Chapter 14

Systematics of Anoxygenic Phototrophic Bacteria

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Summary

Many of the anoxygenic phototrophic bacteria, in particular green sulfur bacteria and purple sulfur bacteria are actively involved in the dissimilatory sulfur cycle by oxidizing reduced sulfur compounds. An introduction to the current state of the systematics of anoxygenic phototrophic bacteria is given here. With the introduction of 16S rDNA sequences, the consideration of genetic relatedness of these bacteria and a great deal of chemotaxonomic properties, the systematic treatment of many of these bacteria has changed over the past decades. Many species and strains have been reclassified and new higher taxa were established that harbour the phototrophic genera.

Four major phylogenetic groups that have significant phenotypic characteristics can be distinguished: (1) the Heliobacteria (*Heliobacteriaceae*), which are Gram-positive bacteria, (2) the filamentous and gliding green bacteria (*Chloroflexaceae*), and (3) the green sulfur bacteria (*Chlorobiaceae*), which each form separate phylogenetic lines within the eubacteria, and (4) the purple sulfur and nonsulfur bacteria (various taxa among the Alpha-, Beta- and Gammaproteobacteria).

This chapter concentrates on the following groups of which major properties and representative genera and species are treated: The **purple sulfur bacteria** are Gammaproteobacteria and treated as *Chromatiales* (*Ectothiorhodospiraceae* and *Chromatiaceae* families). The **purple nonsulfur bacteria** are Betaproteobacteria (*Comamonadaceae* of the Burkholdriales and *Rhodocyclaceae* of Rhodocyeclales) and Alphaproteobacteria (*Rhodospirillaceae*, *Acetobacteraceae*, *Rhodobacteraceae*, *Bradyrhizobiaceae*,

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Hyphomicrobiaceae, *Rhodobiaceae*) and are closely related to non-phototrophic purely chemotrophic relatives and to so-called aerobic bacteriochlorophyll-containg bacteria. The **green sulfur bacteria** form a closely related cluster of genera united in a single family the *Chlorobiaceae*, which is according to its isolated position within the phylogenetic tree of bacteria recognised as a separate phylum, the Chlorobi. Because of the difficulties related to taxonomic treatment and phylogenetic groupings, a list of strains is given indicating old and new taxonomic names of species and genus.

I. Introduction

Phototrophic bacteria are found in major eubacterial branches. The most important common property of these bacteria is the possession of photosynthetic pigments, which is visible in their light absorption spectra, and a photosynthetic apparatus, which enables the performance of light-dependent energy transfer processes. A characteristic unifying property of all of them is the performance of chlorophyll-mediated energy transformation.

On the basis of fundamental physiological differences we distinguish between (i) oxygenic phototrophic bacteria that use water as photosynthetic electron donor and produce molecular oxygen (cyanobacteria), (ii) anoxygenic phototrophic bacteria that use reduced substrates such as sulfide, hydrogen, ferrous iron and a number of simple organic substrates as photosynthetic electron donors but do not produce oxygen during photosynthesis, and (iii) aerobic bacteriochlorophyll-containing bacteria ("ABC-bacteria"), which represent chemoheterotrophic bacteria with the potential to produce photosynthetic pigment-protein complexes and to perform light-mediated photosynthetic electron transport. The cyanobacteria represent a separate major phylogenetic line. The anoxygenic phototrophic bacteria are found in four different major phylogenetic branches, including the filamentous green and gliding bacteria with *Chloroflexus* and relatives, the green sulfur bacteria with *Chlorobium*, the *Heliobacteriaceae* (classified among the *Clostridiales*) and the phototrophic purple bacteria belonging to the Alpha-, Beta- and Gammaproteobacteria. The "ABC-bacteria" are also purple bacteria, closely related to the anoxygenic phototrophic bacteria of the Alpha- and Betaproteobacteria. Characteristic differences in the structure and function of the photosynthetic

Table 1. Diagnostic properties of major groups of phototrophic prokaryotes.

	Chlorobiaceae	*Chloroflexaceae*	Purple bacteria	Heliobacteria	Cyanobacteria (including prochlorophytes)
Photosynthesis	anoxygenic	anoxygenic	anoxygenic	anoxygenic	oxygenic
Type of (bacterio) chlorophyll	bchl c, d, e (+ bchl a)	bchl c, d (+ bchl a)	bchl a, b	bchl g	chl a, chl b*
Phycobilins present	–	–	–	–	+/–
Type of reaction center	I	II	II	I	I + II
Reduction of NAD^+ by primary photosynthetic electron acceptor	+	–	–	+	+
Location of antenna	chlorosomes	chlorosomes	ICM	CM	ICM, phycobilisomes**
Pathway of autotrophic CO_2-fixation	reductive TCA cycle	Hydroxypropionate-pathway	Calvin cycle	–	Calvin cycle
Preferred electron donor	H_2S, H_2	organic compounds (H_2S)	H_2S, H_2 organic compounds	organic compounds	H_2O
Chemotrophic growth	–	–	+/–	–	–/(+)

Abbreviations: – characteristic absent; +/– characteristic present or absent; –/(+) characteristic absent or weak activity present;

* present in prochlorophytes; ** absent in prochlorophytes; CM cytoplasmic membrane; ICM internal membranes bchl bacteriochlorophyll, chl chlorophyll

apparatus, in the pigment content, in important physiological properties as well as 16S rDNA sequence similarities distinguish these major branches of phototrophic bacteria (see Table 1). Quite remarkable is the high variation of the light harvesting structures and of different CO_2-fixation pathways among these groups.

This chapter is concerned with the anaerobic phototrophic bacteria that perform anoxygenic photosynthesis. In these bacteria photosynthesis depends on anoxic or oxygen-deficient conditions, because synthesis of the photosynthetic pigments and the formation of the photosynthetic apparatus are repressed by oxygen. These bacteria are unable to use water as an electron donor, but need more reduced compounds. Most characteristically, sulfide and other reduced sulfur compounds, but also hydrogen and a number of small organic molecules are used as photosynthetic electron donors. Also, the growth with reduced iron as electron donor has been demonstrated in some phototrophic purple bacteria (Widdel et al., 1993; Ehrenreich and Widdel, 1994; Straub et al., 1999).

The anoxygenic phototrophic bacteria are represented by predominantly aquatic bacteria that are able to grow under anoxic conditions by photosynthesis without oxygen production. The various photosynthetic pigments, which function in the transformation of light into chemical energy, give the cell cultures a distinct coloration depending on the pigment content from green, yellowish-green, brownish-green, brown, brownish-red, red, pink, purple, and purple-violet to even blue (carotinoidless mutants of certain purple bacteria containing bacteriochlorophyll *a*). In particular green sulfur bacteria and purple sulfur bacteria are key players in the biological sulfur cycle and form massive blooms under appropriate conditions, when both reduced sulfur compounds and light are available but oxygen is deficient or lacking.

