 Click here to view in 'frames' mode.

The Phototrophic Way of Life

JÖRG OVERMANN
FERRAU GARCIA-PICHEL

Introduction

Photosynthesis is the utilization of radiant energy for the synthesis of complex organic molecules. The phototrophic way of life implies the capture of electromagnetic energy (see Light absorption and light energy transfer in prokaryotes), its conversion into chemical energy (see Conversion of light into chemical energy), and its use for cellular maintenance and growth (see Efficiency of growth and maintenance energy requirements). Photosynthesis may encompass the reduction of carbon dioxide into organic molecules, a mode of growth defined as photoautotrophy. The solar electromagnetic energy reaching the Earth's surface (160 $W \cdot m^{-2}$; see Light energy and the spectral distribution of radiation) surpasses the energy contributed by all other sources by four to five orders of magnitude (electric discharge, radioactivity, volcanism, or meteoritic impacts; ~ 0.0062 $W \cdot m^{-2}$ on primordial Earth; Mauzerall, 1992; present day geothermal energy ~ 0.0292 $W \cdot m^{-2}$; K. Nealson, personal communication).

At present the flux of electromagnetic energy supports a total primary production of 172.5×10^9 tons dry $weight \cdot year^{-1}$ (168 g $C \cdot m^{-2} \cdot year^{-1}$; Whittaker and Likens, 1975). If this global primary production is converted to energy units (39.9 $kJ \cdot g\ C^{-1}$, assuming that all photosynthetic products are carbohydrate), 0.21 $W \cdot m^{-2}$ and thus 0.13 % of the available solar energy flux are converted into chemical energy. Even at this low efficiency, the chemical energy stored in organic carbon still exceeds geothermal energy by at least one order of magnitude. As a consequence, photosynthesis directly or indirectly drives the biogeochemical cycles in all extant ecosystems of the planet. Even hydrothermal vent communities, which use inorganic electron donors of geothermal origin and assimilate CO_2 by chemolithoautotrophy (rather than photoautotrophy), still depend on the molecular O_2 generated by oxygenic phototrophs outside of these systems (Jannasch, 1989).

Several lines of evidence indicate that in the early stages of biosphere evolution, prokaryotic organisms were once responsible for the entire global photosynthetic carbon fixation. Today, terrestrial higher plants account for the vast majority of photosynthetic biomass; the chlorophyll bound in light-harvesting complex LHCII of green chloroplasts alone represents 50% of the total chlorophyll on Earth (Sidler, 1994). In contrast, the biomass of marine primary producers is very low (0.2% of the global value). However, the biomass turnover of marine photosynthetic microorganisms is some 700 times faster than that of terrestrial higher plants. Thus, marine photosynthetic organisms contribute significantly to total primary productivity ($55 \cdot 10^9$ tons dry $weight \cdot year^{-1}$, or 44% of the global primary production). Because the biomass of cyanobacterial

picoplankton (see Habitats of phototrophic prokaryotes) can amount to 67% of the oceanic plankton, and their photosynthesis up to 80% in the marine environment (Campbell et al., 1994; Goericke and Welschmeyer, 1993; Liu et al., 1997; Waterbury et al., 1986), prokaryotic primary production is still significant on a global scale. A single monophyletic group of marine unicellular cyanobacterial strains encompassing the genera *Prochloroccoccus* and *Synechococcus* with a global biomass in the order of a billion of metric tons (Garcia-Pichel, 1999) may be responsible for the fixation of as much as 10–25 % of the global primary productivity. Additionally, prokaryotic (cyanobacterial) photosynthesis is still locally very important in other habitats such as cold (Friedmann, 1976) and hot deserts (Garcia-Pichel and Belnap, 1996) a nd hypertrophic lakes.

Today, the significance of anoxygenic photosynthesis for global carbon fixation is limited for two reasons. On the one hand, phototrophic sulfur bacteria (the dominant anoxygenic phototrophs in natural ecosystems) form dense accumulations only in certain lacustrine environments and in intertidal sandflats. The fraction of lakes and intertidal saltmarshes which harbor anoxygenic phototrophic bacteria is unknown, but these ecosystems altogether contribute only 4% to global primary production (Whittaker and Likens, 1975). In those lakes harboring phototrophic sulfur bacteria, an average of 28.7% of the primary production is anoxygenic (Overmann, 1997). Consequently, the amount of CO_2 fixed by anoxygenic photosynthesis must contribute much less than 1% to global primary production. On the other hand, anoxygenic photosynthesis depends on reduced inorganic sulfur compounds which originate from the anaerobic degradation of or ganic carbon. Since this carbon was already fixed by oxygenic photosynthesis, the CO_2-fixation of anoxygenic phototrophic bacteria does not lead to a net increase in organic carbon available to higher trophic levels. The CO_2-assimilation by anoxygenic phototrophic bacteria has therefore been termed 'secondary primary production' (Pfennig, 1978). Therefore, capture of light energy by anoxygenic photosynthesis merely compensates for the degradation of organic carbon in the anaerobic food chain. Geothermal sulfur springs are the only exception since their sulfide is of abiotic origin. However, because sulfur springs are rather scarce, anoxygenic photosynthetic carbon fixation of these ecosystems also appears to be of minor significance on a global scale.

The scientific interest in anoxygenic phototropic bacteria stems from 1) the simple molecular architecture and variety of their photosystems, which makes anoxygenic phototrophic bacteria suitable models for biochemical and biophysical study of photosynthetic mechanisms, 2) the considerable diversity of anoxygenic phototrophic bacteria, which has implications for reconstructing the evolution of photosynthesis, and 3) the changes in biogeochemical cycles of carbon and sulfur, which are mediated by the dense populations of phototrophic bacteria in natural ecosystems.

All known microorganisms use two functional principles (both mutually exclusive and represent two independent evolutionary developments) for the conversion of light into chemical energy. Chlorophyll-based systems are widespread among members of the domain Bacteria and consist of a light-harvesting antenna and reaction centers. In the latter, excitation energy is converted into a redox gradient across the membrane. In contrast, the retinal-based bacteriorhodopsin system is exclusively found in members of a monophyletic group within the domain Archaea. These prokaryotes lack an antenna system and use light energy for the direct translocation of protons across the cytoplasmic membrane. In both systems, photosynthetic energy conversion ultimately results in the formation of energy-rich chemical bonds of organic compounds.

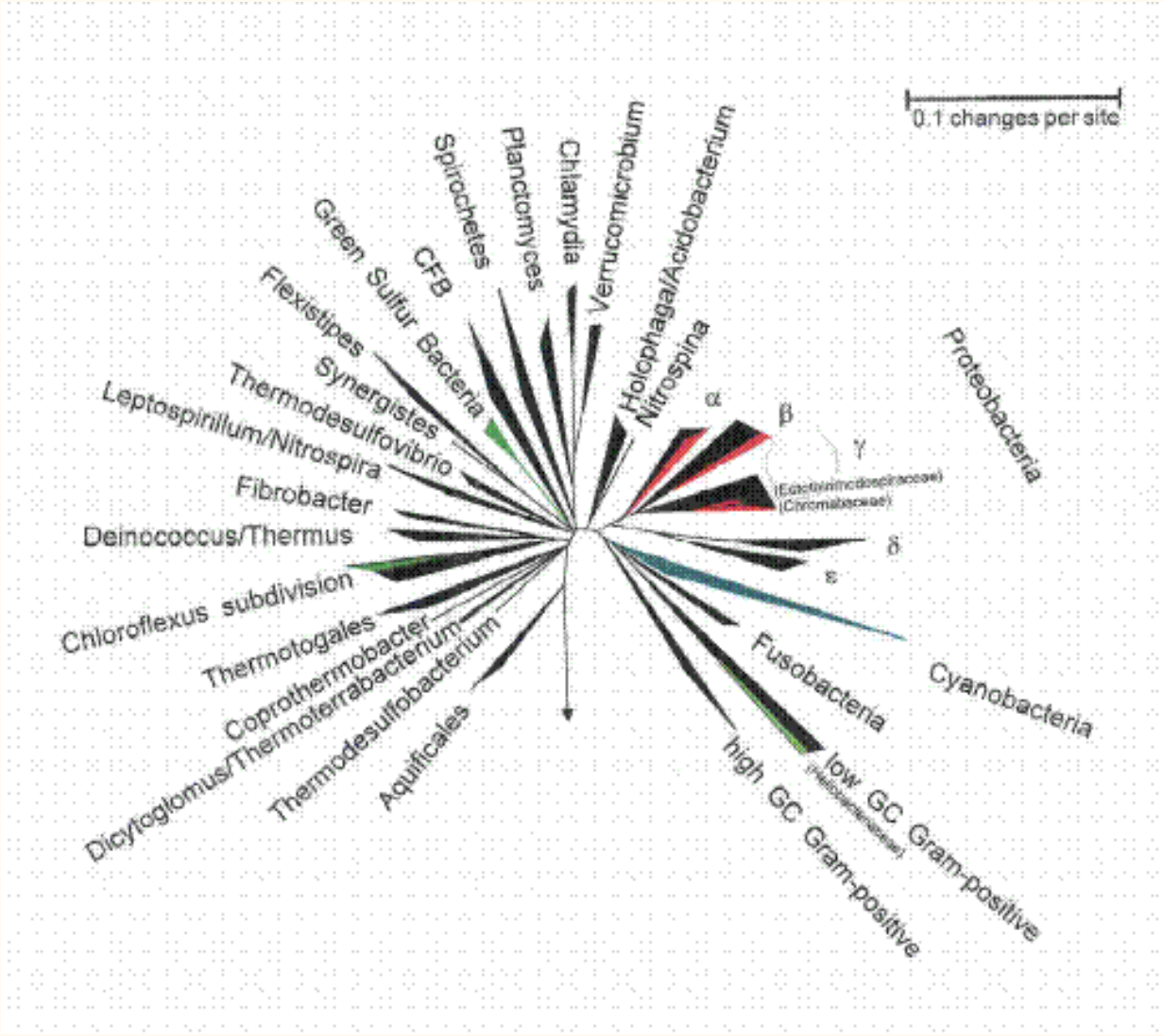
The advent of modern genetic and biochemical methods has led to a considerable gain in knowledge of the molecular biology of phototrophic prokaryotes. At the same time, microbial ecologists have found these microorganisms of considerable interest and now frequently use

molecular methods to investigate natural populations. The present chapter is limited to the discussion of phototrophic bacteria and attempts to link the physiology, ecology, and evolution of phototrophic bacteria to a molecular basis. Emphasis is laid on those molecular structures or functions that have evident adaptive value. This integrating view may provide a more solid foundation for understanding the biology of photosynthetic prokaryotes.

Taxonomy of Phototrophic Prokaryotes

The capacity for chlorophyll-based photosynthetic energy conversion is found in five of the 36 currently recognized bacterial lineages (Fig. 1; Hugenholtz et al., 1998): the *Chloroflexus* subgroup, the green sulfur bacteria, the *Proteobacteria* , the *Cyanobacteria*, and the *Heliobacteriaceae*. With the exception of the *Cyanobacteria*, phototrophic bacteria perform anoxygenic photosynthesis, which is not accompanied by photochemical cleavage of water and therefore does not lead to the formation of molecular oxygen. Based on their phenotypic characters, anoxygenic phototrophic bacteria had been divided previously into the five families Rhodospirillaceae, Chromatiaceae, Ectothiorhodospiraceae, Chlorobiaceae, and Chloroflexaceae (Trüper and Pfennig, 1981). However, 16S rRNA oligonucleotide cataloguing and 16S rRNA sequence comparisons have reveale d that the *Proteobacteria* and the *Chloroflexus*-subgroup both contain nonphototrophic representatives (Woese, 1987; Fig. 1). Therefore the use of light as an energy source for growth is not limited to phylogenetically coherent groups of bacteria. However, nonphototrophic representatives of the green sulfur bacterial and the cyanobacterial lineages have not been isolated to date.

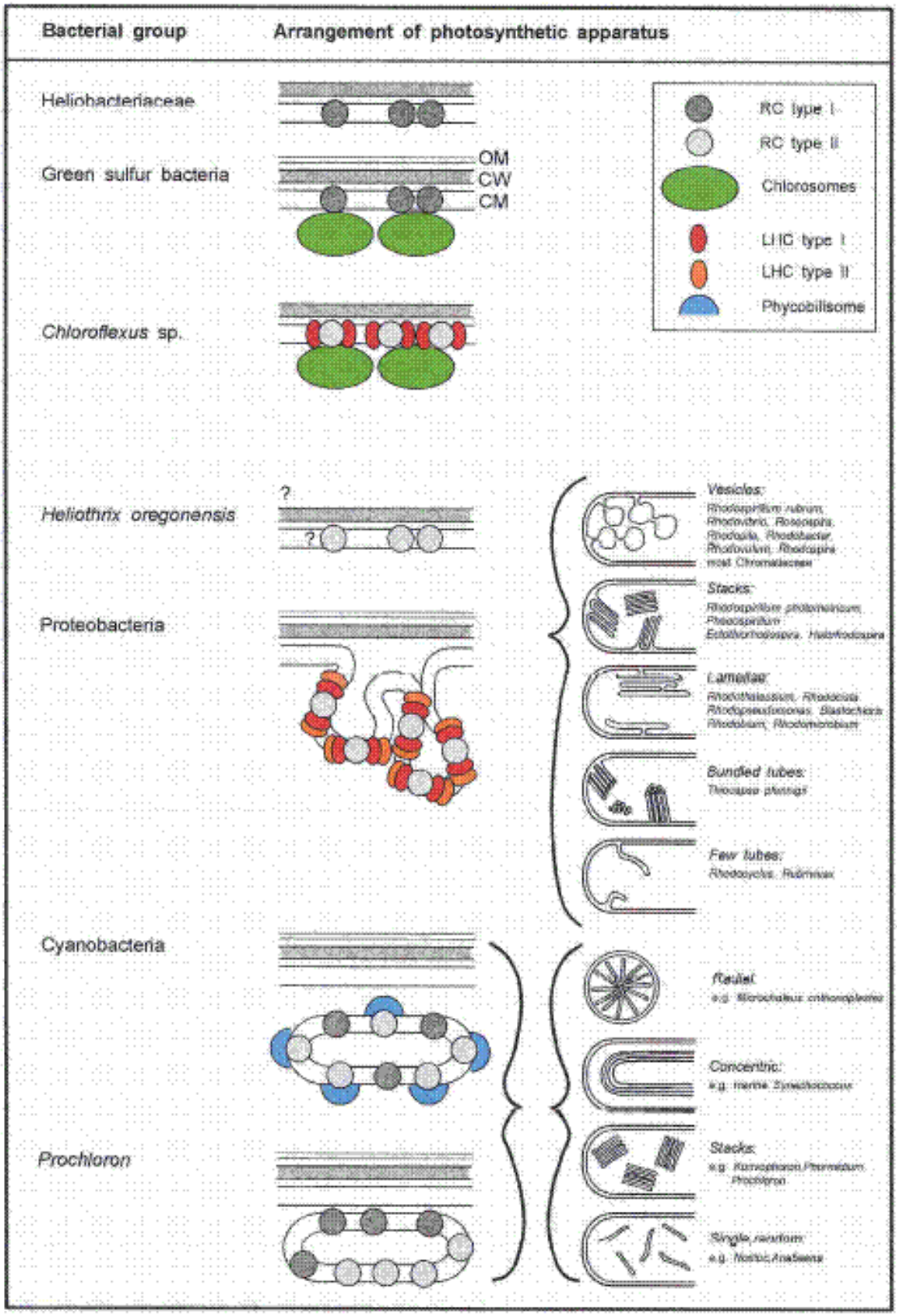
Fig. 1. Phylogenetic tree based on 16S rRNA sequences. All bacterial divisions containing culturable representatives were included in the analyses so that the phototrophic nature of the bacterial strains could be confirmed. Alignments were obtained with CLUSTAL W and pairwise distances calculated with the algorithm of Jukes and Cantor using the DNADIST program of PHYLIP 3.57c. The tree was constructed from evolutionary distances employing the least-squares algorithm of Fitch and Margoliash as implemented by the FITCH program of the package. The Archaeon *Methanopyrus kandleri* DSM 6324 was used as an outgroup to root the tree. (light green) Bacteria containing chlorosomes as light-harvesting antenna. (red) Bacteria containing antenna complexes within the cytoplasmic membrane and quinone/pheophytin-type reaction centers. (medium green) Gram-positive phototrophic bacteria with FeS-type reaction centers. (dark green) Bacteria containing the two types of reaction centers. Width o f colored wedges indicates the phylogenetic divergence.



Within the *Chloroflexus*-subgroup, three different species (*Chloroflexus aurantiacus*, *Chloroflexus aggregans* and *Heliothrix oregonensis*) of filamentous multicellular phototrophs have been described. All three are thermophilic and grow photoorganoheterotrophically. In addition four mesophilic species (*Oscillochloris chrysea*, *Oscillochloris trichoides*, *Chloronema giganteum*, *Chloronema spiroideum*) have been affiliated with the *Chloroflexus*-subgroup based on their multicellular filaments, gliding motility, and the presence of chlorosomes containing bacteriochlorophylls c or d (Pfennig and Trüper, 1989). The phylogenetic position of these latter bacteria has not been investigated so far. With the exception of *He liothrix oregonensis* all species mentioned contain chlorosomes as distinct light-harvesting structures (Fig. 2). Yet to be cultivated axenically, non-thermophilic "*Chloroflexus* -like" organisms are known from intertidal and hypersaline benthic environments (Pierson et al., 1994) and from cold freshwater sulfidic springs (F. Garcia-Pichel, unpublished observation). At least in the case of the hypersaline enrichments, the organisms are closely related to *Heliothrix* in terms of their 16S rRNA sequence (B.K. Pierson, personal communication to FGP). This, together with recent descriptions of *Oscillochloris trichoides* (Keppen et al., 1994) from freshwater sediments indicates a larger diversity and more widespread occurrence of the *Chloroflexaceae* and allied organisms than was previously recognized.

Fig. 2. Organization of the phototrophic apparatus in different groups of phototrophic bacteria. *OM* = outer membrane, *CW* = cell wall, *CM* = cytoplasmic membrane, *RC* = reaction center, *LHC* = light-

harvesting complex. Question marks indicate that the organization of the cell envelope and the organization of the photosynthetic apparatus in *Heliothrix oregonensis* is not exactly known.



