distinguishes them from the purple sulphur bacteria is that they preferentially use a variety of organic molecules rather than hydrogen sulfide as a source of electrons for reducing power;
- All purple nonsulfur bacteria are α-proteobacteria, with the exception of *Rhodocyclus* (β-proteobacteria);

- In the absence of light, most purple nonsulfur bacteria can grow aerobically as chemoorganoheterotrophs. The oxygen inhibits bacteriochlorophyll and carotenoid synthesis, so that cultures growing aerobically in the dark are colorless;
- Most are motile by polar flagella (members of the genera *Rhodospirillum* and *Rhodopseudomonas* are motile by means of polar flagella, whereas those of the genus *Rhodomicrobium* are peritrichously flagellated);
- Purple nonsulfur bacteria vary considerably in morphology. They may be spirals (*Rhodospirillum*), rods (*Rhodopseudomonas*), half circles or circles (*Rhodocyclus*), or they may even form prosthecae and buds (*Rhodomicrobium*);
- They are most prevalent in the mud and water of lakes and ponds with abundant organic matter and low sulfide levels. There also are marine species;
- *Rhodospirillum* and *Azospirillum* (both in the family *Rhodospirillaceae*) are among several bacterial genera capable of forming cysts (resting cells).

Example:

Domain: Bacteria
Phylum: Proteobacteria
Class: Alpha-Proreobacteria
Order: Rhodospirillales
Family: *Rhodospirillaceae* :
Genus: *Rhodospirillum*

2.4. Purple sulfur bacteria

As mentioned previously, the purple photosynthetic bacteria are distributed between three subgroups of the proteobacteria (Tab. 01).

- The purple sulfur bacteria are γ-proteobacteria;
- *Bergey's Manual* divides the purple sulfur bacteria into two families: the *Chromatiaceae* and *Ectothiorhodospiraceae* in the order *Chromatiales.*
- The family *Ectothiorhodospiraceae* contains eight genera. *Ectothiorhodospira* has red, spiral-shaped, polarly flagellated cells that deposit sulfur globules *externally* (Fig. 01). Internal photosynthetic membranes are organized as lamellar stacks.

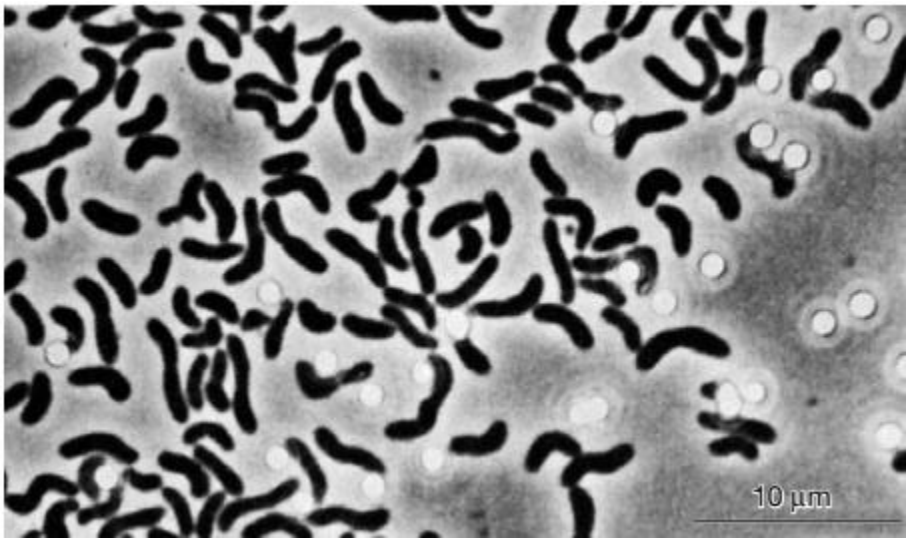

Figure 01: Purple bacteria (*Ectothiorhodospira mobilis*) light micrograph.