A. A Short Overview on the Groups of Anoxygenic Phototrophic Bacteria

The major groups of phototrophic bacteria (Table 1) are well distinguished on the basis of fundamental structural, molecular and physiological properties and characterized by sequence comparison of the 16S rDNA molecule. A fairly complete database of 16S rDNA sequences is available of type strains and additional other strains of the *Chlorobiaceae* (Overmann and Tuschack, 1997; Alexander et al., 2002), of purple sulfur bacteria (Imhoff and Süling, 1996; Guyoneaud et al., 1998; Imhoff et al., 1998b) of filamentous green and gliding bacteria (Keppen et al., 2000), of Heliobacteria (Bryantseva et al., 1999, 2000; Madigan, 2001) and of purple non-sulfur bacteria (Hiraishi and Ueda, 1994; Hiraishi et al., 1995; Imhoff et al., 1998a; Kawasaki et al., 1993). These data have revealed the phylogenetic relationships of the anoxygenic phototrophic bacteria based on the 16S rDNA sequences and are used to determine the phylogenetic position of new isolates.

The ***Heliobacteriaceae*** are anoxygenic phototrophic bacteria that contain bacteriochlorophyll *g* and carotenoids. They are highly sensitive to oxygen and some species form heat resistant endospores. They are phylogenetically related to Gram-positive bacteria and now are classified among the Clostridiales. They grow photoheterotrophically. Growth with reduced sulfur sources has not been observed, although often sulfide is oxidized to sulfur if added to growing cultures (Madigan, 2001).

The **filamentous green and gliding bacteria** (*Chloroflexaceae*) are anoxygenic phototrophic bacteria that contain bacteriochlorophyll *c* or *d* in light-harvesting complexes located in special light-harvesting organelles, the chlorosomes. They move by gliding, are tolerant to oxygen, and grow preferably as photoheterotrophs. Representative species of *Chloroflexus* and *Roseiflexus* are adapted to hot freshwater environments. Some representatives have the capability to oxidize reduced sulfur compounds.

The **green sulfur bacteria** (*Chlorobiaceae*) are anoxygenic phototrophic bacteria that contain bacteriochlorophyll *c*, *d*, or *e* in light-harvesting complexes located in special light-harvesting organelles, the chlorosomes. They are obligately phototrophic, require strictly anoxic growth conditions, and have a low capacity to assimilate organic compounds. Depending on the pigment content, a number of green-colored and corresponding brown-colored strains are known from several species. Reduced sulfur compounds, in particular sulfide and sulfur, are common photosynthetic electron donors in this group of bacteria. In addition, thiosulfate is used by a number of representatives. Species of this group have been

found in marine and hypersaline environments, where under appropriate conditions intensively colored, visible mass developments are formed.

The **phototrophic purple bacteria comprise the purple sulfur bacteria** (*Chromatiaceae* and *Ectothiorhodospiraceae*) and the purple nonsulfur bacteria. Quite characteristic is their capability to grow photoautotrophically and/or photoheterotrophically. The major pigments are bacteriochlorophyll a or b and various carotenoids of the spirilloxanthin, rhodopinal, spheroidene, and okenone series (Schmidt, 1978). The photosynthetic pigments and the structures of the photosynthetic apparatus are located within a more or less extended system of internal membranes that is considered as originating from and being continuous with the cytoplasmic membrane. These intracellular membranes consist of small fingerlike intrusions, vesicles, tubules or lamellae parallel to or at an angle to the cytoplasmic membrane. They carry the photosynthetic apparatus, the reaction centers and light-harvesting pigment-protein complexes surrounding the reaction center in the plane of the membrane (Drews and Imhoff, 1991). Bacteria of this group are the most prominent and abundant anoxygenic phototrophic bacteria in aquatic environments.

- The *Chromatiaceae* are Gammaproteobacteria and grow well under photoautotrophic conditions and use sulfide as photosynthetic electron donor, which is oxidized to sulfate via intermediate accumulation of elemental sulfur, microscopically visible as globules inside the cells. Photoheterotrophic, chemoautotrophic, and chemoheterotrophic growth is possible by several species.
- The *Ectothiorhodospiraceae* are Gammaproteobacteria and can be distinguished from the *Chromatiaceae* by deposition of elemental sulfur outside the cells or in the peripheral periplasmic part of the cells, and their preference for alkaline and saline growth conditions. Some species may also grow chemotrophically under aerobic dark conditions in the dark.
- The purple nonsulfur bacteria are Alpha- and Betaproteobacteria and preferentially grow under photoheterotrophic conditions, though most of them have the ability to grow photoautotrophically with hydrogen and several also with reduced sulfur compounds as electron donors. Only few species are able to completely oxidize sulfide to sulfate.

II. Phototrophic Purple Sulfur Bacteria – Chromatiales

The families *Chromatiaceae* and *Ectothiorhodospiraceae* are classified with the *Chromatiales* (Imhoff, 2005a, b, c). The *Ectothiorhodospiraceae* are purple sulfur bacteria that form sulfur globules outside the cells, while the *Chromatiaceae* exclusively comprise those phototrophic sulfur bacteria able to deposite elemental sulfur inside their cells (Imhoff, 1984a), which is in agreement with Molisch's (1907) definition of the Thiorhodaceae. Quite interestingly, already Pelsh (1937) had differentiated the "Ectothiorhodaceae" from the "Endothiorhodaceae" on a family level. However, because of their illegitimacy, these family names had no standing in nomenclature. Historical aspects of the taxonomy of anoxygenic phototrophic bacteria have been discussed in more detail elsewhere (Imhoff, 1992, 1995, 1999, 2001c).

The two families can also clearly be distinguished by a number of chemotaxonomic properties. Significant differences between *Chromatiaceae* and *Ectothiorhodospiraceae* occur in quinone, lipid and fatty acid composition (see Imhoff and Bias-Imhoff, 1995). Characteristic glucolipids are present in *Chromatiaceae* species, but absent from *Ectothiorhodospiraceae* (Imhoff et al., 1982). While C-16 fatty acids (in particular C-16:1) are the major components in *Chromatiaceae*, C-18 fatty acids (in particular C-18:1) are dominant in *Ectothiorhodo-spiraceae*, and C-16:1 is only a minor component in this latter group. In addition, the lipopolysaccharides are significantly different in members of the two families (Weckesser et al., 1979, 1995). The lipid A of investigated *Chromatiaceae* (*Allochromatium vinosum*, *Thermochromatium tepidum, Thiocystis violacea*, *Thiocapsa roseopersicina* and *Thiococcus pfennigii*) is characterized by a phosphate-free backbone with D-glucosamine as the only amino sugar, which has terminally attached D-mannose and amide-bound 3-OH-C-14:0. In the lipid A of all tested *Ectothiorhodospiraceae* (*Ectothiorhodospira vacuolata*, *Ect. shaposhnikovii*, *Ect. haloalkaliphila* and *Halorhodospira halophila*), phosphate is present, 2,3-diamino-2,3-dideoxy-D-glucose is the major amino sugar (D-glucosamine is also present), D-mannose is

lacking (D-galacturonic acid and D-glucuronic acid are present instead), and quite remarkably, 3-OH-C-10:0 is present as an amide-bound fatty acid (Zahr et al., 1992; Weckesser et al., 1995). These distinctive properties of the lipid A appear to be characteristic features of the two families.