Green sulfur bacteria (see The Family Chlorobiaceae) represent a coherent and isolated group within the domain Bacteria. They are strict photolithotrophs and contain chlorosomes (Fig. 3A). During the oxidation of sulfide, elemental sulfur is deposited extracellularly. Another typical feature

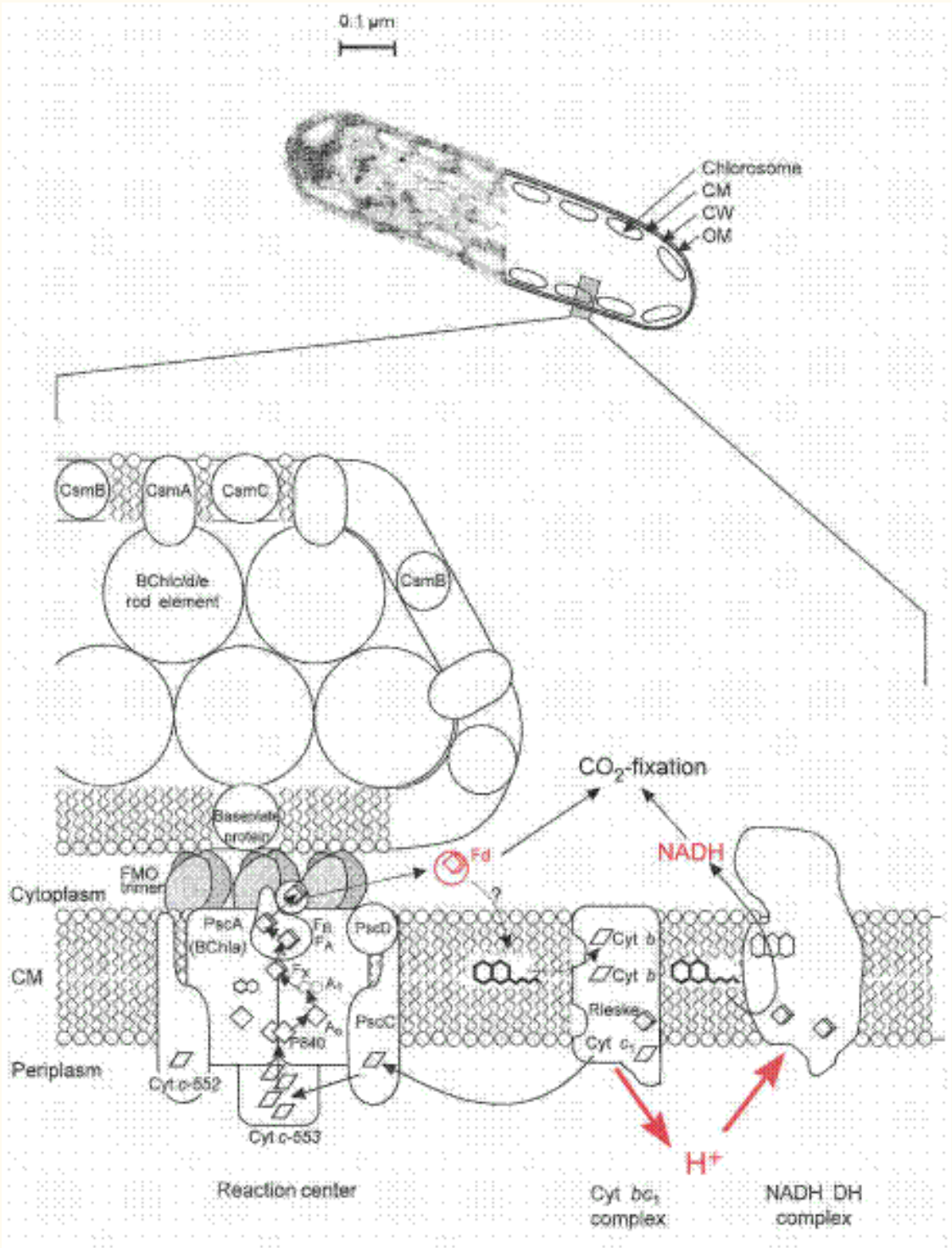
of this group is the very limited physiological flexibility (see Docile Reaction). In the *Proteobacteria*, the α- and β-Proteobacteria comprise photosynthetic representatives (often also called the purple nonsulfur bacteria), which do not form separate phylogenetic clusters but are highly intermixed with various other phenotypes. Characteristically, members of these two groups exhibit a high metabolic versatility and are capable of photoorganotrophic, photolithoautotrophic and chemoorganotrophic growth. Photosynthetic pigments are bacteriochlorophyll *a* or b and a variety of carotenoids. Light-harvesting complexes, reaction centers, and the component s of the electron transport chain are located in intracellular membrane systems of species-specific architecture (Fig. 2; see Light absorption and light energy transfer in prokaryotes).

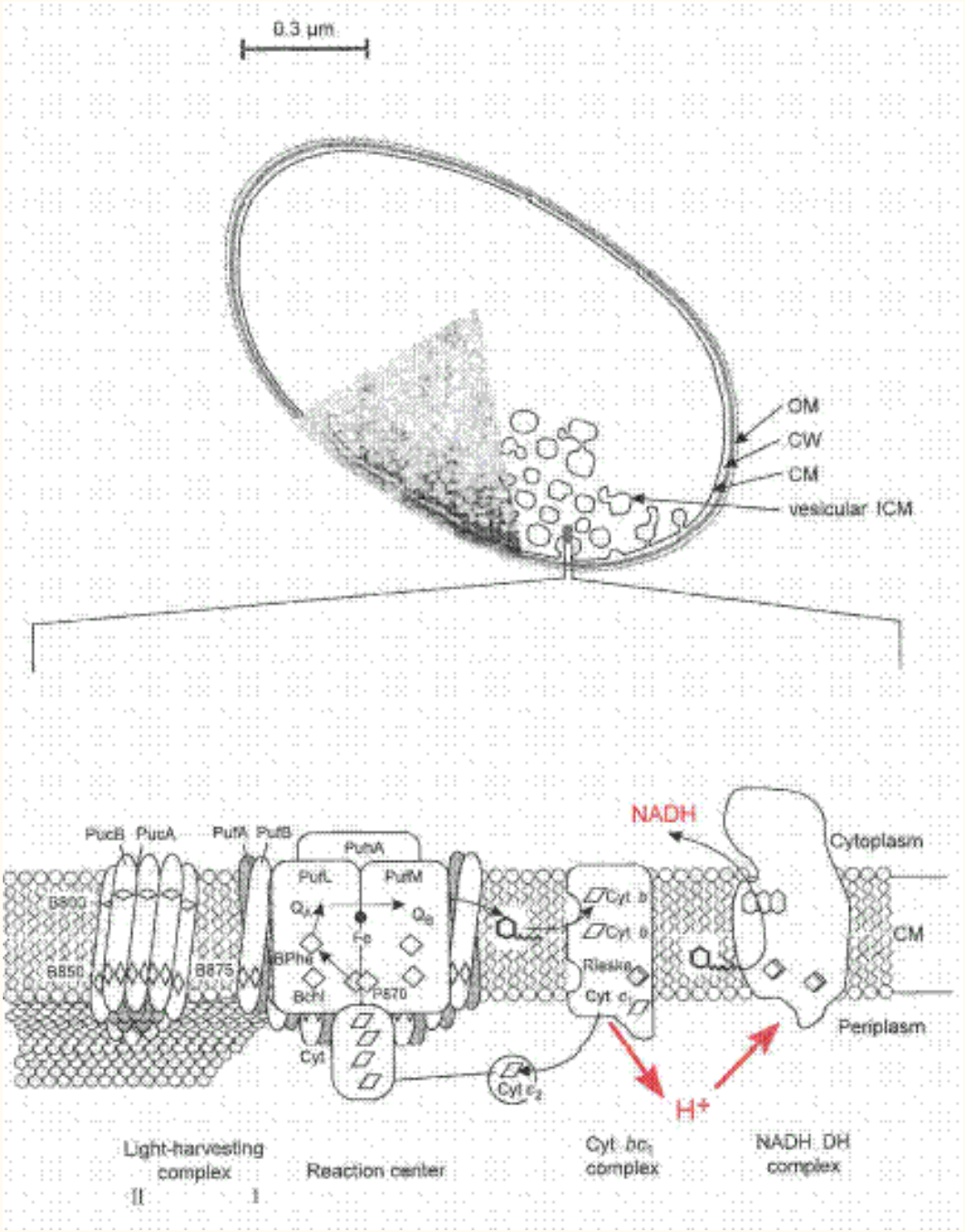
Several members of the α-Proteobacteria are capable of bacteriochlorophyll *a* synthesis but cannot grow by anoxygenic photosynthesis. This physiological group has therefore been designated 'aerobic anoxygenic phototrophic bacteria' (Shimada, 1995; Yurkov and Beatty, 1998), 'aerobic phototrophic bacteria' (Shiba, 1989), or 'quasi-photosynthetic bacteria' (Gest, 1993) and comprises a considerable number of species. So far, the marine genera *Erythrobacter* and *Roseobacter* and the six freshwater genera *Acidiphilium*, *Erythromonas*, *Erythromicrobium*, *Porphyrobacter*, *Roseococcus*, *Sandarcinobacter* (Yurkov and Beatty, 1998) have been described. This group also includes some aerobic facultatively methylotrophic bacteria of the genus *Methylobacterium* and a *Rhizobium* (strain BTAi1; Evans et al., 1990; Shimada, 1995; Urakami and Komagata, 1984). The oxidation of organic carbon compounds is the principal source of metabolic energy. Photophosphorylation can be used as a supplementary source of energy, with a transient enhancement of aerobic growth following a shift from dark to illumination (Harashima et al., 1978; Shiba and Harashima, 1986). Aerobic bacteriochlorophyll-containing bacteria harbor a photosynthetic apparatus very similar to photosystem II of anoxygenic phototrophic Proteobacteria (Yurkov and Beatty, 1998). Photochemically acti ve reaction centers and light-harvesting complexes are present, as are the components of cyclic electron transport (e.g., a cytochrome *c* bound to the reaction center and soluble cytochrome c_2). In contrast to anoxygenic phototrophic bacteria, however, the aerobic phototrophic bacteria cannot grow autotrophically. Intracellular photosynthetic membrane systems as they are typical for anoxygenic phototrophic *Proteobacteria* are absent in most aerobic photosynthetic bacteria; *Rhizobium* BTAi1 being a possible exception (Fleischman et al., 1995). The presence of highly polar carotenoid sulfates and C_{30} carotenoid glycosides is a unique property of this group. All aerobic bacteriochlorophyll *a*-containing species group with the α-subclass of the Proteobacteria, but are more closely related to aerobic non-bacteriochlorophyll-contain ing organisms than to anoxygenic phototrophs (Stackebrandt et al., 1996).

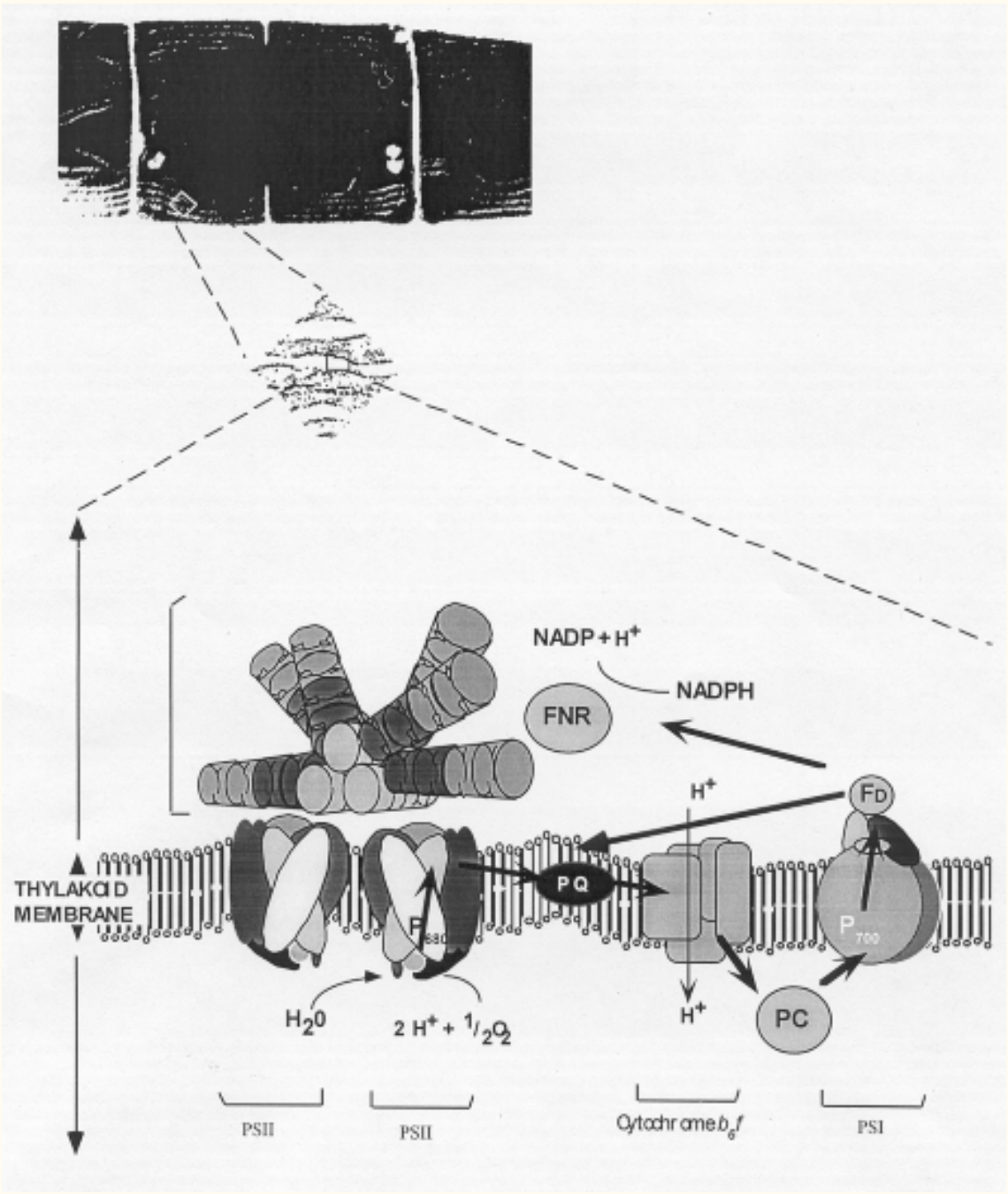
The γ-subclass comprises two families of phototrophic species, the *Chromatiaceae* and *Ectothiorhodospiraceae* (also called purple sulfur bacteria). *Chromatiaceae* accumulate sulfur globules within the cells and represent a conspicuous microscopic feature of these bacteria. With one notable exception (*Thiocapsa pfennigii*), the intracellular membrane system is of the vesicular type (Figs. 2 and 3B). In contrast, members of the *Ectothiorhodospiraceae* deposit elemental sulfur outside of the cells and contain lamellar intracellular membrane systems. Like their relatives of the α- and β-subclass of Proteobacteria, the purple sulfur bacteria contain bacteriochlorophylls *a* and *b*, and all components of the photosynthetic apparatus are located in the intracellular membrane.

Fig. 3. Localization and organization of the photosynthetic apparatus in three major groups of phototrophic bacteria. Electron-donating enzyme systems, like flavocytochrome or sulfide quinone reductase, and ATP formation by the membrane-bound ATP synthase are not shown. A. Green

sulfur bacteria (Chlorobiaceae). B. Purple nonsulfur bacteria and Chromatiaceae. C. Cyanobacteria. *OM* = outer membrane; *CW* = cell wall; *CM* = cytoplasmic membrane; *Cyt* = cytochrome; *P840* and *P870* reaction center special pair = primary electron donor; *B800, B850, B875* = bacteriochlorophyll molecules bound to light-harvesting complexes II and I; A_0 = primary electron acceptor in green sulfur bacteria = Chl *a*; A_1 = secondary electron acceptor in green sulfur bacteria = menaquinone; Q_A, Q_B = ubiquinone; F_X, F_A, F_B = FeS-clusters bound to the reaction center; *Fd* = ferredoxin; *FMO* = Fenna-Matthews-Olson protein, *FNR* = ferredoxin $NADP^+$ reductase; *PQ* = plastoquinone; *PC* = plastocyanin; *PS* = photosystem.




0.3 µm
OM
CW
CM
vesicular ICM
PucB PucA
PufA PufB
PufH
PufL
PufM
B800
B850
B875
BPhe
BcH
P870
Cyt
Cyt b
Cyt b
Rieske
Cyt c1
Cyt c2
NADH
Cytoplasm
CM
Periplasm
H+
Light-harvesting complex II
Reaction center
Cyt bc1 complex
NADH DH complex



No photosynthetic species have been described for the δ- or ε-subclass of the *Proteobacteria*.

Heliobacteriaceae differ from other anoxygenic phototrophic bacteria by their unique light-harvesting and reaction center pigment, bacteriochlorophyll g, and by their phylogenetic affiliation (Fig. 1). The first member of this group, *Heliobacterium chlorum* was described in 1983 by Gest and Favinger (Gest and Favinger, 1983b). Based on peptidoglycan structure studies (Beer-Romero et al., 1988), their high proportion of branched-chain fatty acids (Beck et al., 1990) and 16S rRNA sequencing, the *Heliobacteriaceae* belong to the Gram-positive low GC lineage. A close relatedness can also be deduced from the capability of *Heliobacterium modesticaldum* and *Heliobacterium gestii* to form endospores. However, a detailed phylogenetic analysis also indicated a close relatedness of *Heliobact eriaceae* to the *Cyanobacteria* (Vermaas, 1994). *Heliobacteriaceae* do not contain distinct intracellular structures of the photosynthetic apparatus and the reaction centers are located in the cytoplasmic membrane. Bacteriochlorophyll g confers to the cells a near infrared absorption maximum at 788 nm, which is unique among photosynthetic organisms. The known

species of *Heliobacteriaceae* all grow photoheterotrophically and are strict anaerobes.

Oxygenic photosynthesis is only found in members of a single bacterial lineage out of the five that contain phototrophs (Fig. 1). The *Cyanobacteria* by far comprise the largest number of isolated strains and described species (Table 1). The *Cyanobacteria* (= oxyphotobacteria) are defined by their ability to carry out oxygenic photosynthesis (water-oxidizing, oxygen-evolving, plant-like photosynthesis) based on the coordinated work of two photosystems (Fig. 3C). Phylogenetically, they constitute a coherent phylum that contains the plastids of all eukaryotic phototrophs. They all synthesize chlorophyll *a* as photosynthetic pigment, and most types contain phycobiliproteins as light-harvesting pigments. These multimeric proteinaceous structures are found on the cytoplasmic face of the intracellular thylakoid membranes and contain phycobilins as light-harvesting pigments. All *Cyanobacteria* are able to grow using CO_2 as the sole sou rce of carbon, which they fix using primarily the reductive pentose phosphate pathway (see Carbon metabolism of phototrophic prokaryotes). Their chemoorganotrophic potential typically is restricted to the mobilization of reserve polymers (mainly starch but also polyhydroxyalkanoates) during dark periods, although some strains are known to grow chemoorganotrophically in the dark at the expense of external sugars. Owing to their ecological role, in many cases indistinguishable from that of eukaryotic microalgae, the cyanobacteria had been studied originally by botanists. The epithets "blue-green algae", "Cyanophyceae", "Cyanophyta", "Myxophyceae", and "Schizophyceae" all apply to the cyanobacteria. Two main taxonomic treatments of the *Cyanobacteria* exist, and are widely used, which divide them into major groups (orders) on the basis of morphological and life-history traits. The botanical system (Geitler, 1932 recognized 3 orders, 145 genera and some 1300 spe cies, but it has recently been modernized (Anagnostidis and Komárek, 1989, Komárek and Anagnostidis, 1989). The bacteriological system (Stanier, 1977, Rippka et al., 1979; Castenholz, 1989), relies on the study of cultured axenic strains. It recognizes five larger groups or orders, separated on the basis of morphological characters. Genetic (i.e., mol% GC, DNA-DNA hybridization) as well as physiological traits have been used to separate genera in problematic cases.