Example:

Domain: Bacteria

Phylum: Proteobacteria

Class: Gammaproteobacteria

Order: Chromatiales

Family: *Ectothiorhodospiraceae*

Genus: *Ectothiorhodospira*

- The typical purple sulfur bacteria are located in the family *Chromatiaceae,* which is much larger and contains 26 genera;
- Members of the family *Chromatiaceae* produce carotenoid pigments and may appear orange-brown, red-brown, purple-red, or purple-violet;
- The purple sulfur bacteria are **strict anaerobes** and usually photolithoautotrophs. Some members of the *Chromatiaceae* are potentially mixotrophic (photoautotrophic and heterotrophic), and all strains are capable of photoassimilating simple organic substrates such as acetate;
- They deposit elemental sulphur as a consequence of their utilization of reduced sulphur compounds as electron donors for generating reducing power;
- They oxidize hydrogen sulfide to sulfur and deposit it *internally* as sulfur granules; often they eventually oxidize the sulfur to sulfate. Hydrogen also may serve as an electron donor;

- Because of their color and sulphur metabolism, the *Chromatiaceae* are called the ***purple sulphur bacteria***;
- Typical purple sulfur bacteria are *Thiospirillum*, *Thiocapsa*, and *Chromatium* (Fig. 02). They are found in anoxic, sulfide-rich zones of lakes, bogs, and lagoons where large blooms can occur;
- The cells of *Chromatium*, *Thiocystis*, *Thiosarcina*, *Thiospirillum* and *Thiocapsa* do not contain gas vacuoles, but some genera of the family *Chromatiaceae*, such as *Thiodictyon* and *Thiopedia*, do contain gas vacuoles.

Example:

Domain: Bacteria
Phylum: Proteobacteria
Class: Gammaproteobacteria
Order: Chromatiales
Family: *Chromatiaceae*
Genus: *Chromatium*

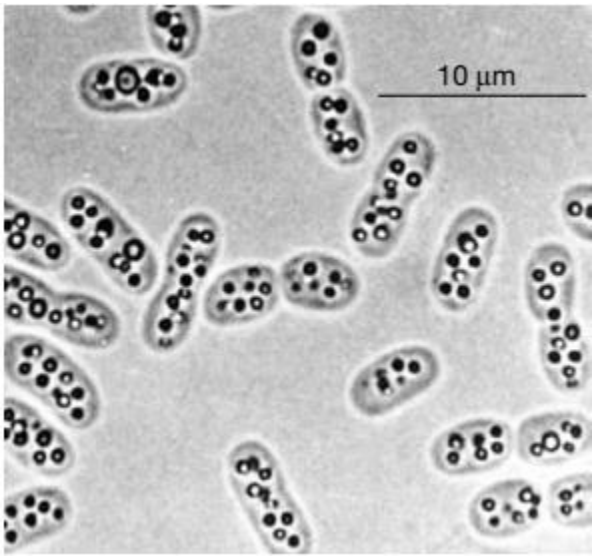

Figure 02: Typical purple sulfur bacteria (*Chromatium vinosum* with intracellular sulfur granules).

Table 01: Characteristics of the major groups of Gram-negative photosynthetic bacteria

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

General metabolic type	Obligately anaerobic photolithoautotrophs	Usually photoheterotrophic; sometimes photoautotrophic or chemoheterotrophic (when aerobic and in the dark)	Obligately anaerobic photolithoautotrophs	Usually anaerobic photoorgano-heterotrophs; some facultative photolithoautotrophs (in the dark, chemo organoheterotrophs).	Aerobic photo-lithoautotrophs
Motility	Nonmotile; some have gas vesicles	Gliding	Motile with polar flagella; some are peritrichously flagellated	Motile with polar flagella or nonmotile; some have gas vesicles	Nonmotile, swimming motility without flagella or gliding motility; some have gas vesicles
Percent G + C	48–58	53–55	45–70	61–72	35–71
Phylum or class	Chlorobi	Chloroflexi	α-, β-, and γ-proteobacteria	α-proteobacteria, β-proteobacteria (*Rhodocyclus*)	Cyanobacteria
Exemple (genus)	*Chlorobium*	*Chloroflexus*	*Chromatium*	*Rhodospirillum*	*Anabaena*

[a] Characteristics of *Chlorobi*.
[b] Characteristics of *Chloroflexus*.
[c] With the exception of *Ectothiorhodospira*