A. Ectothiorhodospiraceae

Ectothiorhodospiraceae (Imhoff, 1984a) represent a group of haloalkaliphilic purple sulfur bacteria that form a separate line of phylogenetic descent related to the *Chromatiaceae. Ectothiorhodospiraceae* are clearly separated from the *Chromatiaceae* by sequence similarity and signature sequences of their 16S rDNA (Imhoff and Süling, 1996; Imhoff et al., 1998b). In a phylogenetic tree based on 16S rDNA data both families form separate but related groups within the Gammaproteobacteria (Fowler et al., 1984; Stackebrandt et al., 1984; Woese et al., 1985; Imhoff and Süling, 1996).

Ectothiorhodospiraceae have been distinguished from the *Chromatiaceae* on the basis of both phenotypic and molecular information (Imhoff, 1984a). During oxidation of sulfide, the *Ectothiorhodospiraceae* deposit elemental sulfur outside their cells. Furthermore, they are distinguished from the *Chromatiaceae* by lamellar intracellular membrane structures, by significant differences of the polar lipid composition (Imhoff et al., 1982; Imhoff and Bias-Imhoff, 1995), and by the dependence on saline and alkaline growth conditions (Imhoff, 1989). *Halorhodospira halophila* is the most halophilic eubacterium known and even grows in saturated salt solutions.

On the basis of sequence similarities and by a number of characteristic signature sequences, two major phylogenetic groups were recognized and classified as separate genera. The extremely halophilic species were reassigned to the genus *Halorhodospira*, including the species *Halorhodospira halophila*, *Halorhodospira halochloris* and *Halorhodospira abdelmalekii*. A new species of this genus, *Halorhodospira neutriphila*, which grows at neutral pH has been described recently (Hirschler-Rea et al., 2003). Among the slightly halophilic species, the classification of strains belonging to *Ectothiorhodospira mobilis* and *Ectothiorhodospira shaposhnikovii* was improved and a close relationship between *Ect. shaposhnikovii* and *Ect. vacuolata* was demonstrated. Based on genetic results, *Ectothiorhodospira marismortui* has been confirmed as a distinct species closely related to *Ect. mobilis*. Several strains which previously had been tentatively identified as *Ectothiorhodospira mobilis* formed a separate cluster on the basis of their 16S rDNA sequences and were recognized as two new species: *Ectothiorhodospira haloalkaliphila*, which includes the most alkaliphilic strains originating from strongly alkaline soda lakes and *Ectothiorhodospira marina*, describing isolates from the marine environment (Imhoff and Süling, 1996).

New alkaliphilic isolates from Siberian and Mongolian soda lakes were found to be distinct from described species of the genera *Ectothiorhodospira* and *Halorhodospira* but more closely related to *Ectothiorhodospira*. Both are regarded as species of the new genera *Thiorhodospira* (Bryantseva et al., 1999) and *Ectothiorhodosinus* (Gorlenko et al., 2004). (In contradiction to these authors, the genus gender should be masculine and therefore the correct species designation is *Ectothiorhodosinus mongolicus*.) In *Thiorhodospira sibirica* sulfur globules remain attached to the cells and according to microscopic observations are located in the cell periphery or the periplasmic space of the cells (Bryantseva et al., 1999).

In addition to the phototrophic genera (*Ectothiorhodospira*, *Thiorhodospira*, *Halorhodospira, Ectothiorhodosinus*), the *Ectothiorhodospiraceae* include genera of purely chemotrophic bacteria unable to perform anoxygenic photosynthesis (*Arhodomonas*, *Nitrococcus*, *Alkalispirillum*).

B. Chromatiaceae

The *Chromatiaceae* (Bavendamm, 1924) (emended description Imhoff, 1984a) comprise those phototrophic purple sulfur bacteria that, under the proper growth conditions, deposit globules of elemental sulfur inside their cells (Imhoff, 1984a). The family represents a quite coherent group of species, based on physiological properties, on the similarity of 16S rDNA sequences (Fowler et al., 1984; Guyoneaud et al., 1998; Imhoff et al., 1998b) and on chemotaxonomic markers such as fatty acid and quinone composition (Imhoff and Bias-Imhoff, 1995) and lipopolysaccharide structures

(Meißner et al., 1988; Weckesser et al., 1995). In addition to the photoautotrophic mode of growth with reduced sulfur compounds as most important photosynthetic electron donors, several species also are able to grow under photoheterotrophic conditions, some even as chemoautotrophs, and a few species also can grow chemoheterotrophically (Gorlenko, 1974; Kondratieva et al., 1976; Kämpf and Pfennig, 1980). All of them oxidize sulfide and elemental sulfur, and some also oxidize thiosulfate and sulfite (Trüper, 1981). Sulfide is oxidized to sulfate as the final oxidation product. During growth of *Chromatiaceae* on sulfide and thiosulfate, sulfur appears in the form of globules inside the bacterial cells. During oxidation of thiosulfate, the sulfur of these globules is entirely derived from the sulfane group of thiosulfate (Smith, 1965; Trüper and Pfennig, 1966). The sulfur in the globules exists in a metastable state and is not true elemental sulfur. It mainly consists of long sulfur chains very probably terminated by organic residues (mono-/bis-organyl polysulfanes) in purple and also in green sulfur bacteria. Most probably, the organic residue at the end of the sulfur chains in the sulfur globules is glutathione or very similar to glutathione (Prange et al., 2002). For a detailed discussion of this topic see the chapters Dahl (chapter 15) and Prange et al. (chapter 23). The sulfur globules are surrounded by a protein monolayer consisting of three different proteins in *Allochromatium vinosum* and two proteins in *Thiocapsa roseopersicina* (Brune, 1995). Evidence is presented, that these sulfur globule proteins contain amino-terminal signal peptides pointing to an extracytoplasmic localization of the sulfur globules (Pattaragulwanit et al., 1998).

During aerobic dark growth, elemental sulfur may support respiration and serve as electron donor for chemolithotrophic growth (Breuker, 1964; Kämpf and Pfennig, 1986). During anaerobic dark, fermentative metabolism, intracellular sulfur serves as an electron sink during oxidation of stored carbohydrates and is reduced to sulfide (Van Gemerden, 1968a, 1968b, 1974). Though growth under these conditions is very poor in *Chromatiaceae*, several species have the capability of a fermentative metabolism that at least allows survival in the absence of light and oxygen (Van Gemerden, 1968a, 1968b; Krasilnikova et al., 1975, 1983; Krasilnikova, 1976).