Previously, a separate group of organisms with equal rank to the cyanobacteria, the so-called 'Prochlorophytes' (with two genera, *Prochloron*, a unicellular symbiont of marine invertebrates, and *Prochlorothrix*, a free-living filamentous form) had been recognized (Lewin, 1981). They were differentiated from cyanobacteria by their lack of phycobiliproteins (Fig. 2) and the presence of chlorophyll *b*. The recently recognized genus *Prochlorococcus* of marine picoplankters could be included here, even though the major chlorophylls in this genus are divinyl-Chl *a* and divinyl-Chl *b*. Fourteen *Prochloron* isolates from different localities and hosts have been found to belong to a single species by DNA-DNA hybridization studies (Stam et al., 1985; Holtin et al., 1990). Some of the original distinctions leading to the separation of the Chl *b*-containing oxyphotobacteria from the cyanobacteria are questionable, since at least in one strain of *Prochloroccoccus marinus*, functional phycoerythrin (Lokstein et al., 1999), and genes encoding for phycobiliproteins have been detected (Lokstein et al., 1999). Additionally, phylogenetic analysis of 16S rRNA genes indicate that the three genera of Chl *b*-containing prokaryotes arose independently from each other and from the main plastid line (see Evolutionary considerations), a result that is supported by the comparative sequence analysis of the respective Chl *a*/*b* binding proteins (Laroche et al., 1996; Vanders taay et al., 1998). Thus "Prochlorophytes" are just greenish cyanobacteria, and are not treated separately here. The recent discovery of Chl *d*-containing symbionts in ascidians (*Acaryochloris marina*, Miyashita et al., 1996) once again demonstrates the evolutionary diversification of light-harvesting capabilities among oxyphotobacteria (see Competition for light). While the phylogenetic affiliation of *Acaryochloris marina* has not been presented as yet, ultrastructural and chemotaxonomic characters predict that *A. marina* belongs to the cyanobacterial radiation as well.

According to phylogenetic analysis of 16S rRNA sequences, the *Cyanobacteria* are a diverse phylum of organisms within the bacterial radiation, well separated from their closest relatives (Giovanonni, 1988; Wilmotte, 1995; Turner, 1887; Garcia-Pichel, 1999; Fig. 1). These analyses support clearly the endosymbiotic theory for the origin of plant chloroplasts, as they place plastids (from all eukaryotic algae and higher plants investigated) in a diverse, but monophyletic, deep-branching cluster (Nelissen et al., 1995). Phylogenetic reconstructions show that the present taxonomic treatments of the cyanobacteria diverge considerably from a natural system that reflects their evolutionary relationships. For example, separation of the orders *Chroococcales* and *Oscillatoriales* (Nelissen et al., 1995; Reeves, 1996), and perhaps also the *Pleurocapsales* (Turner, 1887; Garcia-Pichel et al., 1998) is not supported by phylogenetic analysis. The heterocystous cyanobacteria (comprising the two orders *Nostocales* and *Stigonematales*) form together a monophyletic group, with relatively low sequence divergence, as low as that presented by the single accepted genus *Spirulina* (Nübel, 1999). A grouping not corresponding to any official genus, the *Halothece* cluster, gathers unicellular strains of diverse morphology that are extremely tolerant to high salt and stem from hypersaline environments (Garcia-Pichel et al., 1998). A second grouping, bringing together very small unicellular ope n-ocean cyanobacteria (picoplankton) includes only marine picoplanktonic members of the genera *Synechococcus* and all *Prochlorococcus*. Several other statistically well-supported groups of strains that may or may not correspond to presently defined taxa can be distinguished,. The botanical genus "*Microcystis*" of unicellular colonial freshwater plankton species is very well supported by phylogenetic reconstruction, as is the genus *Trichodesmium* of filamentous, nonheterocystous nitrogen-fixing species typical from oligotrophic marine plankton of the tropics. The picture that emerges from these studies is that sufficient knowledge of ecological and physiological characteristics can lead to a taxonomic system that is largely congruent to the 16S rRNA phylogeny.

A different principle of conversion of light energy into chemical energy is found in the Halobacteria. These archaea are largely confined to surface layers of hypersaline aquatic environments and grow predominantly by chemoorganoheterotrophy with amino or organic acids as electron donors and carbon substrates, generating ATP by respiration of molecular oxygen. In the absence of oxygen, several members are capable of fermentation or nitrate respiration. At limiting concentrations of oxygen, at least three of the described species of Halobacteria (*Halobacterium halobium*, *H. salinarium*, *H. sodomense*) synthesize bacteriorhodopsin (Oesterhelt and Stoeckenius, 1973), a chromoprotein containing a covalently bound retinal. Bacteriorhodopsin is incorporated in discrete patches in the cytoplasmic membrane ("purple membrane"). However, these prokaryotes have only a very limite d capability of light-dependent growth. Only slow growth and one to two cell doublings could be demonstrated experimentally (Hartmann et al., 1980; Oesterhelt and Krippahl, 1983). The fact that rhodopsin-based photosynthesis has been found only in the phylogenetically tight group of Halobacteria may indicate that, because of its lower efficiency, this type of light utilization is of selective advantage only under specific (and extreme) environmental conditions. Further information on the biochemistry, physiology and ecology of this group may be found in the chapters, *Introduction to the Classification of Archaea* and *The Family Halobacteriaceae*.

Table 1. Groups of photosynthetic prokaryotes and their characteristics.

Taxon		Preferred growth mode	Light harvesting	Photochemical reaction
Chloroflexus-subdivision	(3)[a]	Anoxygenic photoorganoheterotroph(cls); BChl *c*, car		Type II reaction center
		Aerobic chemoorganoheterotroph	–	–
Green sulfur bacteria	(15)	Anoxygenic photolithoautotroph	cls; BChl *c*/*d*/*e*, car	Type I reaction center
α-Proteobacteria	(31)	Anoxygenic photoorganoheterotroph	icm; BChl *a*/*b*,car	Type II reaction center
		Aerobic chemoorganoheterotroph	–	–
α-Proteobacteria (aerobic photosynthetic)	(23)	Aerobic chemoorganoheterotroph	BChl *a*	Type II reaction center
β-Proteobacteria	(4)	Anoxygenic photoorganoheterotroph	icm; BChl *a*, car	Type II reaction center
		Aerobic chemoorganoheterotroph	–	–
Chromatiaceae	(31)	Anoxygenic photolithoautotroph	icm; BChl *a*/*b*, car	Type II reaction center
Ectothiorhodospiraceae	(9)			
Heliobacteriaceae	(5)	Anoxygenic photoorganoheterotroph	BChl *g*, car	Type I reaction center
Cyanobacteria	(>>1000)	Oxygenic photolithoautotroph	thy;Chl *a* + PBS or Chl *b*, or Chl *d*; car	Type I + II reaction center
Prochloron, Prochlorothrix	(2)		thy;Chl *a*/*b*, car	
Prochlorococcus	(1)		thy;Chl a_2/b_2, car (PBS)	
Acaryochloris	(1)		thy;Chl*a*,*d*, car (PBS)	
Halobacteria	(3)	Aerobic chemoorganoheterotroph	Purple membrane; bacteriorhodopsin	Bacteriorhodopsin

[a]The numbers of photosynthetic species described for each taxon are given in parenthesis.

BChl = bacteriochlorophyll, car = carotenoids, Chl = chlorophyll, cls = chlorosomes, icm = intracellular membranes, PBS = phycobilisomes, thy = thylacoids

During the past years, culture-independent 16S rDNA-based methods have been used for the investigation of the composition of natural communities of phototrophic prokaryotes. These studies have provided evidence that more than one genotype of *Chloroflexus* occur in one hot spring microbial mat and that four previously unkown sequences of cyanobacteria dominate in the same

environment (Ferris et al., 1996; Ruff-Roberts et al., 1994; Weller et al., 1992). Similarly, nine different partial 16S rDNA sequences of *Chromatiaceae* and green sulfur bacteria, which differed from all sequences previously known, were retrieved from two lakes and one intertidal marine sediment (Coolen and Overmann, 1998; Overmann et al., 1999a).

However, 16S RNA signatures from natural populations were indistinguishable from those of cultured strains in the case of cyanobacteria with conspicuous morphologies, such as the cosmopolitan *Microcoleus chthonoplastes* (Garcia-Pichel et al., 1996) from intertidal and hypersaline microbial mats or *Microcoleus vaginatus* from desert soils (F. Garcia-Pichel, C. López-Cortés and U. Nübel, unpublished observations). In a similar manner, the 16S rRNA sequence of an isolated strain of *Amoebobacter purpureus* (*Chromatiaceae*) was found to be identical to the environmental sequence dominating in the chemocline of a meromictic salt lake (Coolen and Overmann, 1998; Overmann et al., 1999a). Obviously, the limited number of isolated and characterized bacterial strains rather than an alleg ed 'nonculturability,' at least in some cases, accounts for our inability to assign ecophysiological properties to certain 16S rRNA sequence types. This point is illustrated for extremely halotolerant unicellular cyanobacteria by the fact that only after a physiologically coherent group of strains was defined on the basis of newly characterized isolates (Garcia-Pichel et al., 1998) could the molecular signatures retrieved from field samples be assigned correctly.

It has to be concluded that 1) the numbers of species listed in Table 1 do not reflect the full phylogenetic breadth at least in the four groups of anoxygenic phototrophic prokaryotes as well as in morphologically simple *Cyanobacteria*, and 2) that the physiology and ecology of those species of phototrophic prokaryotes that are dominant in the natural environment in some cases may differ considerably from known type strains.

Habitats of Phototrophic Prokaryotes

Bacteria of the *Chloroflexus*-subgroup form dense microbial mats in geothermal springs, often in close association with cyanobacteria. *Chloroflexus aurantiacus* is a thermophilic bacterium which grows optimally between 52 and 60°C and thrives in neutral to alkaline hot springs up to 70–72°C. Of all anoxygenic phototrophic bacteria isolated so far, only *Chloroflexus aurantiacus* is capable of growth up to 74°C. In contrast to the domain Archaea, no hyperthermophilic species are known from the domain Bacteria. The phylogenetically related *Heliothrix oregonensis* grows optimally between 50 and 55°C and is abundant as a flocculant surface layer in a few alkaline springs in Oregon. Hydrothermal springs of 56–66°C, which contain sulfide of geothermal origin, are dominated by a surface layer or a 'unispecific' mat of *Chloroflexus* (Castenholz and Pierson, 1995). Because of the absence of cyanobacteria in some of these systems, *Chloroflexus* presumably grows autotrophically (Pierson and Castenholz, 1995). In the presence of O_2, the mats exhibit an orange color whereas they are green under anoxic conditions (Castenholz and Pierson, 1995). The orange color is the result of the enhanced carotenoid biosynthesis under oxic conditions (see Chemotrophic growth with O_2). In the absence of sulfide, *Chloroflexus* is present as a distinct orange layer beneath a surface layer of cyanobacteria and may utilize their exudates or the fermentation products generated during decomposition of cyanobacteria. Molecular oxygen represses bacteriochlorophyll synthesis in *Chloroflexus* and often is present at saturation levels in the orange layers. Since bacteriochlorop hylls a and c are still present in this layer, however, it must be assumed that bacteriochlorophylls are synthesized at anoxic conditions during nightime (Castenholz and Pierson, 1995).

Green and purple sulfur bacteria often form conspicuous blooms in non-thermal aquatic ecosystems (Figs. 4, 5A, 5B), although moderately thermophilic members of the genera *Chromatium* and *Chlorobium* have been described from hot spring mats (Castenholz et al., 1990). *Chlorobium tepidum* occurs in only a few New Zealand hot springs at pH values of 4.3 and 6.2 and temperatures up to 56°C. *Chromatium tepidum* was found in several hot springs of western North America at temperatures up to 58°C and might represent the most thermophilic proteobacterium (Castenholz and Pierson, 1995). In a recent compilation (van Gemerden and Mas, 1995), 63 different lakes and 7 sediment ecosystems harboring phototrophic sulfur bacteria were listed. Cell densities between 10^4 and $10^7 \cdot ml^{-1}$ and biomass concentrations between 10 and 1000 µg bacteriochlorophyll$\cdot l^{-1}$ are common in pelagic habitats. Of the purple sulfur bacteria, *Chromatiaceae* are typically found in freshwater and marine environments (Fig. 5A, B) whereas *Ectothiorhodospiraceae* inhabit hypersaline waters. The phototrophic sulfur bacteria grow preferentially by photolithoautotrophic oxidation of reduced sulfur compounds and are therefore limited to those environments where light reaches anoxic, sulfide-containing bottom layers. Because light and sulfide occur in opposing gradients, growth of phototrophic sulfur bacteria is confined to a narrow zone of overlap and is only possible if the chemical gradient of sulfide is stabilized against vertical mixing. In pelagic environments like lakes or lagoons, chemical gradients are stabilized by density differences between the oxic and anoxic water layers. Such density differences are either the result of thermal s tratification and mostly transient (as in holomictic lakes) or are caused by high salt concentrations of the bottom water layers, in which case stratification is permanent (meromictic lakes). Pelagic layers of phototrophic sulfur bacteria extend over a vertical distance of 10 cm (van Gemerden and Mas, 1995; Overmann et al., 1991a) up to 30 m (Repeta et al., 1989) and reach biomass concentrations of 28 mg bacteriochlorophyll$\cdot l^{-1}$ (Overmann et al., 1994).

Fig. 4. Bright field photomicrograph of the bacterioplankton community thriving in the chemocline of the meromictic Buchensee (near Radolfzell, Germany) during autumn. The dominant anoxygenic phototroph at this time of the year is the green sulfur bacterium *Pelodictyon phaeoclathratiforme* (brown cells, which appear in chains or netlike colonies). In addition, phototrophic consortia ('*Pelochromatium roseum*,' one consortium in the center) are found. Similar to *Pld. phaeoclathratiforme*, most of the colorless bacterial cells found in the chemocline contain gas vesicles as is evident from their highly refractile appearance in the bright field.

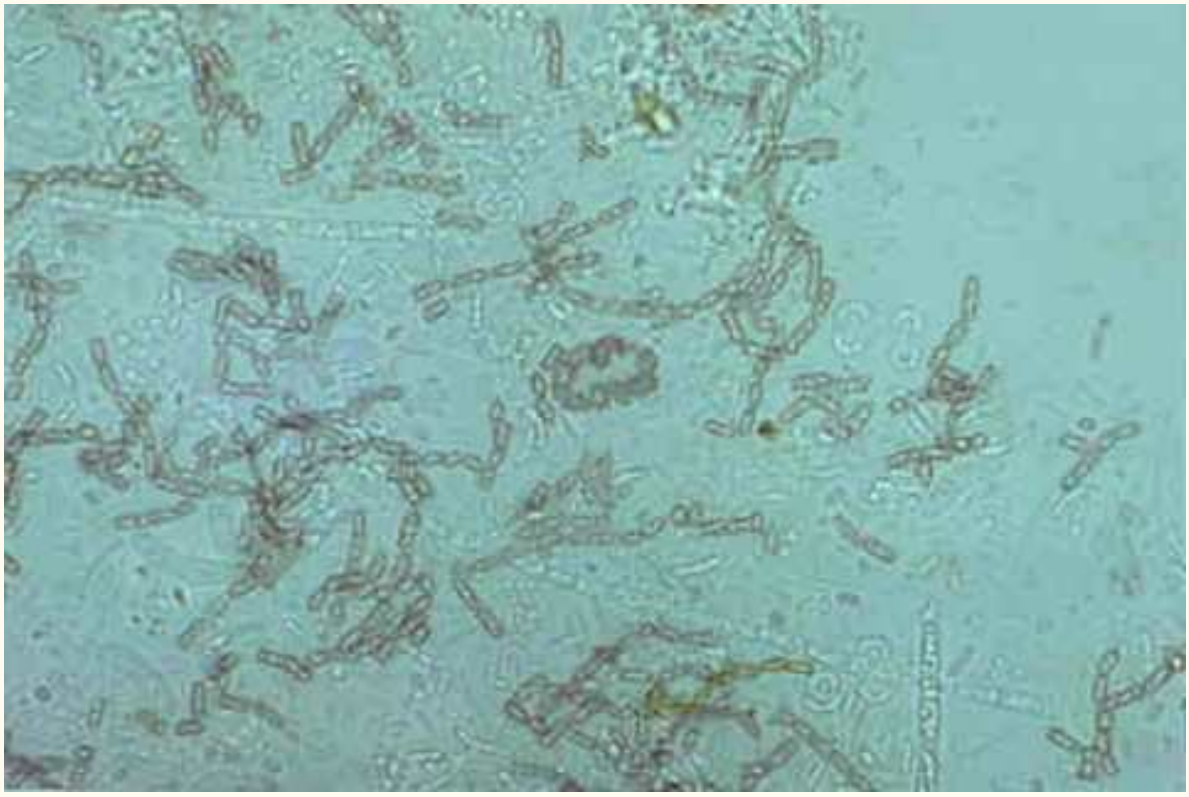
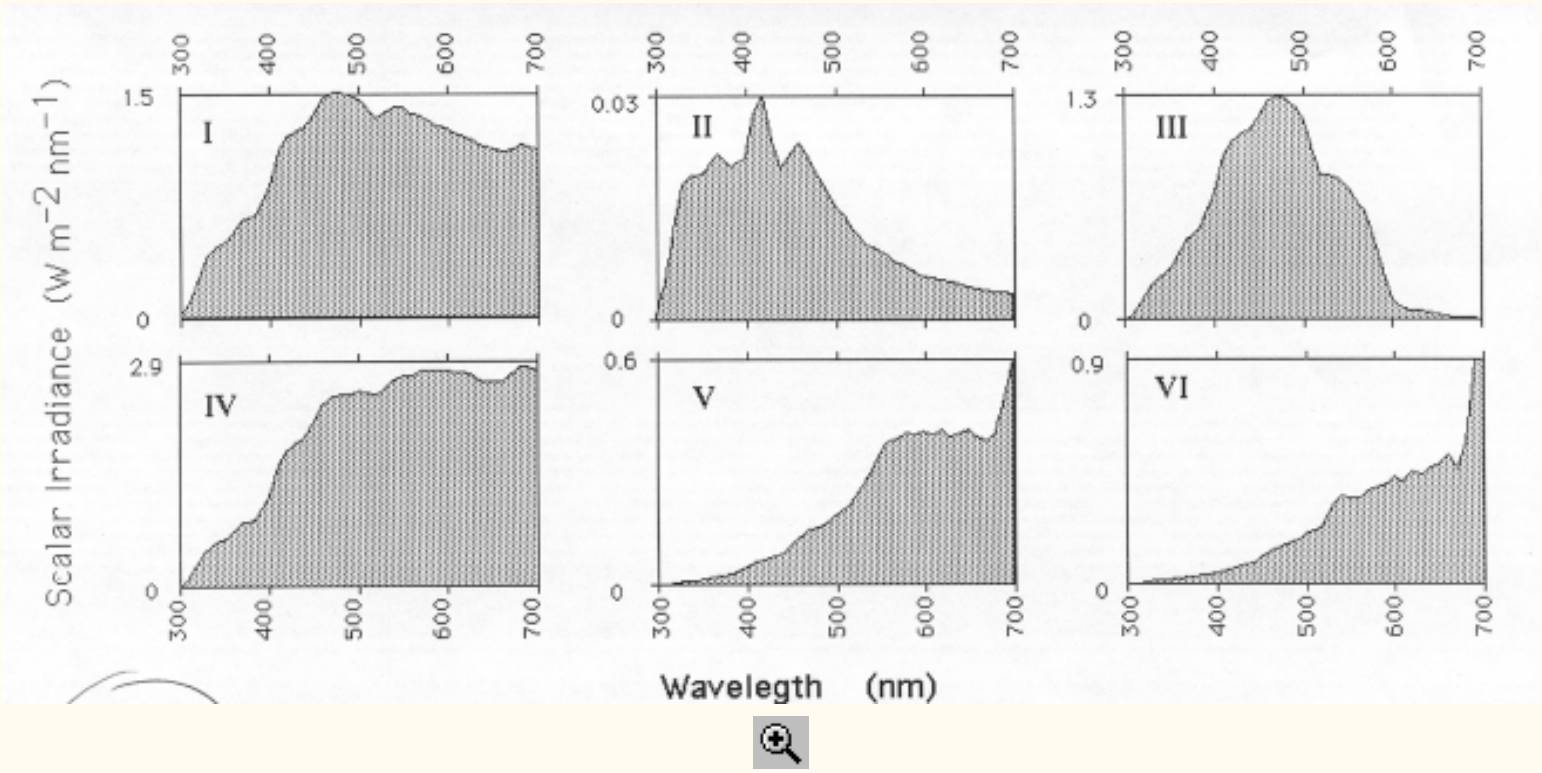