Approaches to the phylogeny of the *Chromatiaceae* were made using full length 16S rDNA sequences. The first complete 16S rDNA sequences were obtained for *Allochromatium vinosum* (DeWeerd et al., 1990) and *Thermochromatium tepidum* (Madigan, 1986). With the description of the new species and genera *Rhabdochromatium marinum* (Dilling et al., 1995), *Halochromatium glycolicum* (Caumette et al., 1997) and *Thiorhodococcus minus* (Guyoneaud et al., 1997), more 16S rDNA sequences became available. With the analysis of complete 16S rDNA sequences from most *Chromatiaceae* species (Guyoneaud et al., 1998; Imhoff et al., 1998b) the phylogenetic relationship of these bacteria was analysed and the existence of major groups of species was established. As a consequence, the reclassification of a number of these bacteria, based on their genetic relationship and supported by diagnostic phenotypic properties was proposed (Guyoneaud et al., 1998; Imhoff et al., 1998b). However, morphological and a number of physiological properties used so far in the classification of these bacteria, have little relevance in a genetically oriented classification system. Apparently, ecological aspects and adaptation of bacteria to specific factors of their habitat, like salinity, are of importance in a phylogenetically oriented taxonomy (see below).

The genetic relatedness determined on the basis of 16S rDNA nucleotide sequences revealed that major phylogenetic branches of the *Chromatiaceae* contain (1) truly marine and halophilic species, (2) species that are motile by polar flagella, do not contain gas vesicles, and are primarily freshwater species, and (3) species with ovoid to spherical cells, the majority of which are non-motile freshwater species containing gas vesicles.

The marine branch includes the genera *Marichromatium*, *Halochromatium*, *Rhabdochromatium*, *Thiorhodococcus*, *Thiococcus*, *Thioflavicocc*us, *Thioalkalicoccus*, *Thiorhodovibr*io, *Thiohalocapsa* and *Isochromatium*. Three genetically related species of this group, which are adapted to the lower range of salt concentrations of brackish and marine habitats (*Thiococcus pfennigii*, *Thioalkalicoccus limnaeus* and *Thioflavicoccus mobilis*), are clearly distinct from all others by containing bacteriochlorophyll *b* and by the presence of tubular internal membranes (Bryantseva et al., 2000; Imhoff and Pfennig, 2001).

The second major branch includes the genera *Chromatium*, *Allochromatium*, *Thermochromatium* and *Thiocystis*, which are motile forms without gas vesicles.

The third branch includes the genera *Thiocapsa*, *Thiolamprovum*, *Thiobaca* and *Lamprocystis* and others as reclassified by Guyoneaud et al. (1998), namely *Thiocapsa pendens* (formerly *Amoebobacter pendens*), *Thiocapsa rosea*, (formerly *Amoebobacter roseus*), *Thiolamprovum pedioformis* (formerly *Amoebobacter pedioformis*) and *Lamprocystis purpurea* (formerly *Amoebobacter purpureus*, Imhoff, 2001b). Unfortunately, *Amoebobacter purpureus* was reclassified on the basis of purely nomenclatural aspects but without supporting data as *Pfennigia purpurea* (see Bergey's Manual of Systematic Bacteriology, Vol. 2B). Because available data were in disagreement with this classification, it had to be reclassified as a species of *Lamprocystis*, *Lamprocystis purpurea* (Imhoff, 2001b). (Attention also has to be given to the different strains assigned to this bacterium (named *Amoebobacter purpureus* or *Lamprocystis purpurea*), because one of the strains according to its 16S rDNA sequence available in databases is misclassified and belongs to a different species.) *Lamprocystis roseopersicina* is one of the rare cases where gas vesicles are formed and the cells are in addition motile by flagella. *Thiobaca trueperi* is a motile rod without gas vesicles (Rees et al., 2002). *Thiocapsa roseopersicina*, one of the best known species of this group, does not form gas vesicles. So far, unpublished sequences of *Thiodictyon* species indicate their association to the group around *Thiocapsa* species.

Because 16S rDNA sequences from *Thiospirillum jenense*, *Lamprobacter modestohalophilus* and *Thiopedia rosea* are presently not available, the phylogenetic assignment of these bacteria is still uncertain.

It was suggested that the salt response is one important taxonomic criterion in such a taxonomic system of the *Chromatiaceae* (Imhoff et al., 1998b), because both the genetic relationship and the salt responses distinguish major phylogenetic branches of the *Chromatiaceae* and single genera. Both the genetic relationship and the salt responses enable to distinguish between, e.g., the halophilic *Halochromatium salexigens* and *Halochromatium glycolicum*, and the marine *Marichromatium gracile* and *Marichromatium purpuratum* from each other and from freshwater species such as *Thiocapsa roseopersicina* and *Allochromatium vinosum* and their relatives. This implies a separate phylogenetic development in the marine and in the freshwater environment and points to the general importance of salt responses and possibly other ecological parameters defining ecological niches for species formation and evolution (Imhoff, 2001a).

III. Phototrophic Purple Nonsulfur Bacteria

Purple nonsulfur bacteria are affiliated with the Alphaproteobacteria and the Betaproteobacteria. The analysis of 16S rDNA sequences revealed a close relationship of these phototrophic bacteria to purely chemotrophic bacteria in numerous cases (e.g. Gibson et al., 1979; Woese et al., 1984a, b; Woese, 1987; Kawasaki et al., 1993; Hiraishi and Ueda, 1994). In addition, a great number of so called "aerobic bacteriochlorophyll-containing bacteria or ABC-bacteria" (not treated here) is associated with these groups.

Bacteria of the phototrophic purple nonsulfur bacteria are able to perform anoxygenic photosynthesis with bacteriochlorophylls and carotenoids as photosynthetic pigments. None of the described species contains gas vesicles. Internal photosynthetic membranes are continuous with the cytoplasmic membrane and consist of vesicles, lamellae, or membrane stacks. Color of cell suspensions is green, beige, brown, brown-red, red or pink.

This is in strict contrast to the "ABC-bacteria". The "aerobic bacteriochlorophyll-containing Alphaproteobacteria" such as *Erythrobacter longus* and others exhibit physiological properties and occupy ecological niches clearly distinct from the phototrophic purple nonsulfur bacteria, because oxygen does not repress synthesis of photosynthetic pigments in these bacteria. Furthermore, these bacteria are strictly aerobic bacteria.

The purple nonsulfur bacteria (*Rhodospirillaceae*, Pfennig and Trüper, 1971) represent by far the most diverse group of the phototrophic purple bacteria (Imhoff and Trüper, 1989). The high diversity of these bacteria is reflected in the organization of the internal membrane systems,

16S rDNA sequence similarities, carotenoid composition, utilization of carbon sources and electron donors. Furthermore, this high diversity is well documented by a number of chemotaxonomic observations, such as cytochrome c_2 amino acid sequences, lipid, quinone and fatty acid composition, as well as lipid A structures (Ambler et al., 1979; Weckesser et al., 1979, 1995; Dickerson, 1980; Hiraishi et al., 1984; Imhoff, 1984b, 1991, 1995; Imhoff et al., 1984; Imhoff and Bias-Imhoff, 1995). As a consequence, it is not appropriate to assign new species to the genera only on the basis of physiological and morphological properties. Chemotaxonomic characteristics and sequence information also have to be taken into consideration. In addition, environmental aspects and ecological distribution should be considered. An outline on recommendations on the description of new species of anoxygenic phototrophic bacteria is given by Imhoff and Caumette (2004).

It was the recognition of the close genetic relationship between phototrophic purple bacteria and chemotrophic bacteria on the basis of 16S rRNA oligonucleotide catalogues and 16S rDNA sequences, respectively, which led C.R. Woese to call the Proteobacteria the Purple Bacteria and their relatives and to discuss the role of phototrophic purple nonsulfur bacteria as ancestors of numerous chemotrophic representatives of these Proteobacteria groups (Woese et al., 1984a, b; Woese et al., 1985; Woese, 1987). With the recognition of their genetic relationships and with the support from chemotaxonomic data and ecophysiological properties, purple nonsulfur bacteria of the Alphaproteobacteria and Betaproteobacteria were taxonomically separated and rearranged according to the proposed phylogeny. Despite the fact that many of the phototrophic purple nonsulfur bacteria are closely related to strictly chemotrophic relatives, the phototrophic capability and the content of photosynthetic pigments is included in the genus definitions of these bacteria.

Members of this group are widely distributed in nature and have been found in freshwater, marine and hypersaline environments that are exposed to the light. They live preferably in aquatic habitats with significant amounts of soluble organic matter, low oxygen tension and moderate temperatures, but also in thermal springs and alkaline soda lakes. They rarely form colored blooms, which are characteristically formed by representatives of purple sulfur bacteria and phototrophic green sulfur bacteria. The preferred mode of growth is photoheterotrophically under anoxic conditions in the light, but photoautotrophic growth with molecular hydrogen and sulfide may be possible, and most species are capable of chemotrophic growth under microoxic to oxic conditions in the dark. While some species are very sensitive to oxygen, others grow equally well aerobically in the dark.

A. Anaerobic Phototrophic Alphaproteobacteria

1. Phototrophic alpha-1 Proteobacteria (Rhodospirillales)

All genera of this group are classified with the *Rhodospirillales*, most of them with the *Rhodospirillaceae* family. *Rhodopila* is classified with the *Acetobacteraceae* (Table 2). Based on 16S rDNA sequence the phototrophic alpha-1 Proteobacteria are phylogenetically distinct from other groups of phototrophic Alphaproteobacteria, though they are closely related to several purely chemotrophic representatives of this group.

Most of the species of the phototrophic alpha-1 Proteobacteria have been previously known as *Rhodospirillum* species and are of spiral shape. They belong to the genera *Rhodospirillum*, *Phaeospirillum*, *Roseospira, Rhodocista*, *Rhodovibrio*, *Rhodospira* and *Roseospirillum* (Imhoff et al., 1998a). The only non-spiral representative of this group is *Rhodopila globiformis*. This acidophilic phototrophic bacterium is phylogenetically closely related to acidophilic chemotrophic bacteria of the genera *Acetobacter* and *Acidiphilium* (Sievers et al., 1994). Also other phototrophic alpha-1-Proteobacteria are closely related to different chemotrophic representatives. *Phaeospirillum* species, e.g. demonstrate close sequence similarity to *Magne-tospirillum magnetotacticum* (Burgess et al., 1993) and *Rhodocista centenaria* reveals strong relations to *Azospirillum* species (Xia et al., 1994; Fani et al., 1995). *Rhodovibrio* and *Rhodothalassium* are distantly related to the other genera and their assignment to higher taxa is currently not without problems (Table 2). *Rhodothalassium* (Imhoff 2005 m) is certainly misclassified within the *Rhodobacteraceae*.

Table 2. Genera of anoxygenic phototrophic bacteria and their classification in higher taxa[a].

Class	Order	Family	Genera[b]
Chloroflexi	*Chloroflexales*	*Chloroflexaceae*	*Chloroflexus, Oscillochloris, Heliothrix, Chloronema, Roseiflexus*
Chlorobi	*Chlorobiales*	*Chlorobiaceae*	*Chlorobium, Chlorobaculum, Prosthecochloris, Chloroherpeton*
Clostridia	*Clostridiales*	*Heliobacteriaceae*	*Heliobacterium, Heliobacillus, Heliophilum, Heliorestis*
Alphaproteobacteria	*Rhodospirillales*	*Rhodospirillaceae*	*Rhodospirillum*
			Phaeospirillum, Rhodocista, Roseospira, Roseospirillum, Rhodospira
			Rhodovibrio[c], *Rhodothalassium*[c]
		Acetobacteraceae	*Rhodopila*
	Rhodobacterales	*Rhodobacteraceae*	*Rhodobacter*
			Rhodobaca, Rhodovulum
	Rhizobiales	*Bradyrhizobiaceae*	*Rhodopseudomonas, Rhodoblastus*
			Blastochloris[c], *Rhodoplanes*[c]
		Hyphomicrobiaceae	*Rhodomicrobium*
		Rhodobiaceae	*Rhodobium*
Betaproteobacteria	*Burkholderiales*	*Comamonadaceae*	*Rhodoferax*
			Rubrivivax[c]
	Rhodocyclales	*Rhodocyclaceae*	*Rhodocyclus*
Gammaproteobacteria	*Chromatiales*	*Chromatiaceae*	*Chromatium, Thermochromatium, Allochromatium, Thiocystis*
			Thiocapsa, Thiolamprovum, Thiobaca, Lamprocystis
			Marichromatium, Halichromatium, Rhabdochromatium, Thiococcus
			Thiorhodococcus, Thioflavicoccus, Thioalkalicoccus, Thiorhodovibrio
			Thiohalocapsa, Isochromatium
			(Thiospirillum, Lamprobacter, Thiodictyon, Thiopedia)[d]
		Ectothiorhodospiraceae	*Ectothiorhodospira*
			Halorhodospira, Ectothiorhodosinus, Thiorhodospira

[a] According to Bergey's Manual on Systematic Bacteriology, 2nd edn. (2001 and 2005).
[b] Only anoxygenic phototrophic genera of these higher taxa are listed here.
[c] In the 2nd edn. of Bergey's Manual of Systematic Bacteriology, unfortunately these genera were assigned as incertae sedis or even misplaced.
[d] These genera have no clear phylogenetic standing, because 16S rDNA sequences (and pure cultures) are not available.

Several chemotaxonomic properties distinguish the phototrophic alpha-1 Proteobacteria from other phototrophic Alphaproteobacteria. Ubiquinones, menaquinones, and rhodoquinones may be present, and the length of their side chain may vary from 7 to 10 isoprene units. They have characteristic phospholipid and fatty acid composition with C-18:1 as the dominant fatty acid and either C-16:1 and C-16:0, C-16:0 and C-18:0, or just C-16:0 as additional major components.

On the basis of distinct phenotypic properties and 16S rDNA sequence similarities of all recognized spiral-shaped purple nonsulfur Alphaproteobacteria, a reclassification of these bacteria had been proposed (Imhoff et al., 1998a). Phylogenetic relations on the basis of 16S rDNA sequences of these bacteria are in good correlation with differences in major quinone and fatty acid composition and also with their growth requirement for NaCl or sea salt. This is in accordance with different phylogenetic lines forming freshwater and salt water representatives. Therefore, these properties were considered of importance in defining

and differentiating these genera. Four of these genera are defined as salt-dependent and three as fresh water bacteria. Only *Rsp. rubrum* and *Rsp. photometricum* were maintained as species of the genus *Rhodospirillum*.