Fig. 5. Multilayered microbial mat as it is regularly found in the sandflats of Great Sippewissett Salt Marsh (Cape Cod, Massachusetts, USA). A. In most instances, the mats consist of a top green layer, an intermediate purple layer, and a grayish to blackish bottom layer. B. Fully developed microbial mats consist (from top) of an olive-green layer of diatoms and cyanobacteria, a green layer consisting mostly of cyanobacteria, a purple layer of purple sulfur bacteria, a peach-colored layer formed by BChl *b*-containing purple sulfur bacteria (morphologically similar to *Thiocapsa pfennigii*), and a greyish to blackish bottom layer.


1
2
3
4
5

Littoral sediments represent the second type of habitat of phototrophic sulfur bacteria. In these systems, turbulent mixing is largely prevented by the sediment matrix, and diffusion is the only means of mass transport. Gradients of light and sulfide are much steeper, and the fluxes of sulfide much larger compared to the pelagic environment. These conditions allow layers of phototrophic sulfur bacteria in sediments to reach much higher biomass densities (up to 900 mg bacteriochlorophyll·dm^{-3}; van Gemerden et al., 1989) than in lakes. At the same time, the layers are very narrow (1.3–5 mm; van Gemerden and Mas, 1995; Fig. 5A). This vertical distribution of anoxygenic phototrophic biomass ultimately determines the significance of microbial sulfide oxidation for the sulfur cycle in these ecosystems (see Significance of anoxygenic photosynthesis for the pelagic carbon and sulfur cycles). The spectral compos ition of light available for anoxygenic photosynthesis is considerably different between pelagic and benthic habitats (Fig. 6) and selects for different species of anoxygenic phototrophic bacteria. Whereas light of the blue to yellow-green wavelength bands dominates the depths of most lakes, infrared light is an important source of energy in benthic microbial mats (see Light energy and the spectral distribution of radiation).

Fig. 6. Effects of the habitat on the physical exposure of cyanobacteria. The spectral scalar irradiance (sun and sky radiation) incident at ground level at noon in a clear midsummer day at 41° N is plotted in Plate I. The rest of the plates depict the in situ scalar irradiance experienced by cyanobacterial cells thriving in several habitats exposed to the incident fluxes in plate I (note different scales). Plate II: a "strong shade" habitat (North-facing surface illuminated by extremely diffuse sky radiation only), where scalar irradiance is very low but the relative importance of UV is enhanced. Plate III: a planktonic habitat (under 1 m of clear open-ocean water), where all fluxes remain fairly high and UVB and visible are more strongly attenuated than UVA. Plate IV: the surface of beach (quartz, feldspar) sand, where all UVB, UVA, and visible are higher than incident (by 120, 150, and 205%, respectively) due to light trapping effects. Plate V: 300-µm deep in a wet topsoil, where UVB and U VA have been attenuated below 5% of incident but ca. 20% of the visible light remains. Plate VI: scalar irradiance within the thallus of the terrestrial cyanobacterial lichen *Collema* sp. Modified from Castenholz and Garcia-Pichel, 1999, after data from the following sources: F. Garcia-Pichel (unpublished observation); Garcia-Pichel, 1995; Büdel et al., 1997; and Smith and Baker, 1981.



The dominance of certain species of green sulfur bacteria (Fig. 4) or *Chromatiaceae* in pelagic environments in many cases can be explained by their specific light-harvesting capabilities (see Light absorption and light energy transfer in prokaryotes and Competition for light) and other phenotypic traits. Typically, those species that have been isolated from natural blooms in lakes are obligately photolithotrophic, lack assimilatory sulfate reduction, cannot reduce nitrate, and assimilate only few organic carbon sources (see Carbon metabolism of phototrophic prokaryotes). This applies not only to all green sulfur bacteria but also to the dominant species of *Chromatiaceae*. Obviously, in the chemocline of lakes the metabolic versatile *Chromatiaceae* species have no selective advantage. As judged from the physiological characteristics of strains of phototrophic sulfur bacteria isolated from sediments, the pronounced diurnal variations in oxygen concentrations and salinity, together with the different light quality, select for different species composition in benthic microbial mats. The purple sulfur bacterium *Chromatium* (and the multicellular gliding colorless sulfur bacterium *Beggiatoa*) are found in many microbial mats and exhibit diurnal vertical migrations in response to the recurrent changes in environmental conditions (Jørgensen, 1982; Jørgensen and Des Marais, 1986). Microbial mats of intertidal sediments are typically colonized by

the immotile purple sulfur bacterium *Thiocapsa roseopersicina* and small motile thiobacilli (van den Ende et al., 1996).

In contrast to the phototrophic members of the γ-Proteobacteria, purple nonsulfur bacteria of the α- and β-subclasses of *Proteobacteria* do not appear to form dense accumulations under natural conditions (Biebl and Drews, 1969; Swoager and Lindstrom, 1971; Steenbergen and Korthals, 1982). However, purple nonsulfur bacteria can be readily isolated from a wide variety of marine, lacustrine and even terrestrial environments (Imhoff and Trüper, 1989; J. Overmann, unpublished observation). While comprehensive comparative quantitation of the ecological importance of purple nonsulfur bacteria is still lacking, as many as ca. 10^6 c.f.u. of purple nonsulfur bacteria could be cultivated per cm^3 of sediment in coastal eutrophic settings (Guyoneaud et al., 1996).

Generally, aerobic phototrophic bacteria thrive in eutrophic marine environments. Obligately aerobic bacteria containing bacteriochlorophyll *a* have been isolated from beach sand and seaweeds (thalli of *Enteromorpha linza* and *Sargassum horneri*; Shiba et al., 1979), and in some cases also from freshwater ponds and microbial mats. At least some of the aerobic phototrophic bacteria apparently can survive in situ temperatures of up to 54°C (Yurkov and Beatty, 1998). Aerobic phototrophic bacteria were isolated from hydrothermal plume water of a black smoker 2000 m below ocean surface (Yurkov and Beatty, 1998); acidophilic strains could be isolated from acidic mine drainage. Typically, *Methylobacterium* species are isolated from foods, soils and leaf surfaces (Shimada, 19 95). Photosynthetic *Rhizobium* strains are widely distributed in nitrogen-fixing stem nodules of the tropical legume *Aeschynomene* spp. where they are present as symbiosomes. Similar strains have also been found in root and hypocotyl nodules of *Lotononis bainesii* (Fabaceae). These photosynthetic rhizobial and regular symbiosomes differ in that the former contains only one large spherical bacteroid. The photosynthesis of these endosymbionts may provide energy for nitrogen fixation and permit a more efficient growth of the host plant, since up to half of the photosynthate produced by legumes is allocated to nitrogen fixation (Fleischman et al., 1995).

Heliobacteriaceae appear to be primarily soil bacteria and have been isolated from dry paddy fields or other soils throughout the world (Madigan and Ormerod, 1995). Bacteria of this family may even represent the dominant anoxygenic phototrophic bacteria in soil (Madigan, 1992). Occasionally, strains also have been isolated from lakeshore muds and hot springs (Amesz, 1995; Madigan and Ormerod, 1995). *Heliobacterium modesticaldum* grows up to 56°C (Kimble et al., 1995). Spore formation may offer a selective advantage to *Heliobacterium modesticaldum*, *Heliophilum fasciatum*, and *Heliobacterium gestii* in their main habitat (rice field soil), which undergoes periodic drying and concomitantly becomes oxidized (Madigan, 1992). During growth of the rice plants, organic compounds excreted by their roots could provide sufficient substrates for photoheterotrophic growth of the *Heliobacteriaceae*.

Cyanobacteria as a group exhibit the widest range of habitats of all phototrophic prokaryotes due to the ubiquity of water, their preferred electron donor for the reduction of CO_2. In principle, cyanobacteria can thrive in any environment that has, at least temporarily, liquid water and sunlight. They are known from Antarctic endolithic habitats and from hot springs. More than 20 species of cyanobacteria (Castenholz and Pierson, 1995) are thermophilic. Effectively, however, no cyanobacteria are known from acidic environments (below pH 4.5) and competition with eukaryotic microalgae or higher plants may restrict their growth in other environments. Cyanobacteria are found in the plankton of coastal and open oceans and in freshwater and saline inland lakes. They thrive in the benthos of marine intertidal (Fig. 5B), lacustrine and fluvial waters and in a large

variety of terrestrial habitats (soils, rocks, trees). Symbiotic associations are common.

In the marine plankton, the phycoerythrin-containing *Synechococcus* often represents a major fraction of all primary producers. The same holds true for *Prochlorococcus* (Campbell and Vaulot, 1993; Chisholm et al., 1988; Olson et al., 1990b). Compared with the high number of cyanobacterial species found in freshwater plankton, intertidal areas, and hypersaline environments, the diversity of this group is very limited in the open ocean (Carr and Mann, 1994). The predominant group invariably consists of small (<2 µm) mostly nonmotile, non-nitrogen-fixing single cells assigned to the genus *Synechococcus*, which is found in the photic zone of all oceans except in the coldest areas. As a characteristic feature, the cells contain phycoerythrin as accessory photopigment which confers an orange autofluorescence on the cells. Despite their similar phenotype, marine *Synechococcus* strains are genetically heterogenous (Waterbury et al., 1986). An important component of the phytoplankton in tropical and subtropical oceans are the filamentous *Trichodesmium* spp. (Carr and Mann, 1994). The bundle and aggregate forming *Trichodesmium* typically develop into blooms that can extend kilometers long and are detected on the surface of oligotrophic tropical and subtropical oceans with the naked eye or with satellite imagery from space. The success of *Trichodesmium* can be mainly traced to the highly efficient nitrogen-fixing capacity of these nonheterocystous cyanobacteria. Their activities attain global magnitude for the nitrogen cycle (Capone et al., 1977). Heterocystous, nitrogen-fixing cyanob acteria of the genera *Nodularia*, *Anabaena*, and *Aphanizomenon* bloom in mesotrophic and eutrophic fresh and brackish waters. Together with the blooms of the nonheterocystous genus *Microcystis*, these cyanobacteria have become a real environmental concern, not only because of their effects of overall water quality but also because of their ability to produce toxins, which are known to have caused the deaths of humans and cattle. In the chemocline of stratified lakes, deep blooms of cyanobacteria occur frequently.

Edaphic cyanobacteria are also distributed worldwide, especially in soils of basic pH; sheathed oscillatorian forms (*Microcoleus vaginatus*, *"Schizothrix"* spp.), along with heterocystous ones (*Nostoc*, *Scytonema*) are of major ecological relevance in arid and semiarid regions where growth of higher plants is restricted. In such environments, cyanobacteria adopt a life strategy of resistance to desiccation (Potts, 1994) making use of the few occasions in which liquid water is available from rain or dew. Very intense productivity spurts occur in a matter of minutes after wetting (Garcia-Pichel and Belnap, 1996). The so-called 'cyanobacterial desert crusts' contribute significantly to the biogeochemistry and to the physical stability of arid soils. Other important terrestrial habitats of cyanobacteria are the surface or subsurfa ce of rocks: extensive endolithic cyanobacterial communities, usually dominated by members of the genus *Chroococcidiopsis*, have been described from tropical, desert and polar environments (Friedmann, 1982, Wessels and Büdel, 1995).

In the course of evolution, cyanobacteria have entered into symbiotic associations with a multitude of organisms. These have reached a wide range in the degree of interdependence between partners (see Symbiosis between phototrophic bacteria and eukaryotes).

Principles and Prerequisites of Photosynthesis

Bacterial photosynthesis can be divided into two different types of reactions 1) the light reaction, in which light energy is trapped and converted into ATP (via a proton-motive force ΔP) and a reduced redox carrier $R_{red} \cdot H^+$, and 2) the so-called dark reaction of biosynthetic carbon reduction.

Light reaction: $2\ H_2A + 2\ R_{ox} + light \rightarrow 2\ A + 2\ R_{red}{\cdot}H + \Delta P$

$ADP + P_I + \Delta P \rightarrow ATP + H_2O$

Dark reaction: $CO_2 + ATP + 2\ R_{red}{\cdot}H + H_2O \rightarrow <CH_2O> + ADP + Pi + 2\ R_{ox}$

Sum: $CO_2 + 2\ H_2A \rightarrow <CH_2O> + H_2O + 2\ A$

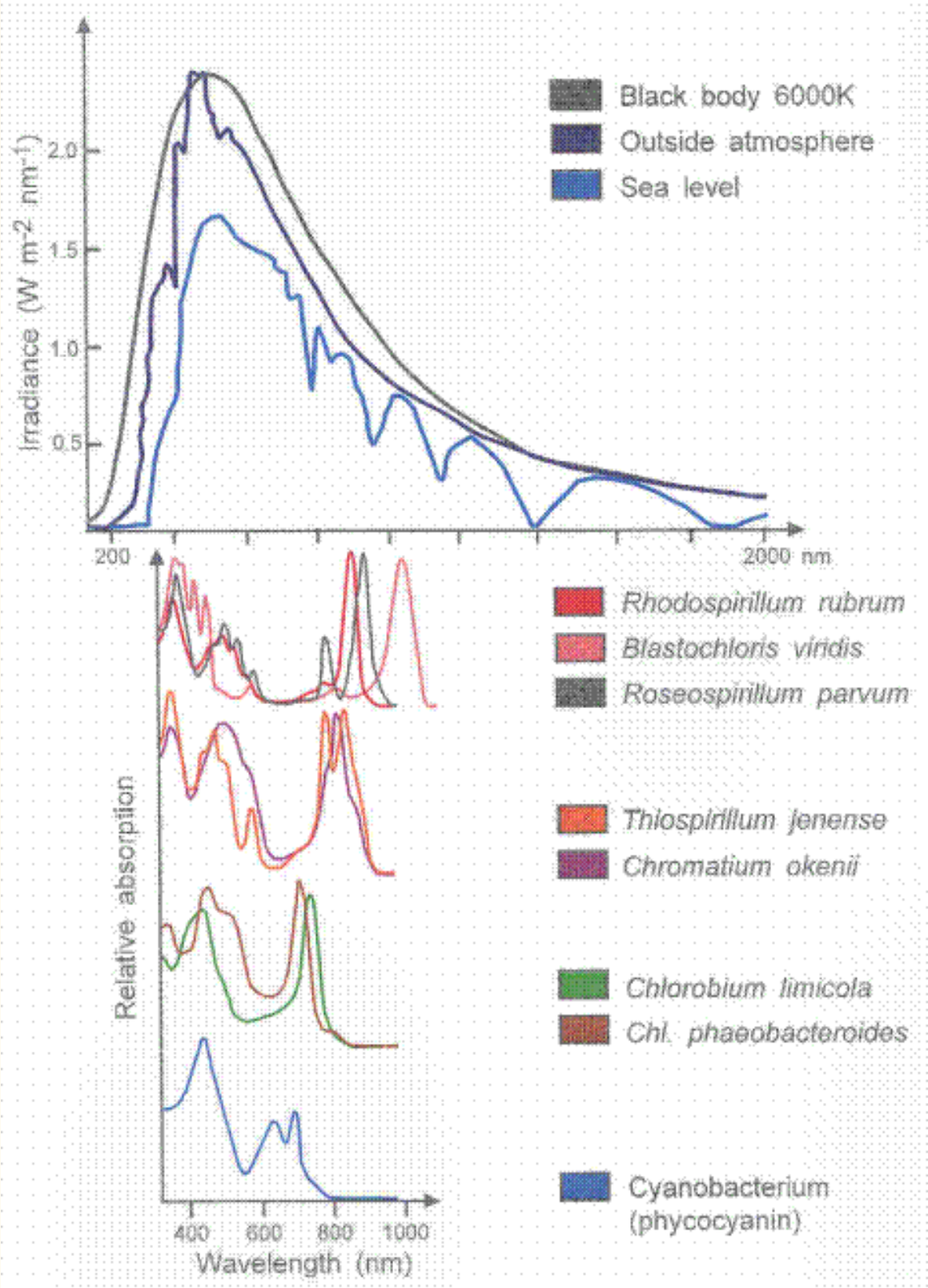
(van Niel equation)

Microorganisms have found different ways to accomplish these two tasks.