2. Phototrophic Alpha-2 Proteobacteria (Rhizobiales)

Most of the species of the phototrophic alpha-2 Proteobacteria have been previously known as *Rhodopseudomonas* species and have rod-shaped motile cells. They belong to the genera *Rhodopseudomonas, Rhodobium, Rhodoplanes, Rhodoblastus*, *Blastochloris* and *Rhodomicrobium*. Based on analysis of 16S rDNA sequences, the phototrophic Alphaproteobacteria of the order *Rhizobiales* are well separated from other groups of phototrophic Alphaproteobacteria; however, they are closely related to several purely chemotrophic Alphaproteobacteria of the order *Rhizobiales. Rhodopseudomonas palustris*, for example, is most closely related to *Nitrobacter* species.

A number of morphological and chemotaxonomic properties distinguishes the phototrophic alpha-2 Proteobacteria from other purple nonsulfur bacteria. Most characteristic is their budding mode of growth and cell division which comes along with lamellar internal membranes that are lying parallel to the cytoplasmic membrane. There is variation in the presence of either ubiquinone alone, ubiquinone together with either rhodoquinone or menaquinone, or ubiquinone with both menaquinone and rhodoquinone as major components. Most species have 10 isoprenoid units in their side chains (except *Blastochloris* species). As far as known, either small or large "mitochondrial type" cytochrome c_2 is present. Characteristic phospholipids are present and among the fatty acids C-18:1 is the dominant fatty acid and either C-16:1 and C-16:0, C-16:0 and C-18:0 or just C-16:0 are additional major components (see Imhoff and Bias-Imhoff, 1995).

Outstanding properties which distinguish *Rhodomicrobium* from other alpha-2 Proteobacteria are the filament formation and the characteristic growth cycle. Other distinguishing characteristics are the composition of the lipid A, of polar lipids and fatty acids. Among the closest phylogenetic relatives of *Rhodomicrobium* based on 16S rDNA sequence analysis is *Hyphomicrobium vulgare* (Kawasaki et al., 1993).

In the second edition of Bergey's Manual of Systematic Bacteriology, *Rhodobium* (Imhoff and Hiraishi, 2005) is assigned to the *Rhodobiaceae*, *Rhodomicrobium* (Imhoff, 2005j) to the *Hyphomicrobiaceae* and *Rhodoblastus* and *Rhodopseudomonas* (Imhoff, 2005g, h) to the *Bradyrhizobiaceae*. Unfortunately and in contrast to the author's opinion, *Blastochloris* and *Rhodoplanes* (Imhoff, 2005i; Hiraishi and Imhoff, 2005b) have been misplaced in this edition. Both should be included into the *Bradyrhizobiaceae* together with the genera *Rhodoblastus* and *Rhodopseudomonas*.

3. Phototrophic Alpha-3 Proteobacteria (Rhodobacterales)

Phototrophic alpha-3 Proteobacteria have a number of characteristic chemotaxonomic properties that enable their diagnosis. All investigated species have a large type cytochrome c_2 (Ambler et al., 1979; Dickerson, 1980) and as sole quinone component Q-10 (Imhoff, 1984b; Hiraishi et. al., 1984). Those species that are able to assimilate sulfate use the pathway via 3′-phosphoadenosine-5′-phosphosulfate (PAPS, Imhoff, 1982). C-18 and C-16 saturated and monounsaturated fatty acids are major fatty acids, C-18:1 the predominant component (Imhoff, 1991). The lipopolysaccharides of investigated species contain in their lipid A moieties glucosamine as sole amino sugar, have phosphate, amide-linked 3-OH-14:0 and/or 3-oxo-14:0 and ester-linked 3-OH-10:0 (Weckesser et al., 1995). A differentiation of the genera and species of *Rhodobacter*, *Rhodovulum* and *Rhodobaca* is possible on the basis of 16S rDNA sequences and by DNA–DNA hybridization.

The phototrophic alpha-3 Proteobacteria are phylogenetically well separated from other groups of phototrophic Alphaproteobacteria, though they are closely related to purely chemotrophic alpha-3 Proteobacteria. The majority belongs to the genera *Rhodobacter* and *Rhodovulum* (Pfennig and Trüper, 1974; Imhoff et al., 1984; Hiraishi and Ueda, 1994). The former are freshwater bacteria and the latter true marine bacteria and species of both genera have distinct 16S rDNA sequences (Hiraishi and Ueda, 1994, 1995; Hiraishi et al.,

1996; Straub et al., 1999). The recently described new bacterium *Rhodobaca bogoriensis* is an alkaliphilic slightly halophilic bacterium from African soda lakes and is phylogenetically associated to *Rhodobacter* (Milford et al., 2000). All three genera (Imhoff, 2005d, e, f) are classified with the Rhodobacteraceae of the *Rhodobacterales*.

Characteristic properties of *Rhodobacter*, *Rhodobaca* and *Rhodovulum* species are the ovoid to rod-shaped cell morphology, the presence of vesicular internal membranes (except *Rba. blasticus*) and the content of carotenoids of the spheroidene series. Most *Rhodobacter* species are distinct from *Rhodovulum* species by the lack of a substantial NaCl requirement for optimal growth, i.e. they show a typical response of freshwater bacteria. The salt requirement for optimal growth of *Rhodovulum* species on the other hand does not preclude that some of these bacteria also may grow in the absence of salt.

Species of *Rhodobacter* and *Rhodovulum* not only are well characterized by phenotypic properties, but also are established on the basis of 16S rDNA sequences and DNA–DNA hybridization studies. Comprehensive DNA/DNA hybridization studies have been performed both with *Rhodobacter* and *Rhodovulum* species. A first detailed study including 21 strains of the species known at that time gave support for the recognition of strains of *Rba. veldkampii* as a new species and in addition revealed the diversity of marine isolates of this group (DeBont et al., 1981). This study also demonstrated the identity on the species level of a denitrifying isolate of *Rba. sphaeroides* and other non-denitrifying strains of this species (Satoh et al., 1976; DeBont et al., 1981). Similarly, several marine and halophilic isolates were shown to be related to *Rhv. euryhalinum* by DNA–DNA hybridization but significantly distinct from *Rhv. sulfidophilum*, *Rba. sphaeroides* and *Rba. capsulatus* (Ivanova et al., 1988). DNA–DNA hybridization also allowed the genetic distinction of 4 strains of the denitrifying *Rba. azotoformans* from *Rba. sphaeroides* and other *Rhodobacter* species (Hiraishi et al., 1996). Several strains of *Rhodovulum strictum*, which according to 16S rDNA sequence is most similar to *Rhv. euryhalinum* (96.8%), were shown to have low DNA–DNA homology (less than 30%) to type strains of all other *Rhodovulum* species, including *Rhv. euryhalinum* (Hiraishi and Ueda, 1995).