Light Energy and the Spectral Distribution of Radiation

The present day solar irradiance at the average distance of Earth to the sun and outside the atmosphere (the so-called *solar constant*) is 1353·W m^{-2} (Kirk, 1983). The spectral energy distribution of this solar radiation approximates that of a black body at 6000°K (the surface temperature of the sun). According to Wien's Law, a black body at this temperature has a maximum emission of electromagnetic energy at about 480 nm. The actual spectral energy distribution of solar radiation exhibits minima which reflect the absorption bands of hydrogen in the outer atmosphere of the sun (Fig. 7). The total light energy received by the Earth is $5.46{\cdot}10^{24}$ J·$year^{-1}$, which would correspond to 339.4 W· m^{-2}. The actual solar (time and space-averaged) irradiance reaching the surface of the Earth amounts only to 160 W·m^{-2} (Gates, 1962; Dietrich et al., 1975). This large reduction is due to Raleigh scattering by air molecules and dust particles, and of light absorption by water vapor, O_2, O_3 and CO_2 during the passage of radiation through the Earth's atmosphere. Concomitantly, the spectral distribution of solar irradiance is changed especially because water vapor absorbs infrared light (Fig. 7). At sea level, light of the wavelength regions 400–700 nm (PAR, photosynthetically available radiation) constitutes 50% of this irradiance (Kirk, 1983).

Fig. 7. Spectral energy distribution of solar radiation outside the atmosphere and at sea level as compared to the absorption spectra of various phototrophic bacteria. Absorption spectra of the purple nonsulfur bacterium *Rhodospirillum rubrum* (containing BChl *a*, spirilloxanthin), *Blastochloris viridis* (BChl *b*, 1,2-dihydroneurosporene), and *Roseospirillum parvum* (BChl *a*, spirilloxanthin, lycopenal), of the Chromatiaceae species *Thiospirillum jenense* (BChl *a*,lycopene, rhodopin) and *Chromatium okenii* (BChl *a*, okenone), of the Chlorobiaceae species *Chlorobium limicola* (BChl *c*, chlorobactene) and *Chlorobium phaeobacteroides* (BChl *e*, i sorenieratene) and of a cyanobacterium (Chl *a*, phycocyanin) are depicted.



Based on estimates for global primary productivity, only 0.13 % of the flux of solar energy reaching the surface of the Earth is converted into chemical energy by photosynthesis (Odum, 1983; see Introduction). Under natural conditions, photosynthesis of the various groups of phototrophic prokaryotes is limited by different environmental factors including light, reduced sulfur compounds, organic carbon substrates, oxygen, and temperature. The physical characteristics of the medium have, through processes of absorption and scattering, a large influence on the available radiation (see Competition for light). As a second major limiting factor, the availability of nutrients limits the growth of phototrophic bacteria and as a consequence,

photosynthetic energy conversion.

Surface environments exposed to sky radiation (as in strong shades) may be enriched in blue and UV radiation (Fig. 6). Water is the major light-absorbing component only in very clear open ocean and inland lakes. It strongly absorbs light of the ultraviolet, red and especially infrared (wavelengths around 745 and 960 nm). As a consequence, tens of meters below the surface of clear waters the spectrum is enriched in blue wavelengths. Several meters below coastal or most lacustrine water surfaces, the spectrum is enriched towards the green wavelengths, and deep (several millimeters) in the photic zones of sediments and soils infrared wavelengths dominate. Yellow substance in lakes is mostly of terrestrial origin and particularly absorbs light of the ultraviolet and blue portion of the spectrum (Kirk, 1983). In dystrophic lakes in which high concentrations of humic compounds are the major light-absorbing components, light of the red wavelength range prevails such that green-co lored species of green sulfur bacteria have a selective advantage over their brown-colored counterparts or purple sulfur bacteria (Parkin and Brock, 1980a).

In benthic and soil ecosystems, light quality differs fundamentally from that in the pelagic environment. In the visible wavelength range, radiation is strongly attenuated by mineral and biogenic particles. In sandy sediments light attenuation occurs preferentially in the wavelength range of blue light due to the reflection by sand grains (Jørgensen and Des Marais, 1986; Kühl and Jørgensen, 1992). The presence of iron minerals results in an enhanced attenuation of UV and blue wavelengths (Garcia-Pichel and Belnap, 1996). In contrast, absorption of infrared light by sediment particles is low and absorption by water is negligible due to the short optical pathlength. As a consequence of the optical properties of the sediment particulates, the red and infrared portion of the spectrum penetrate to the deepest levels. Multiple scattering causes the light fields to become rapidly diffuse, so that bacteria thriving within these environments receive light from all directions. The parameter measuring light received at a point in space from all directions is called scalar irradiance (E_0, or photon fluence rate). A third important, but counterintuitive, phenomenon is the presence of maximum irradiance values close to the surface, which are even larger than the incident scalar irradiance (Fig. 6). Below this surficial zone where the E_0 maximum occurs, E_0 attenuates exponentially (Jørgensen and Des Marais, 1986; Jørgensen and Des Marais, 1988; Kühl and Jørgensen, 1992; Lassen et al, 1992). For visible light, the measured photic depths (depths where E_0 is attenuated to 1% of the incident) varied between 3.1 mm for quartz sand and 0.45 mm for silty muds (Garcia-Pichel and Bebout, 1996b). In the ultraviolet (UV) at 310 nm, the corresponding depths were only 1.25 and 0.23 mm.

Light Absorption and Light Energy Transfer in Prokaryotes

Principle

The chlorophyll-based photosystems of bacteria convert electromagnetic energy into a redox gradient. The redox reactions are initiated by absorption of electromagnetic energy, leading to a transition of specific molecules into an excited electronic state. An increase in the electronic energy of a molecule requires more energy than changes in vibrational or rotational states. Since the

energy of light quanta is inversely related to their wavelength (Planck's Law), molecules absorb electromagnetic radiation of short wavelengths (ultraviolet and visible light) during changes in electronic energy, and longer wavelengths during changes in vibrational (near infrared radiation) and rotational energy (far infrared radiation and microwaves). Changes in the electronic state of molecules, and thus photochemically driven redox reactions by light absorption, can only occur by absorption of quanta of wavelengths <1240 nm (i.e., an energy larger than 1 eV per electron). This fact obviously limits the wavelength range that is usable for photochemical reactions. The major fraction of solar energy is present in the wavelength range between 400 and 750 nm. These wavelengths can only be harvested by organic molecules containing delocalized π-electrons in conjugated double bonds (Fig. 7).

Pigments and Light-harvesting Complexes

To capture light for photosynthesis, phototrophic organisms employ three classes of pigment molecules: magnesium porphyrins (chlorophylls and bacteriochlorophylls, also called chlorins), open-chain tetrapyrrole bilin pigments (phycobilins), and carotenoids. However, other types of chromophores may be used in non-photosynthetic light-harvesting, as is the case of the flavins and pterines of DNA-photolyase (Tanada et al., 1997) and in specific regulatory photoreceptors (Halobacteriaceae, bacteriorhodopsin). Until recently it appeared that only the magnesium-containing chlorin molecules were employed as the major photosynthetic pigment. The aerobic photosynthetic bacterium *Acidiphilium rubrum* is the first photosynthetic organism known to employ zinc-containing bacteriochlorophyll *a* as the photochemically active pigment (Wakao et al., 1996).

Free molecules remain in the excited singlet state for as little as 10^{-8} to 10^{-9} sec and rapidly return to the ground state (fluorescence). Through the multiplicity of vibrational and rotational states associated with each electronic energy level, two different electronic energy states may overlap. In such molecules the lowermost electronic energy level (the lowest excited singlet state) is reached in a rapid series of radiationless transitions with a concomitant small decrease in free energy. The wavelengths emitted during the subsequent return of the electron to the ground state therefore is longer than those wavelengths that were absorbed (Stokes shift). Chlorophylls and bacteriochlorophylls exhibit two major absorption bands (Table 2) and, when excited in the dissolved state, a corresponding red (685 nm for chlorophyll a) or infrared (786 nm for bacteriochlorophyll *a*) fluorescence. In photosynthetically active c ells, however, only about 1% of the absorbed light energy is lost by fluorescence. It is a characteristic of the photosynthetic apparatus of living organisms, that fluorescence (hence loss of already absorbed energy) is minimized. Instead, most of the energy absorbed by the antenna pigments is channeled by vectorial and radiationless inductive dipole resonance toward the reaction centers, where it drives the photochemical redox reactions. The specific coordination of pigment molecules in photosynthetic organisms favors inductive resonance and photochemical reactions over fluorescence. Within the photosynthetic antenna, a fine modulation of the absorption properties of the pigments occurs because of differences in their binding to the antenna proteins, so that the vectorial excitation cascade is thermodynamically favored (i.e., in a sequence involving pigments with progressively longer absorption maxima). The resulting small differences in the energy level of antenna pigments directs the transfer of excitatio n energy more or less to the reaction center.

A second consequence of the interactions between pigment molecules and proteins is the shift of the absorption peaks of the former towards longer wavelengths. In the case of chlorophyll *a*, the shift is comparatively small while it is larger in bacteriochlorophyll-protein complexes (up to 650 nm in bacteriochlorophyll *b*-containing phototrophic bacteria; Table 2). The shift for most

carotenoids in association with proteins is as small as for chlorophyll *a*. In intact cells, carotenoids absorb mainly in the 420–550 nm wavelength region. In contrast, binding of one type of porphyrin pigment (bacteriochlorophyll *a*) by different apoproteins has led to a considerable diversification of the long-wavelength absorption maxima in purple sulfur and nonsulfur bacteria (Fig. 7). Obviously the role of proteins in pigment-protein-complexes is not confined to the proper coordination of pigment molecules but als o can represent a means to exploit wavelength regions not utilized by other phototrophic organisms. Especially in intertidal microbial mats, variations in the fine structure of the pigment-protein complexes is a means of ecological niche separation (see Competition between phototrophic bacteria). The absorption spectra of whole cells of phototrophic bacteria seem to have evolved in such a way that almost the entire electromagnetic spectrum suitable for electrochemical reactions can be exploited (Fig. 7).

The first step of porphyrin synthesis is the formation of 5-amino levulinic acid (δ-ALA). In *Chloroflexus aurantiacus*, β- and γ-Proteobacteria, *cyanobacteria*, *Heliobacteriaceae*, and green sulfur bacteria, δ-ALA is synthesized from glutamate (C5-pathway), which therefore appears to represent the more ancestral pathway. In contrast, α-Proteobacteria as well as yeasts, fungi, and animals form δ-ALA by the ALA synthase-mediated condensation of glycine with succinyl-CoA (Beale, 1995; Oh-Hama, 1989; Oh-hama et al., 1991).

All (bacterio)chlorophylls exhibit two major absorption bands (Table 2), leaving a considerably wide gap in the absorption spectrum. The latter is partially complemented by the absorption spectrum of carotenoids found in all phototrophic bacteria or by a range of phycobiliproteins in most cyanobacteria. Owing to the presence of up to 15 conjugated double bonds, carotenoids absorb light at the short wavelength end of the visible range.

Table 2. Major absorption maxima of chlorins in whole cells and in the dissolved state, and fluorescence maxima of whole cells of phototrophic prokaryotes.

Chlorin	Absorption maxima (nm)	Fluorescence maxima (nm)	
	Whole cells	Acetone extracts	Whole cells
Chl *a*	670–675	435, 663	680–685
Chl *b*	n.d.	455, 645	(in acetone 652)
Chl *d*	714–718	400, 697	(in acetone 745)
BChl *a*	375, 590, 805, 830–911	358, 579, 771	907–915
BChl *b*	400, 605, 835–850, 986–1035	368, 407, 582, 795	1040 nm
BChl *c*	457–460, 745–755	433, 663	775
BChl *d*	450, 715–745	425, 654	763
BChl *e*	460–462, 710–725	459, 648	738
BChl *g* [a]	375, 419, 575, 788	365, 405, 566, 762	n.d.

[a] Bacteriochlorophyll *g* of the Heliobacteriaceae shows structural relationships to chlorophyll *a* because it contains a vinyl group on tetrapyrrole ring I. Like in bacteriochlorophylls *a* and *b*, pyrrole ring II is reduced, however, and the esterifying alcohol is farnesol as in bacteriochlorophylls of green sulfur bacteria. As for bacteriochlorophyll *a* or *b*, the reduced state of ring II in bacteriochlorophyll *g* causes an additional though smaller absorption maximum, the Q_x band at about 567 nm.
n.d., not determined.

The light-harvesting antenna complexes of green sulfur bacteria and *Chloroflexus* are extramembranous ovoid organelles, so-called chlorosomes, which are attached to the inner surface of the cytoplasmic membrane and contain bacteriochlorophylls *c*, *d*, or *e*. Chlorosomes are exceptional in that proteins do not seem to be involved as ligands for most of the antenna bacteriochlorophyll molecules. Instead, interactions between the bacteriochlorophylls themselves govern the absorptive properties of the photosynthetic antenna in green sulfur bacteria (Blankenship et al., 1995; Fig. 3A). In all other phototrophic prokaryotes studied, chlorins and carotenoid molecules occur in complexes with proteins.

Chlorins in pigment-protein complexes are noncovalently bound by histidine imidazole residues, which ligate the central magnesium atom of the porphyrin (Drews and Golecki, 1995). In some cases (e.g., heliobacterial reaction center protein; Vermaas, 1994) the histidine residues are replaced by asparagine, glutamine or arginine, which may function as ligands. Noncovalent binding of carotenoids seems to be mediated largely by hydrophobic interactions. In the purple nonsulfur bacteria, the *Chromatiaceae*, and *Ectothiorhodospiraceae*, all antenna complexes (and reaction centers) are located within intracytoplasmic membranes that are differentiated from, but contiguous to, the cytoplasmic membrane of the cell. In purple nonsulfur bacteria, *Chromatiaceae*,

and *Ectothiorhodospiraceae*, intracellular membranes occur as vesicles, stacks, lamellae, or tubules (F igs. 2 and 3B). Most photosynthetic species of the α-Proteobacteria (*Rhodocyclus purpureus*, *Rhodocyclus tenuis*, *Rubrivivax gelatinosus*) do not form extensive intracellular membrane systems. The photochemical apparatus of purple nonsulfur bacteria is confined to the intracellular membrane system, whereas the enzyme complexes of the respiratory chain and transport systems are located in the cytoplasmic membrane (Bowyer et al., 1985). This functional differentiation does not seem to exist in purple sulfur bacteria (*Allochromatium vinosum*, *Ectothiorhodospira mobilis;* Drews and Golecki, 1995). With one known exception, the photosynthetic apparatus in *cyanobacteria* is located on specialized intracellular membranes (thylakoids). Thylakoids may be either single or stacked, a nd are distributed concentrically (parallel to the cytoplasmatic membrane), radially, or randomly (Fig. 2). Like in chloroplasts, lateral heterogeneity (spatial separation of photosystem I in stroma lamellae and of photosystem II in grana stacks) has been found in 'Prochlorophytes.'

In *Heliothrix*, the *Heliobacteriaceae*, some purple nonsulfur bacteria (e.g., *Rhodocyclus tenuis*; Wakim and Oelze, 1980) and one cyanobacterium (*Gloeobacter violaceus*), the photosynthetic apparatus is located in the cytoplasmic membrane.

The light-harvesting antenna complexes of purple nonsulfur and purple sulfur bacteria are composed of two small, membrane-spanning α- and β-polypeptides to which bacteriochlorophyll *a* or *b*, and carotenoids are noncovalently bound. The polypeptide monomers aggregate within the membrane to form ring structures of 16 (LHI) or 9 (LHII) subunits, respectively (McDermott et al., 1995; Fig. 3B). According to the current structural model, the ring of 16 LHI-subunits surrounds one reaction center. Several LHII-aggregates transfer energy to this supercomplex.

In *Cyanobacteria*, light-harvesting chlorophyll *a* is present in two different types of protein complexes. The CP43 and CP47 core-antenna complexes are tightly associated with photosystem II (Barry et al., 1994). In photosystem I, however, antenna chlorophylls are an integral part of the reaction center itself (Golbeck, 1994; Fig. 3C).

A third class of light-harvesting complexes are phycobilisomes. They occur in the division *Cyanobacteria* (and in the plastids of red algae and some other groups of eukaryotic algae), and in most species are the main light-harvesting antenna structures of these bacteria. Under the electron microscope, phycobilisomes appear as hemidiscoidal to cylindrical particles attached to the cytoplasmic side of the thylacoids. In *Gloeobacter violaceus*, the cytoplasmic membrane is underlain by a continuous subcortical layer containing the phycobilisomes. Light energy absorbed by phycobilisomes is transferred preferentially to photosystem II, with chlorophyll *a* serving as antenna for photosystem I. However, short-term or partial spillover may occur, as the phycobilisomes are quite mobile (van Thor, J.J., et al., 1998). While the blue and red wavelength range is absorbed mainly by chlorophyll; the phycobilisomes harvest the blue-green, yellow, and orange regions (450–655 nm) of the light spectrum, thereby extending the spectral range of photosynthetic light-harvesting considerably (Fig. 7). The capacity of forming phycobilisomes is of selective advantage for the colonization of low light aquatic habitats (see Competition between phototrophic bacteria). Most (80%) of the phycobilisome mass is water-soluble phycobiliproteins, which contain open-chain tetrapyrrole chromophores (the phycobilins). Four types of phycobilins are known, the blue-colored phycocyanobilin (PCB), red-colored phycoerythrobilin (PEB), yellow-colored phycourobilin (PUB), and purple-colored phycobiliviolin (PXB, also sometimes abbreviated CV). They are found in various molar ratios, and form part of four recognized types of phycobiliproteins: allophycocyanin (APC), phycocyanin (PC), phycoerythrocyanin (PEC), and phycoerythr in (PE). In contrast to (bacterio)chlorophylls, the chromophores are covalently bound

by thioether linkages to cysteine residues of the apoproteins. Up to three chromophores may be bound to a single α- or β-polypeptide. The phycobiliproteins are heteromonomers forming $(\alpha\beta)_3$ trimeric disks. Together with chromophore-free linker polypeptides, these disks are assembled in aggregates, the phycobilisomes, which are attached to the cytoplasmic side of photosystem II (Fig. 3C). Peripheral rod elements consisting of phycoerythrin (which harbors PEB, and sometimes also PUB) or phycoerythrocyanin (with PCB and PXB), and phycocyanin (with PCB, and in some cases small amounts of PEB) are arranged in a hemidiscoidal fashion around a core substructure consisting largely of allophycocyanin (with PCB). The different absorption properties of the phycobilins are the result of differences in the number of conjugated double-bonds (the conjugated π-electron system is shorter for PEB and PUB), in the side chains of the tetrapyrrole prosthetic groups, including also chemically distinct chromophore-protein linkages, and in the protein environments of the chromophores (Sidler, 1994). Light energy is absorbed mainly by the peripheral rods, and transferred rapidly by radiation-less downhill energy transfer from phycoerythrin (absorption maximum 495–575 nm) or phycoerythrocyanin (575 nm) to phycocyanin (615–640 nm). Finally, allophycocyanin (650–655 nm) transfers the energy to photosystem II.

Not all cyanobacteria possess all of these different phycobiliproteins. Those synthesizing exclusively APC and PC appear blue-green. Many heterocystous cyanobacteria also produce PEC in addition to APC and PC (Bryant et al., 1982); these strains never produce PE. Dark-colored strains of many benthic genera contain large amounts of PC and PE. Red cyanobacteria, typical for deep lacustrine and marine waters produce large amounts of PE, and only small amounts of PC. Marine open ocean cyanobacteria (*Synechoccus*, *Trichodesmium*) contain large amounts of a PUB-rich PE, with absorbance maxima around 495–500 nm.

In Chl *b*-producing cyanobacteria (the former 'Prochlorophytes'), the photosynthetic antennae are intrinsic to the membrane, and in *Prochlorothrix hollandica*, they contain chlorophyll *a* and β-carotene (PSI; photosystem I), or chlorophylls a and b, and zeaxanthin (PSII; photosystem II). In contrast to the other two known species, *Prochlorococcus marinus* contains divinyl-chlorophyll *a* and divinyl-chlorophyll *b*. The presence of chlorophyll *b* and zeaxanthin and their functional connection to the reaction center of PSII enables these bacteria to absorb light in the wavelength range of 460–500 nm, and is of selective advantage under light conditions present in the lower euphotic zone of oligotrophic oceans (see Competition for light). However, chlorophyll *b* represents only a minor fraction of the photosynthetic pigments. In *Prochloron*, the ratio of chlorophyll *a*/ chlorophyll *b* is between 2.6 and 12.0 (Thorne et al., 1977); this ratio is even higher in *Prochlorothrix* (10–18), in which the ratio of PSI to PSII is > 3:1. In *Prochlorothrix hollandica*, cells grown at low light intensities exhibit the lowest chlorophyll *a*/chlorophyll *b* ratios (Matthijs et al., 1994).

A very interesting variation is exemplified by *Acaryochloris marina*, where Chl *d* is the major antenna chlorin (2% of the dry weight, whereas Chl *a* is only 0.1%) harvesting light for both photosystems (Schiller et al., 1997). *A. marina* also contains traces of a Chl *c*-like pigment in addition to more typically cyanobacterial carotenoids (α-carotene—found also in *Prochlororococcus* —and zeaxanthine—found in many cyanobacteria) and phycobiliproteins (APC and PC; Miyachi et al., 1997).

In purple bacteria, the size of the photosynthetic antenna is in the range of 20–200 bacteriochlorophyll *a* per reaction center (Zuber and Cogdell, 1995). The specific bacteriochlorophyll *a* content of aerobic bacteriochlorophyll-containing bacteria reaches only 5–10% of that of anoxygenic phototrophic bacteria (Yurkov and Beatty, 1998). At least in one strain

(*Rhizobium* BTAi1), the size of the photosynthetic unit is similar to that of anoxygenic phototrophic bacteria (Evans et al., 1990), indicating that the low pigment content is due to a low number of reaction centers. In PSII of cyanobacteria, the antenna comprises 300–800 phycobilin chromophores and 47 chlorophyll *a* molecules (Sidler, 1994, Matthijs et al., 1994), whereas the reaction center protein PsaA of PSI binds 110 chlorophyll *a* molecules (Golbeck, 1994). The photosynthetic antenna of green sulfur bacteria is significantly larger than that of other anoxygenic phototrophs and comprises about 1000 bacteriochlorophyll molecules connected to one reaction center (see The family Chlorobiaceae, Physiology). This appears to be one major reason for the competitive success of green sulfur bacteria in low-light environments (see Competition for light). Antenna size is smaller in *Chloroflexus* (Olsen, 1998). About 35 molecules of bacteriochlorophyll g are associated with one reaction center in *Heliobacteriaceae* (Amesz, 1995).

Efficiency of Light Harvesting

The light absorption capabilities of photosynthetic prokaryotes can be judged best by calculating which fraction *f* of the light impinging on a single cell is actually absorbed. This fraction is considerable for purple sulfur and other bacteria. The highest bacteriochlorophyll-specific attenuation coefficient k_B has been determined for a population of *Amoebobacter purpureus* (0.050 $m^2 \cdot (mg\ BChl\ a)^{-1}$; Overmann et al., 1991a). For comparison *Prochlorococcus* has a chlorophyll-specific attenuation coefficient of 0.0147–0.0232 $m^2 \cdot (mg\ Chl\ a^{-1}$ (Moore et al., 1998). For *Amoebobacter*, *f* is 0.36, or 36%, as calculated from Beer's Law and using the value of k_B, the intracellular c oncentration of light-harvesting pigments C (10.3×10^6 mg BChl$\cdot m^{-3}$, calculated from a content of 85 µg BChl$\cdot$(mg protein)$^{-1}$; van Gemerden and Mas, 1995; Watson et al., 1977) and the average optical pathlength d of a cell (2 µm):

$$f = 100 \times \exp(-k_B \times C \times d)$$

Of the photosynthetic pigments that absorb this high fraction of incident light, the majority (typically >97%) serves in light-harvesting and transfers excitation energy to the photochemical reaction centers. The combination of antenna complexes with one reaction center constitutes the photosynthetic unit. The efficiency of energy transfer within the photosynthetic unit and its size determine the fraction of the quantum flux that is harvested.

Large concentrations of pigments result in self-shading and thus a reduced efficiency of light absorption per mole of pigment. At the cell size and intracellular pigment concentrations typical of most prokaryotic phototrophs, this decrease in efficiency is not very important (Garcia-Pichel, 1994a), but it might be significant in some extremely low-light adapted anoxygenic phototrophs like the green sulfur bacterial strain isolated from the Black Sea chemocline (Overmann et al., 1991a).

Close proximity of photosynthetic pigments enables an efficient transfer of excitation energy but at the same time also causes a so-called 'package effect' (Kirk, 1983) by which self-shading of the pigment molecules exceeds that predicted by the Lambert-Beer law. The package effect is seen clearly in a flattening of absorption peaks, commonly observed when recording absorption spectra of whole cells (see The Family Chlorobiaceae, Identification). Because the energy requirement for biosynthesis of additional antenna structures is rather constant, the net energy gain for a photosynthetic cell must decrease at higher intracellular pigment concentrations, which restricts

the amount of light-harvesting structures a photosynthetic cell can synthesize. Polypeptides of the photosynthetic machinery (a significant fraction of the total cell protein) amount to 20% in purple nonsulfur bacteria and >50% in phycobiliprotein-containing cyanobacteria. Interestingly, the total protein content of cyanobacterial cells is comparable to other phototrophic bacteria. Possibly, cyanobacteria contain reduced levels of proteins involved in nonphotosynthetic processes to compensate for the high energy and nitrogen expenditure of the antenna proteins.

The biosynthesis of proteins requires a major fraction of the energy expenditure of the bacterial cell (Gottschalk, 1986). In chlorosomes, the mass ratio of protein:bacteriochlorophyll is significantly lower than in other light-harvesting complexes (Table 3). Probably this is one major reason for the larger antenna size and the lower light energy requirements of green sulfur bacteria as compared to their purple and cyanobacterial counterparts (see Competition between phototrophic bacteria), and might help explain the competitive advantage gained by *Prochlorococcoccus* over their close relatives *Synechococcus* in the open oceans.

Table 3. Pigment:protein ratio in different photosynthetic antenna complexes.

Antenna complex type	Protein:pigment	
	Mass ratio	Per pigment molecule (in Da)
Chlorosomes	0.5–2.2	420–1840
B806-866 complex[a]	3.9–5.8	3550–5290
B800-850 LHII	4.4	4000
B820 LHI	6.7	6100
Phycobilisomes	~22.4	~12,300

[a] *Chloroflexus aurantiacus*

Data from Olson, 1998 or calculated from Sidler, 1994, Loach and Parkes-Loach, 1995, Zuber and Cogdell, 1995. Carotenoids have been neglected in these calculations because of their lower numbers as compared to bacteriochlorophylls (B800-850 LHII), their absence in phycobilisomes, and the controversy concerning their functional significance in light-harvesting (chlorosomes). Only antenna complexes which are separate entities from reaction centers were considered. Photosystem I does not contain a distinct antenna structure; the PsaA protein of the reaction center binds 110 chlorophyll *a* molecules.

Conversion of Light into Chemical Energy

Principle

The unifying principle of bacterial and archaeal photosynthesis is the light-driven generation of a proton-motive force (PMF). The PMF is subsequently used by ATP synthase to form ATP, or for active transport and motility.

In chlorophyll-based photosynthesis, redox reactions and charge separation precede the establishment of the PMF. In addition, reducing power ($NAD(P)H + H^+$) is generated as a primary product of the light reaction in *Cyanobacteria*. In the photochemical reaction, only the energy of the lowest excited singlet state (see Light absorption and light energy transfer in prokaryotes) of the chlorophylls is used. Consequently, all absorbed light quanta have the same effect irrespective of their original energy (wavelength). When comparing the light energy available in different habitats, or the light adaptation of different phototrophic bacteria, it is therefore more meaningful to express irradiances in units of $\mu mol\ quanta \cdot m^{-2} \cdot s^{-1}$ rather than $W \cdot m^{-2}$ (see Competition for light).

The standard free energy for the reduction of CO_2 depends on the redox potential of the photosynthetic electron donor employed (Table 4, Fig. 8). If this energy requirement for electron transfer is compared with the energy available after absorption of photons of different wavelengths, it becomes clear that oxygenic photosynthesis is not feasible in photosystems containing the known types of chlorin pigments, and requires the absorption of two photons per electron (Fig. 8).

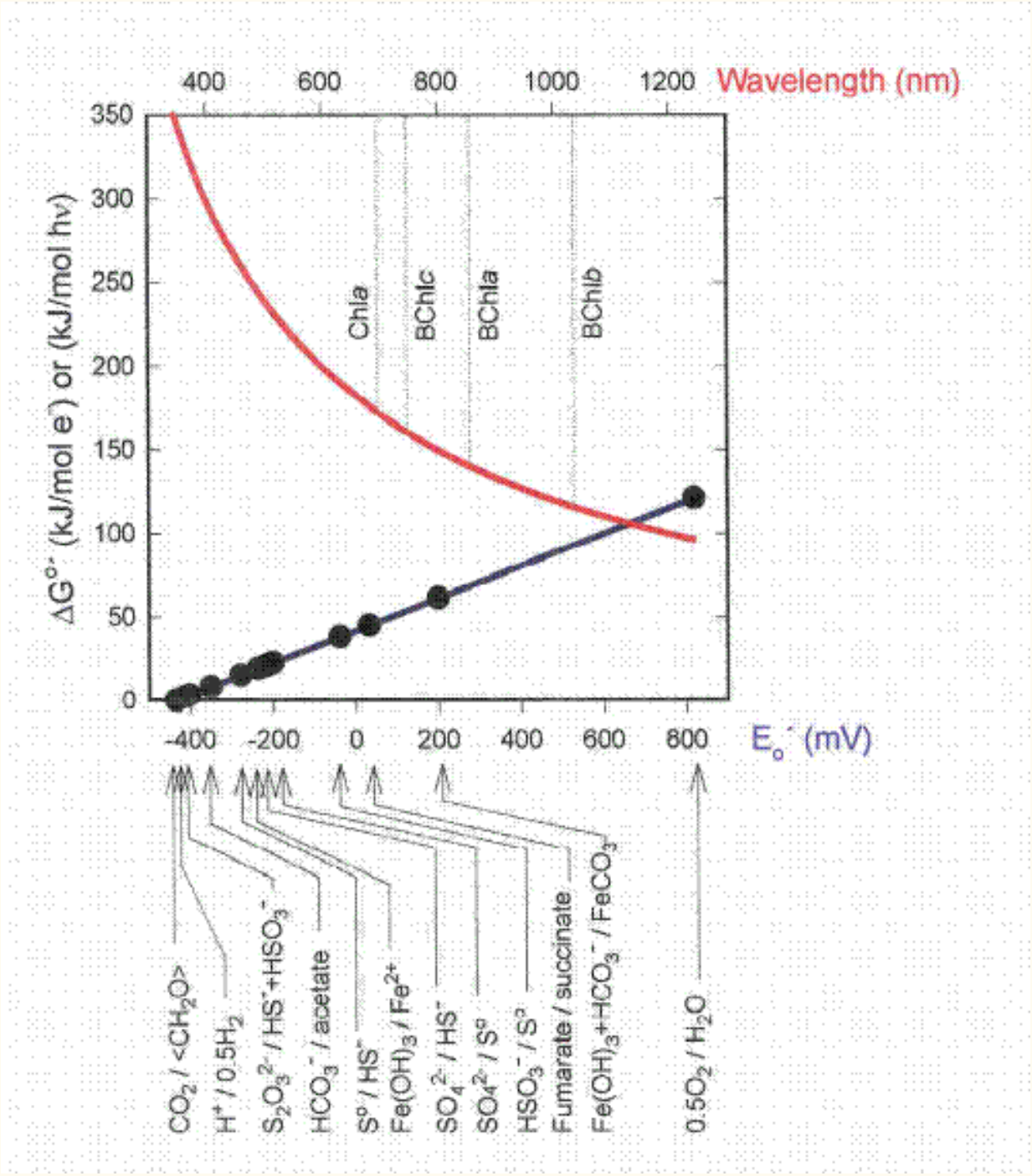
Table 4. Standard redox potentials of different electron donors of the photosynthetic light reaction. a

Electron donor	E_0' [mV]
½ O_2/H_2O	+ 820
$Fe(OH)_3$ + HCO_3–/$FeCO_3$	+ 200
Fumarate/Succinate	+ 33
HSO_3/ S^o –	– 38
SO_4^{2-}/ S^o	– 200
SO_4^{2-}/ HS^-	– 218
$Fe(OH)_3/Fe^{2+}$	– 236
S^o/HS^-	– 278
HCO_3^-/acetate	– 350
$S_2O_3^{2-}/HS^-$ + HSO_3^-	– 402
$H^+/½H_2$	– 414
Electron acceptor	**E_0' [mV]**
$CO_2/<CH_2O>$	– 434

[a]Taken from Brune, 1989;Widdel et al., 1993; Thauer et al., 1977; Zehnder and Stumm, 1988.

Fig. 8. Free energy of one mol quanta calculated from Planck's constant h (6.63×10^{-34} J·s), the speed of light c (2.99×10^8 m·s^{-1}), the wavelengths of light λ, and the Avogadro constant N_A=

6.023×10^{23} mol^{-1} according to $\Delta G^{o'}_{h\nu} = N_A \cdot h \cdot c \cdot \lambda^{-1}$. Free energy required for the transfer of 1 mole of electrons from an electron donor with standard redox potential $E^{o'}_d$ (see Table 4) to CO_2 calculated according to $\Delta G^{o'}_{el} = -F \cdot (-470 - E^{o'}_d)$ using the Faraday constant F (96.5 $kJ \cdot V^{-1} \cdot mol^{-1}$). Dotted vertical lines indicate the energy that is available after absorption of light by the long wavelength Q_y absorption bands of different photosynthetic pigments.



The biological conversion of light into chemical energy has been found to be remarkably efficient: the number of charge separation events per absorbed photon is 1.0 (Kok, 1973; Wraight and Clayton, 1973) and the efficiency of the entire photoconversion process of a red photon to chemical energy by oxygenic photosynthetic organisms is 43% (Golbeck, 1994). Whereas the efficiency of energy transfer between antenna bacteriochlorophyll and the reaction center in most cases is close to 100% (Amesz, 1995), the transfer between antenna carotenoids and the reaction center can be

significantly lower, 70% in *Heliobacteriaceae* (Amesz, 1995) and even 20% in a purple nonsulfur bacterium (Angerhofer et al., 1986). When carotenoids serve as the only light-harvesting pigments, 2.5 t imes higher irradiances are required by *Rhodopseudomonas acidophila* to attain the same growth rates as compared to light-absorption by bacteriochlorophyll (Göbel, 1978). In aerobic phototrophic bacteria, most of the highly diverse carotenoids do not function as light-harvesting molecules but might serve in quenching of toxic oxygen radicals (Noguchi et al., 1992; Yurkov et al., 1994). The same has been proposed recently for the carotenoid isorenieratene/β-isorenieratene in brown-colored green sulfur bacteria (J. B. Arellano, J. Psencik, C. M. Borrego, R. Guyoneaud, C. A. Abella, L. J. Garcia-Gil, T. Gillbro, personal communication).

One prerequisite for the photoconversion process is the presence of a membrane that is impermeable to protons and separates two different cell compartments. Three integral membrane multisubunit protein complexes participate in the generation of ATP in all phototrophic bacteria: the photosynthetic reaction center, a cytochrome complex, and an ATP synthase. All three are highly conserved within the bacterial radiation. Reaction centers have a dimeric core and consist of two closely associated integral membrane polypeptides plus additional proteins (Fig. 3). The special protein environment of the reaction center stabilizes the excited state and prevents back reaction after charge separation by enforcing ultrafast electron transfer to other electron acceptors nearby. The transfer of excitation energy from the antenna complexes to the reaction center initiates a charge separation at a special bacteriochlorophyll dimer (special pair), which is located on the periplasmic (or lumen) side of the photosynthetic mem brane. It is this endergonic process of charge separation that is ultimately driven by light energy; all the following redox reactions are exergonic. An electric potential is established across the membrane (inside negative). In its excited state, the special pair becomes a powerful reductant and ultimately reduces a quinone (in pheophytin-type reaction centers) or ferredoxin (in FeS-type reaction centers) on the cytoplasmic side of the photosynthetic membrane. The quinol or reduced ferredoxin leaves the reaction center complex and in turn donates electrons to a membrane-bound cytochrome complex or NADH dehydrogenase. A series of redox reactions results in the establishment of a proton-motive force across the photosynthetic membrane. Finally, the PMF is converted to ATP by ATPase.

In contrast to the (bacterio)chlorophyll-based systems of bacteria, light energy conversion of Halobacteria does not involve redox reactions and is limited to a vectorial transport of protons by bacteriorhodopsin. Upon excitation by light, the prosthetic retinal undergoes a series of reversible photochemical transformations (an isomerization from the all-*trans* to the 13-*cis* form) and releases a proton into the extracellular space. The PMF thus generated is used for ATP synthesis by ATPase. Due to its low solubility, O_2 in the concentrated salt solution is present in significantly lower amount than in freshwater. Rhodopsin-mediated formation of ATP may become the sole source of energy for growth under anaerobic conditions in the light (Oesterhelt and Krippahl, 1983) and has therefore been viewed as an adaptation to the natural brine habitat of Halobacteria. Because of its distinct m echanism, archaeal 'photosynthesis' is not discussed in further detail in the present section. Additional information can be found in chapters titled Introduction to the Classification of Archaea and The Family Halobacteriaceae.

Molecular Architecture of the Reaction Center

All bacteria which perform anoxygenic photosynthesis possess—or (in the case of cyanobacteria which are capable of using sulfide as electron donor) employ—only a single photosystem. The decrease in redox potential that a single photosystem can undergo upon excitation appears to be limited (Blankenship, 1992, compare Fig. 8). A combination of two different photosystems is

required for the thermodynamically unfavorable utilization of water as an electron donor for photosynthesis (Fig. 3C). With the relatively simple architecture of their photosystems, all anoxygenic phototrophic bacteria depend on electron donors that exhibit standard redox potentials more negative than water (e.g., H_2S, H_2, acetate; Table 4). This molecular feature is one major reason for the narrow ecological niche of anoxygenic phototrophic bacteria in extant ecosystems (see Habitats of phototrophic prokaryotes).