B. Anaerobic Phototrophic Betaproteobacteria (Rhodocyclales & Burkholderiales)

The phototrophic Betaproteobacteria comprise species of three genera, *Rhodocyclus*, *Rubrivivax* and *Rhodoferax*. Based on 16S rDNA sequences, the phototrophic Betaproteobacteria represent different phylogenetic lines within the Betaproteobacteria (Hiraishi, 1994). *Rhodocyclus* (Imhoff, 2005l) is classified in the family *Rhodocyclaceae* of the order *Rhodocyclales*, *Rhodoferax* (Hiraishi and Imhoff, 2005a) is classified with the *Comamonadaceae* of the order *Burkholderiales*, and *Rubrivivax* (Imhoff, 2005k) is presently classified as genus incertae sedis.

Sequences of 16S rDNA clearly classify these bacteria as belonging to the Betaproteobacteria (Hiraishi, 1994; Maidak et al., 1994). They are freshwater bacteria common in stagnant waters that are exposed to the light and have an increased load of organic compounds and nutrients and are deficient in oxygen. Internal photosynthetic membranes are much less developed than in other phototrophic purple bacteria appearing as small fingerlike intrusions and are not always evident. Growth preferably occurs under photoheterotrophic conditions, anaerobically in the light. All species known so far do not use reduced sulfur compounds as photosynthetic electron donor and sulfide is growth inhibitory already at low concentrations. Sulfate can be assimilated as sole sulfur source and is reduced with adenosine-5′-phosphosulfate (APS) as an intermediate (Imhoff, 1982). NADH is used as a cosubstrate in the GS/GOGAT reactions and HIPIP is present (Ambler et al., 1979).

Prior to the establishment of the phylogenetic relationship among the phototrophic Betaproteobacteria, these species had been included in the *Rhodospirillaceae* together with the phototrophic Alphaproteobacteria (Pfennig and Trüper, 1974). Three species were known as *Rhodopseudomonas gelatinosa*, *Rhodospirillum tenue* (Pfennig and Trüper, 1974) and *Rhodocyclus purpureus* (Pfennig, 1978). In addition to a clear phylogenetic separation (Hiraishi, 1994), both of these groups show significant differences in a number of chemotaxonomic properties. As a consequence, *Rhodospirillum tenue* (Pfennig, 1969) was transferred to *Rhodocyclus*

tenuis (Imhoff et al., 1984). *Rhodopseudomonas gelatinosa* was transferred to *Rhodocyclus gelatinosus* (Imhoff et al., 1984) and later assigned to a new genus as *Rubrivivax gelatinosus* (Willems et al., 1991). Additional new bacteria have been isolated since then that are also members of the Betaproteobacteria and have been described as the new species and genus *Rhodoferax fermentans* (Hiraishi and Kitamura, 1984; Hiraishi et al., 1991) and as additional species of this genus, *Rhodoferax antarcticus* (Madigan et al., 2000) and *Rhodoferax ferrireducens* (Finneran et al., 2003).

The phototrophic Betaproteobacteria have ubiquinone and menaquinone (or rhodoquinone) derivatives with eight isoprenoid units in the side chain (Q-8, RQ-8 and MK-8); they have a "small type" cytochrome c_{551} (in contrast to the phototrophic Alphaproteobacteria; Ambler et al., 1979; Dickerson, 1980); they have characteristic phospholipid and fatty acid compositions with the highest proportions of C-16 fatty acids (16:0 and 16:1) among all phototrophic purple bacteria and correspondingly very low ones of 18:1 (Hiraishi et al., 1991; Imhoff, 1984b; Imhoff and Bias-Imhoff, 1995; Imhoff and Trüper, 1989). Lipopolysaccharides of phototrophic Betaproteobacteria characteristically contain significant amounts of phosphate and amide-linked 3-OH-capric acid (3-OH-C-10) in their lipid A moiety (Weckesser et al., 1995). In *Rfx. fermentans* 3-OH-C-8:0 was found instead (Hiraishi et al., 1991).

IV. Phototrophic Green Sulfur Bacteria – *Chlorobiales*

The green sulfur bacteria, represented by the family *Chlorobiaceae*, form a branch of bacteria that is phylogenetically distinct from other main phylogenetic lines, and is therefore treated as a separate phylum (the Chlorobi) in *Bergey's Manual of Systematic Bacteriology* (Overmann, 2001). Traditionally, the taxonomic classification of these bacteria was based on morphological and easily recognizable phenotypic properties (Pfennig, 1989; Pfennig and Overmann, 2001a, b). Such properties include cell morphology, pigment composition and absorption spectra, and metabolic properties. However, some of these properties appear to be problematic or even misleading in a phylogenetically oriented systematic system. In particular, (i) the formation of gas vesicles has been used to distinguish between genera; (ii) brown-colored forms have been distinguished as species from their green-colored counterparts, and are distinct in their bacteriochlorophyll and carotenoid composition; and (iii) subspecies were recognized on the basis of utilization of thiosulfate as a photosynthetic electron donor. Although these properties are easily recognizable and have allowed a phenotypic differentiation, they are not in accord with the phylogenetic relationship of these bacteria (Figueras et al., 1997; Overmann and Tuschak, 1997). Therefore, in a systematic taxonomy of green sulfur bacteria based on phylogenetic relationships, they can not be used for the differentiation of species.

Phylogenetic relationships of green sulfur bacteria were established by using 16S rRNA and *fmo* (Fenna–Matthews–Olson protein, FMO protein) gene sequences, including important signatures of amino acid and nucleotide sequences (Alexander et al., 2002). Both 16S rRNA and *fmo* gene sequence information is available for most of the type strains. In addition, a larger number of 16S rDNA sequences and *fmo* gene sequences of non-type strains are known (Figueras et al., 1997; Overmann and Tuschak, 1997; Alexander et al., 2002). The congruent phylogenetic relationships found with two independent gene sequences provide a solid basis for the phylogeny of these bacteria, and for a phylogeny-based taxonomy (Imhoff, 2003).

The phylogenetic studies revealed almost-identical grouping in trees constructed from 16S rDNA and *fmoA* sequences. This suggests a largely congruent evolution of FMO and 16S rDNA (Alexander et al., 2002) and gives strong support to the 16S rDNA-based phylogeny of these bacteria. The assignment of strains into phylogenetic groups is further supported by characteristic signatures in the amino acid sequence of the FMO protein (Alexander et al., 2002). The phylogenetic grouping of the green sulfur bacteria is not in accord with their traditional classification. Therefore, the reclassification of these bacteria was necessary and included a complete reassignment of strains and species (Imhoff, 2003) (Table 3). Three examples demonstrate this: (i) species and strains formerly assigned to the genus *Chlorobium* were found in all phylogenetic groups, those of the genus

Table 3. Species names and properties of strains of *Chlorobium*, *Prosthecochloris* and *Chlorobaculum* species[a].