Two different types of reaction centers occur in photosynthetic bacteria. Based on the chemical nature of the early electron acceptors, a pheophytin/quinone-type reaction center and a FeS-type reaction center are distinguished (Blankenship, 1992; Fig. 3A,B). The first type is found in green gliding *Chloroflexus* species, phototrophic members of the α- and β-Proteobacteria, *Chromatiaceae*, *Ectothiorhodospiraceae*, and in PSII of *Cyanobacteria*. The reaction center of *Proteobacteria* consists of three protein subunits (L, M, H) which bind four bacteriochlorophylls, two bacteriopheophytins, two quinones and one high-spin nonheme Fe^{2+} (Lancaster and Michel, 1996; Fig. 3B). Many species (e.g., *Chloroflexus aurantiacus*, *Blastochloris viridis* and *Allochromatium vinosum*) contain an additional tetraheme cytochrome c polypeptide attached to the periplasmic side of the reaction center.

Following the transfer of the electrons by ubiquinol or plastoquinol, the redox reactions at the cytochrome bc_1 (or b_6f) complex drive proton transport across the cytoplasmic membrane. Protons are translocated either into the extracellular space (anoxygenic phototrophic bacteria) or the intrathylacoidal space (cyanobacteria). The ratio of protons translocated to electrons transferred (H^+/e^- ratio) is 2. The reaction center and cytochrome bc_1 in pheophytin-type reaction centers of *Proteobacteria* and *Chloroflexus* are functionally linked by two diffusible electron carriers, ubiquinone in the hydrophobic domain of the membrane and cytochrome c_2 or auracyanin (Meyer and Donohue, 1995) in the periplasmic space. The liberated electron is transferred back to the special pair via quinone, the cytochrome bc_1 complex and soluble periplasmic soluble electron carrie r (often cytochrome c_2). Owing to this cyclic electron transport, the only primary product of photosynthesis is the proton-motive force, and the reduced pyridine nucleotide required for photosynthetic CO_2 fixation is generated by energy-dependent reverse electron flow (Fig. 3).

In oxygenic phototrophic bacteria, plastoquinone is the electron acceptor of PSII and donates electrons to the cytochrome b_6f-complex. The special pair is reduced by the manganese-containing water-splitting system located at the lumenal side of the transmembrane PSII complex (Fig. 3C).

In the pheophytin-type reaction centers of aerobic phototrophic bacteria, photoinduced charge separation occurs only in the presence of O_2 (Okamura et al., 1985). It has been proposed (Yurkov and Beatty, 1998) that oxic conditions are required for photochemical activity because the primary acceptor ubiquinone has a significantly higher midpoint redox potential than in anoxygenic photosynthetic bacteria (65 to 120 mV more positive). The primary acceptor therefore may stay in its oxidized, electron-accepting state only in the presence of O_2.

The second type of reaction center contains iron-sulfur clusters as early electron acceptors and occurs in green sulfur bacteria (Fig. 3A), *Heliobacteriaceae*, and in the photosystem I of *Cyanobacteria*. Functionally, the reaction centers of green sulfur bacteria, *Heliobacteriaceae*, and PSI of cyanobacteria are therefore similar. However, the former two are homodimeric and only one reaction center gene has been detected, whereas the reaction center of PSI of cyanobacteria and green plants contains two nonidentical, but similar, subunits (PS I-A and PS I-B; Vermaas, 1994). In FeS-type reaction centers, the redox potential of the special pair in its reduced state (P*) is

sufficiently low to permit a transfer of electrons to ferredoxin. Until recently, it has therefore been assumed that noncyclic electron flow can directly reduce $NAD(P)^+$ and does not require further energy expenditure not only in cyanobacteria but also in green sulfur bacteria. However, the sequencing of the whole genome of *Chlorobium tepidum* has not provided any indications for the presence of a ferredoxin-NADP+ oxidoreductase (D.A. Bryant, personal communication).

Electron Donors

Anoxygenic phototrophic bacteria of the α- and β-Proteobacteria use a wide variety of reduced organic carbon compounds as electron-donating substrates (see Carbon metabolism; Table 4; Fig. 8). Most phototrophic sulfur bacteria are capable of using sulfide as photosynthetic electron donor. Other inorganic electron donors utilized include H_2, polysulfides, elemental sulfur, thiosulfate, sulfite, and iron (Widdel et al., 1993). Sulfide is oxidized to zero-valent sulfur, which in *Chromatiaceae* appears to be deposited as polysulfides or polythionates rather than in the form of S_8 rings (Steudel, 1989; Steudel et al., 1990). In addition, thiosulfate is formed as an oxidation product by some species (see The Family Chlorobiaceae; Sulfur metabolism; Steudel et al., 1990). The photosynthetic sulfide oxidation rates of purpl e sulfur bacteria are higher than required for growth and remains constant at all growth rates. As a result, storage of sulfur is at maximum at low growth rates (van Gemerden and Mas, 1995). Zero-valent sulfur is further oxidized to sulfate. In microbial mats, polysulfides and organic sulfur compounds may be significant as photosynthetic electron donor. Polysulfide oxidation has been reported for *Chlorobium limicola* f.sp. *thiosulfatophilum*, *Allochromatium vinosum*, *Thiocapsa roseopersicina*, while dimethylsulfide is utilized and oxidized to dimethylsulfoxide by the two purple sulfur bacteria *Thiocystis* sp. and *Thiocapsa roseopersicina* (van Gemerden and Mas, 1995). In addition to reduced sulfur compounds, hydrogen serves as electron donor in the majority of green sulfur bacteria, and in the metabolically more versatile species of purple sulfur bacteria (such as *Allochromatium vinosum*, *Thiocapsa roseopersicina*). In green sulfur bacteria which lack assimilatory sulfate reduction, a reduced sulfur source is required during growth with molecular hydrogen. Finally, a few species of purple nonsulfur bacteria, of *Chromatiaceae*, and of the green sulfur bacteria have been found to utilize ferrous iron as photosynthetic electron donor (Widdel et al., 1993; Heising et al., 1999).

Sulfide acts as a strong poison of PSII activity in many algae and cyanobacteria. The ability of some *Cyanobacteria* to conduct anoxygenic photosynthesis with sulfide as an electron donor to PSI (Cohen et al., 1975; Padan, 1979; Padan and Cohen, 1982), or to continue oxygenic photosynthesis in the presence of sulfide (Cohen et al., 1986), may be one of the key traits that extend the habitat of sulfide-utilizing cyanobacteria into the temporarily anoxic, sulfide-containing, layers of hot springs (Castenholz and Utkilen, 1984), marine microbial mats (De Wit and van Gemerden, 1987a; De Wit et al., 1988), and the chemoclines of meromictic lakes (Jørgensen et al., 1979, Camacho et al., 1996). Sulfide is an inhibitor of PSII and induces the synthesis of a sulfide-oxidizing enzyme system. In contrast to phototrophic sulfur bacteria, cyanobacteria oxidize sulfide to elemental sulfur or thiosulfate but do not form sulfate (De Wit and van Gemerden, 1987b). However, the use of sulfide by cyanobacteria in anoxygenic photosynthesis must be regarded as a detoxification mechanism, since their low affinity for sulfide (De Wit and van Gemerden, 1987b, Garcia-Pichel and Castenholz, 1990) renders them unable to compete with purple or green sulfur bacteria for sulfide as an electron donor.

In the natural habitat, growth of phototrophic sulfur bacteria is limited mainly by light and sulfide. Sulfide often becomes the growth-limiting factor at the top of the phototrophic sulfur bacterial

layers where light intensities are highest, while sulfide has to diffuse through the remainder of the community. The affinity for sulfide during photolithotrophic growth varies between the different groups of anoxygenic phototrophs (including cyanobacteria growing with sulfide) and has been shown to be of selective value during competition experiments. Green sulfur bacteria and *Ectothiorhodospiraceae* exhibit 5 to 7 times higher affinities for sulfide than *Chromatiaceae* (van Gemerden and Mas, 1995). On the contrary, affinities for polysulfides are comparable between green sulfur bacteria and *Chromatiaceae*.

Efficiency of Growth and Maintenance Energy Requirements

For any photochemical reaction, the quantum yield is defined as the number of molecules converted per light quantum absorbed. The quantum efficiency is the ratio of energy stored in a compound, to the radiant energy absorbed for its formation. The quantum requirement is the reciprocal of the quantum yield. For CO_2 fixation of purple sulfur bacteria, a quantum requirement of 8 and 10.5 mol quanta· (mol CO_2)$^{-1}$ is theoretically expected (Brune, 1989), considering that reverse electron transport is necessary. Experimentally, a quantum requirement of 12± 1.5 and 11.7 mol quanta·(mol CO_2^{-1} was determined, which corresponds to a quantum yield of 0.083 (Wassink et al., 1942 in Brune, 1989; Göbel, 1978).

In contrast, calculated values for the quantum requirements of green sulfur bacteria lie between 3.5 and 4.5 mol quanta·(mol CO_2)$^{-1}$, if noncyclic electron transport is assumed. However, earlier measurements had yielded much higher values (9–10; Brune, 1989). This discrepancy may be explained by the very recent finding that a gene for ferredoxin-$NADP^+$ oxidoreductase does not seem to be present in the genome of *Chlorobium tepidum* (D. A. Bryant, personal communication), which makes noncyclic electron transport rather unlikely also for green sulfur bacteria.

The quantum yield for CO_2-fixation determined for *Prochlorococcus* isolates incubated in daylight spectrum fluorescent light was between 0.086 and 0.128 mol C·(mol quanta)$^{-1}$ (Moore et al., 1998), thus reaching Emerson's theoretical maximum for O_2 evolution in oxygenic photosynthesis. In cyanobacteria, typically thriving in oxic environments where only oxidized sources of nitrogen and sulfur are available, a large proportion of the reducing power generated in the light reactions must be diverted to assimilatory nitrate or sulfate reduction, or to nitrogen fixation, so that the quantum requirement for CO_2 fixation can be substantially lower than that for oxygen evolution.

In a careful study of *Rhodobacter capsulatus* and *Rba. acidophilus* grown with lactate as electron donor in a light chemostat, a value for the maintenance light energy requirement of m_q = 0.012 mol quanta·(g dry weight·h)$^{-1}$ was determined (Göbel, 1978). The maintenance energy requirements of green sulfur bacteria are significantly lower compared to their purple conterparts (van Gemerden and Mas, 1995). This may be explained by the fact that protein turnover is highly energy demanding and that the protein content of the green sulfur bacterial antenna is much lower than in purple sulfur bacteria (Table 3).

Response to Changes in Light Intensity and Quality

Phototrophic bacteria acclimate to changes in light intensity and quality by diverse mechanisms. Anoxygenic phototrophic bacteria as well as cyanobacteria respond to a step-down in irradiance by increasing the specific pigment content and vice versa (references compiled in Sánchez et al., 1998). These changes can be accomplished either by varying the number of photosynthetic units per cell, the size of the individual photosynthetic unit, or both (see Long-term adaptations to changes in light intensity). Besides long-term biochemical changes in the composition and the amount of light-harvesting complexes, short-term redistribution of antenna capabilities (see State transitions) occur in oxygenic phototrophs.

Many species use vertical migration, mediated by tactic responses (see Movement by flagella) and formation of gas vesicles to regulate their vertical position and exposure to light. Especially in the stably stratified pelagic habitats of phototrophic sulfur bacteria, the difference in buoyant density from the surrounding water would cause a sedimentation of bacterial cells out of the photic zone and towards the lake bottom. The minimum buoyant density, which has been determined for phototrophic cells devoid of gas vesicles, was 1010 $kg \cdot m^{-3}$ (Overmann et al., 1991b). Actively growing cells, which contain storage carbohydrate and—in the case of *Chromatiaceae*—elemental sulfur, can easily attain much higher buoyant densities (up to 1046 $kg \cdot m^{-3}$; Overmann and Pfennig, 1992). By comparison, freshwater has a considerably lower density (e.g., 996 $kg \cdot m^{-3}$; Overmann et al., 1999c). As a consequence, sedimentation losses are significant for natural populations of several species of phototrophic sulfur bacteria (Mas et al., 1990). Phototrophic bacteria have developed two ways to adjust their vertical position along gradients of light intensity and spectral composition. For purple sulfur bacteria, motility in response to changes in irradiance is known to be of ecological significance in both planktonic and benthic situations. In benthic and terrestrial cyanobacteria, vertical locomotion by gliding is common. Planktonic cyanobacteria inhabiting stratified waters perform vertical migrations by changing their cellular gas vesicle content and ballast mass (intracellular carbohydrates and protein) and hence their buoyant density. Planktonic anoxygenic phototrophic bacteria do not seem to perform vertical migrations mediated by changes in gas vesicle content but rather use these cell organelles t o maintain their position within the chemocline (Overmann et al., 1991b; Overmann et al., 1994; Parkin and Brock, 1981).

Long-term Adaptations to Changes in Light Intensity

In those photosynthetic bacteria in which the entire photosynthetic apparatus is confined to the membrane, light absorption often is increased by formation of intracellular membrane systems (Fig. 2). In *Rhodobacter capsulatus*, the number of intracellular membrane vesicles increases by a factor of 6.3 when the cells are shifted from high to low light intensities. As a result, the area of intracellular membranes under these conditions is 2.7-fold larger than the area of the whole cytoplasmic membrane. Photosynthetic species of the β-Proteobacteria which do not form extensive intracellular membrane systems (*Rhodocyclus purpureus*, *Rhodocyclus tenuis*, *Rubrivivax gelatinosus*) increase the density of photosynthetic units in their cytoplasmic membrane (Drews and Golecki, 1995). Intracellular membranes appear to be absent in *Heliobacteriaceae* and *Heliothrix*, where pigments are confined to the cytoplasmic membrane (Fig. 2). In *Chloroflexus aurantiacus*, the increase in cellular concentrations of bacteriochlorophylls a and c is mediated by an increase in the number and volume of chlorosomes, and the percentage of cell membrane surface covered by chlorosomes (Golecki and Oelze, 1987). In a similar manner, green sulfur

bacteria adapt to low light intensities by increasing the size and the cellular number of chlorosomes (see The family Chlorobiaceae, Physiology).

During induction of the photosynthesis apparatus in *Proteobacteria*, invaginations of the cytoplasmic membrane, increases in the number and size of the photosynthetic units, and bacteriochlorophyll synthesis occur simultaneously. Under anoxic conditions, the amount of pigment synthesized by anoxygenic phototrophic bacteria is inversely related to the available light intensity and varies by a factor of up to 6.6 (Göbel, 1978). After a shift to low light intensity, the ratio of light-harvesting complex I per reaction center remains constant (at about 30 bacteriochlorophylls per reaction center), whereas the relative amount of the peripheral light-harvesting complex II increases. As a result, the size of the photosynthetic unit changes by a factor of two to five. Conversely, the specific NADH dehydrogenase activity decreases as does the amount of cytochrome and ubiquinone per reaction center. In *Rba. capsulatus* and *Rba. spheroides* these changes take about 2–3 generations and the growth rate is lowered during adaptation due to energy limitation. In the purple sulfur bacterium *Allochromatium vinosum*, low-light adaptation is also accomplished by increasing the size of the photosynthetic unit (Sánchez et al., 1998). Species like *Rhodospirillum rubrum* and *Blastochloris viridis*, which harbor only one type of light-harvesting complex, increase the number of photosynthetic units (Drews and Golecki, 1995).

Similar to anoxygenic phototrophic bacteria, changes in both the number and the size of the photosynthetic unit have also been decribed for cyanobacteria. In marine *Synechococcus* strains, the cellular content of the light-harvesting phycoerythrin can be varied by a factor of 20 and decreases with increasing light intensity. In marine benthic *Microcoleus chthonoplastes*, an increase in the content of total phycobilines and a change in the ratio of PEC to PC occurs with decreasing light intensity. The latter increase the ratio of phycocyanin to chlorophyll *a* during low-light adaptation (Foy and Gibson, 1982; Post et al., 1985). Acclimation to very low light intensities usually involves an increase in the size of the photosynthetic unit, such as in metalimnetic *Oscillatoria (Leptolyngbya) redekei* and *Oscillatoria agha rdii*. Changes in both the number and the size of the photosynthetic units seem to occur in *Microcystis* (Zevenboom and Mur, 1984).

Adaptations to Low Light Intensities

The capability to adapt to low light intensities represents a competitive advantage for phototrophic organisms. An estimate of the minimum irradiance I_{min} required for survival of phototrophic cells in the environment can be calculated from a few physiological parameters, namely the pigment content of the cells, P (in mg bacteriochlorophyll·g C^{-1}); the maintenance energy requirement, m_q (in µmol quanta·g $C^{-1}·s^{-1}$); the (bacterio)chlorophyll-specific attenuation coefficient, k (in m^2·mg BChl a^{-1}); the cellular dry weight content, D (in g C·m^{-3}); and the mean optical pathlength of one cell d:

$$I_{min} = m_q \cdot D \cdot d / [1 - \exp(-k \cdot D \cdot P \cdot d)]$$

Employing the appropiate values for m_q (see Efficiency of growth and maintenance energy requirements), k and P (see Light energy and the spectral distribution of radiation), D ($1.21·10^5$ g C·m^{-3}; Watson et al., 1977) and d (0.5 µm for the smaller anoxygenic phototrophs), this yields a minimum irradiance (I_{min}) of 2 µmol quanta·$m^{-2}·s^{-1}$. In many natural habitats of anoxygenic phototrophic bacteria, irradiances of this order of magnitude or lower have been measured.

Prochlorococcus has been found at deep water layers down to 300 m. However, these bacteria do not grow at light intensities below 3.5 µmol quanta·m^{-2}·s^{-1} (Moore et al., 1998) and thus appear to be less low-light adapted than the green sulfur bacterial strain MN1 isolated from the Black Sea which grows a t light intensities as low as 0.25 µmol quanta·m^{-2}·s^{-1} (Overmann et al., 1991a). Lower irradiances could be used by phototrophic prokaryotes after a decrease of m_q or an increase of P or both. Both adaptations are present in strain MN1 (Overmann et al., 1991a).