Genus and species name	old name	Strain number	Thio sulfate used	Cell size [µm]	Salt required	Vitamins	Major Bchl	G + C values mol%	Gas vesicles	carotenoid
Chlorobium										
Chl. limicola	*Chl. limicola*	DSM 245^T	–	0.7–1.1	no	–	c	51.0	–	clb
Chl. limicola	*Chl. limicola*	DSM 246	–		no	B_{12}	c	52.0	–	clb
Chl. limicola	*Chl. limicola f. thios.*	1630	+		no	B_{12}	c	52.5	–	
Chl. limicola	*Chl. limicola f. thios.*	9330	+		no	–	c	52.0	–	
Chl. limicola	*Chl. phaeobacteroides*	DSM 1855	–		no	B_{12}	e	o	–	iso
Chl. limicola	*Chl. limicola*	DSM 247	–		no	B_{12}	c	51.5	–	
Chl. limicola	*Chl. limicola*	DSM 248	–		no	B_{12}	c	51.5	–	
Chl. limicola	*Chl. limicola f. thios.*	DSM 257	+		no	–	c	52.5		
Chl. phaeobacteroides	*Chl. phaeobacteroides*	DSM 266^T	–	0.6–0.8	no	B_{12}	e	49.0	–	iso
Chl. phaeobacteroides	*Chl. phaeobacteroides*	DSM 267	–		no	B_{12}	e	50.0		iso
Chl. clathratiforme	*Pld. phaeoclathrathiforme*	DSM 5477^T	+	0.8–1.1	no	B_{12}	e	47.9	+	iso
Chl. clathratiforme	*Pld. clathratiforme*	PG	–	0.7–1.2	no	o		(48.5)	+	clb
Chl. ferrooxidans	*Chl. ferrooxidans*	DSM 13031^T	o	0.5	no	o	c	o	–	clb
Chl. luteolum	*Pld. luteolum*	DSM 273^T	–	0.6–0.9	>1%	B_{12}	c	58.1	+	clb
Chl. luteolum	*Chl. vibrioforme*	DSM 262	–	0.5–0.7	>1%	B_{12}	d	57.1	–	clb
Chl. phaeovibrioides	*Chl. phaeovibrioides*	DSM 269^T	–	0.3–0.4	>1%	B_{12}	e	53.0	–	iso
Chl. phaeovibrioides	*Chl. vibriof. f.thios.*	DSM 265	–	0.5–0.7	>1%	B_{12}	d+c	53.5	–	
Chl. phaeovibrioides	*Chl. vibrioforme*	DSM 261	–		>1%	B_{12}	d	52.0	–	
Chl. phaeovibrioides	*Chl. phaeovibrioides*	DSM 270	–		>1%	B_{12}	e	52.0	–	
Prosthecochloris										
Ptc. aestuarii	*Ptc. aestuarii*	DSM 271^T	–	0.5–0.7	2–5%	B_{12}	c	52–56.1	–	clb
Ptc. spec.	*Ptc. aestuarii*	2K	–		+	o			–	
Ptc. vibrioformis	*Chl. vibrioforme*	DSM 260^T	–	0.5–0.7	>1%	B_{12}	d+c	53.5	–	clb
Ptc. vibrioformis	*Chl. phaeovibrioides*	DSM 1678	–		>1%	o	e	o	–	
Ptc. vibrioformis	*Chl. vibrioforme*	CHP 3402	o			o			–	
Chlorobaculum										
Chlorobaculum tepidum	*Chl. tepidum*	ATCC49652^T	+	0.6–0.8	no		c	56.5	–	clb
Cba. limnaeum	*Chl. phaeobacteroides*	DSM 1677^T	–		no	B_{12}	e	o	–	
Cba. limnaeum	*Chl. phaeobac.*	1549	–		no				–	

(continued)

Table 3. (continued)

Genus and species name	old name	Strain number	Thio sulfate used	Cell size [μm]	Salt required	Vitamins	Major Bchl	G + C values mol%	Gas vesicles	carotenoid
O	*Chl. limic.*	UdG 6040	o	0.8–1.0			c		−	clb
O	*Chl. limic.*	UdG 6042	o	0.8–1.0			c		−	clb
O	*Chl. limic.*	UdG 6045	o	0.7–1.0			c		−	clb
O	*Chl. limic.*	UdG 6038	o	0.7–1.0			c		−	clb
Cba. thiosulfatiphilum	*Chl. limic. f.thios.*	DSM 249^T	+	0.7–1.0	no	−	c	58.1	−	clb
Cba. thiosulfatophilum	*Chl. limic. f.thios.*	1430	+		no	−	c	58.1	−	
Cba. parvum	*Chl. vibriof. f.thios.*	DSM 263^T	+	0.7–1.1	>1%	o	d	56.6	−	clb
Cba. parvum	*Chl. vibriof. f.thios.*	NCIB 8346	+		>1%	o	d	56.1	−	
Cba. chlorovibrioides	*Chl. chlorovibrioides*	UdG 6026	−	0.3–0.4*	2–3%	B_{12}	c	54.0	−	clb
Cba. chlorovibrioides	*Chl. vibrioforme*	UdG 6043	o	0.7–0.8	5%	o	c		−	clb

[a] According to Imhoff, 2003.

Pelodictyon in two of them (Table 3); (ii) prior to their reassignment, strains of several of the old species (including *Chlorobium limicola*, *Chlorobium phaeobacteroides*, *Chlorobium vibrioforme* and *Chlorobium phaeovibrioides*) appeared in at least two of the phylogenetic groups (Table 3); (iii) *Chlorobium limicola* subsp. *thiosulfatophilum* and *Chlorobium vibrioforme* subsp. *thiosulfatophilum*, as represented by their defined type strains (again prior to reassignment), were different from their reference species at the genus level (Table 3).

The major groups of species of green sulfur bacteria recognized by Alexander et al. (2002) were used as a basis for the definition of genera. *Chloroherpeton thalassium* forms a clearly separate phylogenetic line from all other species and genera of green sulfur bacteria and therefore was not involved in the rearrangement of strains and species. The type strain of the recognized type species *Prosthecochloris aestuarii* of group 1 (Alexander et al., 2002) formed the basis of assigning other species clustering with this species to the genus *Prosthecochloris*. The groups 2 and 3 of Alexander et al. (2002) were not significantly separated from each other and treated as a single genus. The recognized type strain of *Chlorobium limicola* (included in group 3) was the basis to maintain *Chlorobium* as the genus name for this group with *Chlorobium limicola* as type species. Group 4 was represented by a number of strains and species formerly assigned to the genus *Chlorobium*, but phylogenetically distant from the type strain and species *Chlorobium limicola* and the group of bacteria that clusters with this species. Consequently, the bacteria of group 4 were assigned to a novel genus, for which the name *Chlorobaculum* was proposed (Imhoff, 2003) (Table 3). The type species of this genus is *Chlorobaculum tepidum*, the former *Chlorobium tepidum* (Wahlund et al., 1991). On the basis of 16S rDNA and fmoA sequences, the phylogenetic groups and their representatives can be recognized and distinguished in natural samples and their specific distribution in nature has been studied (Alexander and Imhoff, 2006).

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