Adaptations to High Light Intensities

Sessile cyanobacteria living on the surface of benthic microbial mats are typically adapted to very high light conditions and contain large amounts of sunscreen pigments. For oxygenic phototrophs, special adaptations to oxygen-dependent photoinhibition of photosynthesis are of particular relevance. The protein D1 of PSII, coded by the *psbA* gene, has been identified as the central target of photoinhibition at high light intensities. In *Synechococcus* PCC 7942, *psbA* contains actually a multigene family coding for three different forms of the protein D1, which are differentially expressed according to the light conditions. Analysis of mutants showed that the isoforms expressed under high light conditions allow for optimal performance of PSII under photoinhibitory conditions (Golden, 1994). In addition, carotenoids probably play a central role in avoiding oxygen-mediated pho tosensitized bleaching of photosynthetic pigments and photooxidation of fatty acids under high light conditions.They function as antioxidant quenchers of excited molecules (such as triplet state chlorins and singlet oxygen) in many organisms and perhaps also as inhibitors of free-radical reactions (Britton, 1995). The photoprotective xanthophyll cycle typical of green algae and higher plants is not present in cyanobacteria, but judging from its increased specific content at high light intensity, zeaxanthin seems to play an important photoprotective role in some strains (Kana et al., 1988; Masamoto and Furukawa, 1997; Millie et al., 1990). Glycosylated myxoxanthophylls seem to attain the same role in others (Nonnengießer et al., 1996; Garcia-Pichel et al., 1998, Ehling-Schulz et al., 1997). Because there is a considerable photooxidation of carotenoids themselves at high light intensities, the maintenance of high carotenoid contents requires an increased expression of their biosynthetic genes.

Chromatic Adaptation

Several species of cyanobacteria are capable of changing the amount of peripheral phycoerythrin in response to changes in the spectral composition of light. During growth in white or green light, red-pigmented PE hexamers are added to the peripheral rods whereas additional blue-pigmented PC is added under red light (Sidler, 1994). This complementary chromatic adaptation is found only in strains capable of forming PE, but not in those forming PEC. The complementary change in antenna pigment composition optimizes the light-harvesting capabilities of populations of *Oscillatoria* spp., which thrive in deeper layers of stratified lakes where light is predominantly in the blue-green to green wavelength range (Utkilen et al., 1985; Fig. 6).

Genetic Regulation in Response to Light

The synthesis of the photosystem is especially energy consuming because of the high amount of light-harvesting and reaction center protein present in phototrophically grown cells of phototrophic

Proteobacteria (20% in purple nonsulfur bacteria). The maintenance energy requirements seem to be increased in low-light adapted cells (Sánchez et al., 1998). An effective regulation of photosynthesis gene expression therefore would prevent futile synthesis of cellular proteins. The synthesis of the photosystem in anoxygenic phototrophic bacteria is under the control of a complex regulatory network (Bauer and Bird, 1996).

The expression of light-harvesting complex I and reaction center genes is controlled 1) by the linkage of genes in superoperons, 2) at the level of transcription initiation, and 3) posttranscriptionally by the decay rate of mRNA (Bauer, 1995).

In *Rhodobacter capsulatus*, the genes coding the structural, biosynthetic and regulatory proteins for light-harvesting I and reaction center complexes are found assembled in a 46 kb-long photosynthetic gene cluster (Alberti et al., 1995). The arrangement of the genes within the cluster seems to be conserved among different phototrophic species of the α-Proteobacteria, like *Rhodobacter sphaeroides*, *Rhodocista centenaria* and *Rhodospirillum rubrum* (Bauer et al., 1993). Only the *pucBA* operon which codes for structural α- and β-polypeptides of light-harvesting complex II is found in a distant location on the bacterial chromosome (about 18 kb of the *puhA* in *Rhodobacter capsulatus*; Suwanto and Kapl an, 1989).

In anoxygenic phototrophic bacteria, transcription of the photosynthesis genes occurs only under anoxic conditions. Different photosynthesis genes exhibit varying levels of expression and degrees of regulation (Bauer and Bird, 1996). The *pufA,B,L,M* genes (coding for the α- and β-polypeptide of the light-harvesting complex I and the reaction center L and M structural polypeptides) as well as *puhA* (coding for the structural polypeptide subunit H) are tightly coregulated, transcribed at a high rate under anoxic conditions and strongly regulated (15- to 30-fold). An inverted repeat sequence located between *pufA* and *pufL* affects the longevity of the respective mRNA primary transcript. A reduction of light leads to an activation of *puf* and *puh* gene expression by the *hvrA* gene product , which probably directly interacts with the two promoter regions. Light of 450 nm exhibits the most severe repressing effect, indicating that a flavin-binding protein (possibly HvrA itself) is the photoreceptor. Notably in aerobic phototrophic bacteria, a blue light sensitive system seems to regulate biosynthesis of bacteriochlorophyll *a* (Shimada, 1995).

The intracellular bacteriochlorophyll concentrations appear to affect *puf* and *puc* gene expression not only at the transcriptional but also the posttranscriptional level in *Rhodobacter capsulatus* (Rödig et al., 1999). The polycistronic organization allows the coordinate expression of the structural polypeptides of light-harvesting complex I and the two integral membrane-proteins of the reaction center. Since, however, many light-harvesting I complexes are required per reaction center in *Proteobacteria*, additional regulatory mechanisms must exist. Differential degradation of various portions of the polycistronic mRNA are one means to regulate the stoichiometry of different components of the photosynthetic apparatus. The synthesis of different amounts of gene products is achieved by posttranscriptional regulation (Rödig J. et al., 1999). Because of a h ighly stable secondary terminator structure at its 3´-end and the absence of specific recognition sites for endonucleolytic cleavage, the mRNA coding the two light-harvesting polypeptides has much higher stability than that of the entire *puf* gene transcript. The degradation of the downstream *pufLM* section of the mRNA is mediated by an endonuclease. A similar regulation mechanism may exist for the polycistronic mRNA of bacteriochlorophyll synthesis genes (*bchFNBHLM-F1696*) and the *puhA*, and operate in regulation of light-harvesting complex II expression.

A shift to low light intensities results in an increase especially of light-harvesting complex II. The corresponding *pucBA* operon is highly expressed but only moderately regulated (4-fold). In the

purple nonsulfur bacterium *Rhodobacter capsulatus*, four-fold less *puc* mRNA but at the same time four times as many light-harvesting II complexes were detected after a shift from high to low-light conditions (Zucconi and Beatty, 1988). Therefore regulation by light most likely involves posttranscriptional regulation. A posttranscriptional regulation appears to occur (Bauer, 1995).

Bacteriochlorophyll and carotenoid biosynthesis genes are only weakly expressed and moderately (2 to 4-fold) regulated. Light intensity may control the rate of bacteriochlorophyll degradation (by oxidative degradation of bacteriochlorophyll; Biel, 1986) rather than the rate of synthesis (Biel, 1995). This is another distinct difference from the regulation by oxygen, where inhibition of δ-aminolevulinate synthase by molecular oxygen appears to occur (see Chemotrophic growth with O_2). Bacteriochlorophyll may be stabilized by insertion in pigment-protein complexes, however. The promotor of the bacteriochlorophyll synthesis gene *bchC* is of the sigma-70 type and leads to one large superoperon (Yurkov and Beatty, 1998). In contrast, an alternative sigma factor appears to recognize the strongly regulated structural *puf* and *puh* genes (Bauer, 1995). These differences explain the independent and different levels of regulation observed for the two classes of genes.

Recently the promoter for the carotenoid biosynthesis genes *crtB* and *crtP* were identified in *Synechocystis* PCC 6803, and shown to be light regulated (Fernández-González et al., 1998).

State Transitions

In cyanobacteria, state transitions involve redirecting the pathways of excitation energy transfer from light-harvesting complexes to both photosystems, and can be recognized by fluorescence analysis. Cyanobacteria can reach two energetically different states, in which one of the photosystems is preferentially excited. This is achieved with fast changes in the coupling between the light-harvesting complexes and the reaction center (van Thor et al., 1999). Evidence is accumulating that at least in the chlorophyll *b*-containing phototrophic bacteria ('Prochlorophytes'), the short-term regulation occurs by a mechanism similar to that in green chloroplasts (Matthijs et al., 1994). In the latter, polypeptides of the PSII antenna (LHCII) are rapidly phosphorylated during overexcitation of this photosystem, and as a consequence detach from PSII and migrate to the stromal thylakoids. This mechanisms ensures a bala nced energy distribution between PSII and PSI. The net result of state transitions is the balanced function of both photosystems and an optimization of the quantum yield for photosynthesis during short-term changes, such as those that planktonic cells might experience during vertical transport by water currents.

Movement by Flagella

Phototrophic *Proteobacteria* swim by means of flagella, whereas one species of the green sulfur bacteria (*Chloroherpeton thalassium*), members of *Chloroflexus* subgroup and cyanobacteria move by gliding. Of the α-Proteobacteria, most phototrophic species are motile. Peritrichous or lateral flagella are only found in *Rhodomicrobium vannielii* and the swarming phase of *Rhodocista centenaria*. About two thirds of the known *Chromatiaceae* species are motile. Larger forms (*Chromatium okenii*, *Chr. weissei*, *Chr. warmingii*, *Chr. buderi*, *Thiospirillum jenense*) are motile by means of bipolar multitrichous tufts of flagella. *Thiospirillum jenense* is bipolarly flagellated. Forms with smaller cells are monotrichously flagel lated (small *Chromatium* species, *Lamprocystis*, *Thiocystis*, *Thiorhodococcus*, *Thiorhodovibrio*). All *Ectothiorhodospiraceae* are flagellated. A new mode of motility has been described for a unicellular cyanobacterium which moves in a similar

fashion to flagellated bacteria but apparently lacks a flagellum (Waterbury et al., 1985).

True phototaxis is the ability to move towards or away from the direction of light. Cyanobacteria are the only prokaryotes displaying true phototaxis (Garcia-Pichel and Castenholz, 1999). Phototaxis may not be of competitive value for microorganisms adapted to live at low light intensities in the subsurface of sediments, soils and mats because the light fields may be close to diffuse deep below the surface. However, directed movements can still be of much use in microorganisms dwelling at or close to the sediment surface, where the light fields contain a significant downward directionality. Photophobic responses are changes in the direction of movement in reaction to abrupt changes in light intensity (Castenholz, 1982; Häder, 1987). In the step-up photophobic response, organisms will reverse direction when sensing an increase in light intensit y, which results in a net accumulation of organisms at lower light intensities. In a step-down photophobic (or scotophobic) response, the organisms will tend to accumulate in the region of higher light intensity. Photophobic responses are the basis of photomovement in all flagellated bacteria (Armitage, 1997), and in most gliding cyanobacteria (Castenholz, 1982).

In swimming cells of phototrophic *Proteobacteria*, a decrease in light intensity triggers a reversal of flagellar rotation (*Rhodospirillum rubrum*, *Chromatium* spp.) or an increase in stopping frequency (*Rhodobacter sphaeroides*). Owing to a memory effect, cells of the latter species retain a higher stopping frequency for up to 2 min, which prevents the cells from being trapped in the dark but instead permits reorientation of the cells and a return to higher light intensities (Armitage et al., 1995). As a result of this scotophobic response, the cells accumulate in the light and at wavelengths corresponding to the absorption maxima of photosynthetic pigments. A change in light intensity of as little as 2% can be sensed (Armitage et al., 1995). Active electron transport is required for the scotophobic response.

The formation of flagella in *Chromatium* species is induced by low sulfide concentrations and low light intensities. These two environmental variables are mutually dependent: the lower the light intensity, the higher the sulfide concentration at which a given strain can persist in its motile stage (Pfennig and Trüper, 1989). In the natural environment of purple sulfur bacteria, gradients of light and sulfide are opposed to each other. The control of motility by the two interdependent environmental variables (instead of only one) enables *Chromatium* cells to return either from low sulfide/high light environment above the chemocline or from the high sulfide/low light environment below the chemocline back to their habitat.

In its pelagic habitat, *Chromatium okenii* may display diurnal migrations with a vertical amplitude of about 2 m (Sorokin, 1970). In other lakes, vertical migrations of *Chromatium minus* extended over a distance of 30–35 cm (Lindholm et al., 1985; Pedrós-Alió and Sala, 1990). Vertical migration of nonthermophilic *Chromatium*, and of *Chromatium tepidum* also has been observed in ponds and in intertidal or hot spring microbial mats (Castenholz and Pierson, 1995; Jørgensen, 1982; Pfennig, 1978). In the latter environments, *Chromatium* cells migrate upwards to the surface of the mat and enter the overlaying water as a result of positive aerotaxis during the night. The cells contain high amounts of intracellular sulfur globules, which are formed during incomplete sulfide oxidation by anoxygenic photosynthesis during daytime. It is assumed that migration into microoxic layers enables the cells to grow chemoautotrophically by oxidation of sulfide or intracellular sulfur with molecular oxygen (Jørgensen, 1982; Castenholz and Pierson, 1995).

If phototrophic sulfur bacteria would solely follow the light gradient, their scotophobic response would ultimately lead them into oxic water layers. Both the scotophobic behavior and aerotaxis respond to the rate of intracellular electron flow (presumably sensed as changes in the redox state

of an intermediate). Because the two tactic reponses interact through a common signal, a combination of light and molecular oxygen elicits a differential response. *Rhodobacter sphaeroides* exhibits pronounced aerotaxis when precultivated aerobically, but negative aerotaxis when grown anaerobically in the light. Conversely, cells only swim towards higher light intensities in anoxic medium. A pulse of oxygen in the light causes a transient fall in the membrane potential which probably represents the primary tactic signal. As a result, the bacteria move towards environments where electron transport rate is increased (Armitage et al., 1995).

Rhodocista centenaria exhibits a characteristic swarming behavior. In liquid media, cells move with a single polar flagellum. Upon contact with solid agar media, formation of a large number of lateral flagella is induced. Lateral flagella allow whole colonies to swarm towards or away from the light (Ragatz et al., 1994). The supposedly true phototaxis of these swarming colonies (Ragatz et al., 1995) has later been proven to actually be aerotaxis following microgradients within the colonies (Sackett et al., 1997). The light sensing system in this species appears to be more complex, since infrared light leads to positive, and visible light to negative phototaxis. In microbial mats, infrared light penetrates to much greater depths than light of the visible wavelength range (see Competition for light). It has been suggested that the ratio of visible to in frared light may be used to maintain an optimum position in such environments (Armitage et al., 1995; Ragatz et al., 1995).

Cyanobacteria are the only prokaryotes displaying true phototaxis (Garcia-Pichel and Castenholz, 1999). Surface dwelling cyanobacteria such as *Lyngbya* spp. from hot springs mats and intertidal sediments and the motile phases (hormogonia) of terrestrial *Nostoc* spp. from desert soils exhibit this type of movement. The bundle-forming *Microcoleus chthonoplastes* also is able to display a "populational phototaxis" in that bundles of trichomes of this cyanobacterium are able to steer in the direction of the incoming light, whereas single trichomes are apparently not able to do so (Prufert-Bebout and Garcia-Pichel, 1994). True phototaxis is a mechanism for the orientation of cells at or close to the sediment surface, where the light field contains a significant downward directionality. In contrast, phototaxis does not provide a selective advantage for bacteria thriving in the subsurface of sediments, soils and mats because of the diffuse light field. In natural microbial mats photophobic responses to changes in light intensity are probably involved in the migrations of gliding bacteria (Nelson and Castenholz, 1982; Pentecost, 1984). In microbial mats, some strains of cyanobacteria are able to migrate vertically following their optimal light intensity over the diel cycle (Garcia-Pichel et al., 1996). The upward migrations of cyanobacteria in mats is preferentially prevented by short wavelengths, especially by UV radiation (Garcia-Pichel and Castenholz, 1994b; Bebout and Garcia-Pichel, 1995, Kruschel and Castenholz, 1988) and not by red nor green light.

Phototrophic consortia are structural associations between a colorless central bacterium and several surrounding cells of pigmented epibionts (see Interactions between phototrophic bacteria and chemotrophic bacteria; The family Chlorobiaceae; Fig. 5). Intact consortia of the type "Chlorochromatium aggregatum" exhibit a scotophobic response and accumulate in a spot of white light. In phototrophic consortia, only the central colorless bacterium carries a flagellum (J. Glaeser and J. Overmann, unpublished observation). The action spectrum of scotophobic accumulation corresponds to the absorption spectrum of the green sulfur bacterial epibionts, however. It has to be concluded that a rapid signal transfer exists between the light-sensing but immotile epibionts and the colorless motile rod (Fröstl and Overmann, 1998).

Gas Vesicles

Buoyancy-conferring gas vesicles are common in green sulfur bacteria, *Chromatiaceae*, and cyanobacteria. Gas vesicles are cylindrical structures with conical ends; their length and width are variable and species-specific. The sheath of gas vesicles are composed of proteins (Walsby, 1994). The gas mixture within the gas vesicles is the same as in the surrounding medium and is at the same partial pressures. Gas vesicles occur in a third of the species of *Chromatiaceae* (belonging to the genera *Amoebobacter*, *Lamprobacter*, *Lamprocystis*, *Thiodictyon*, *Thiopedia*, *Thiolamprovum*) and some green sulfur bacteria (genera *Ancalochloris*, *Pelodictyon*, *Chloroherpeton*). Of the *Ectothiorhodospiraceae*, only *Ectothiorhodospira vacuolata* forms gas vesicles during stationary phase. This reflects the distribution of both families of purple sulfur bacteria in nature, where *Chromatiaceae* typically colonize low-light stratified aquatic environments, whereas *Ectothiorhodospiraceae* typically inhabit more shallow saline ponds and sediments. Gas vesicles also are present in *Prochlorothrix hollandica*. In planktonic habitats, cells of cyanobacteria and phototrophic sulfur bacteria often contain gas vesicles, which indicates a selective advantage of this cellular property.

Gas vesicle formation in the green sulfur bacterium *Pelodictyon phaeoclathratiforme* is induced exclusively at light intensities < 5µmol quanta·m^{-2}·s^{-1} (Overmann et al., 1991b). This appears to be the reason for the rare observation of gas vesicles in pure cultures of green sulfur bacteria which routinely are incubated at much higher light intensities. A transfer of *Amoebobacter purpureus* strain ML1 to the dark results in an increase of the gas vesicle volume by a factor of nine (Overmann and Pfennig, 1992). Ambient temperature controls gas vesicle formation in *Thiocapsa pendens* (Eichler and Pfennig, 1986).

The buoyancy of many species of *Cyanobacteria* is regulated by the formation of gas vesicles. Highly buoyant cells may float towards the surface of stagnant water bodies. When the turgor pressure within the surrounding cytoplasm rises, such as by accumulation of low molecular weight photosynthates during periods of intense photosynthesis, the critical pressure may be exceeded and the gas vesicles collapse. New vesicles are formed by de novo synthesis rather than by re-inflation of collapsed vesicles. Short-term regulation of cell buoyant density occurs in cyanobacterial species thriving in stratified lakes, like *Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, and green-colored *Oscillatoria* spp. (Konopka et al., 1978; Oliver and Walsby, 1984; Utkilen et al., 1985). In these species, the proteinaceous gas v esicle sheaths are weak enough to permit a collapse at high intracellular turgor pressures as they are reached during periods of intense photosynthesis. By this mechanism, cells lose buoyancy within 30 minutes and thus can sink out of surface layers of stratified lakes. After de novo synthesis of gas vesicles in lower water layers, utilization of photosynthates, and a decrease of turgor pressure, cells rise back to the surface during the night. Rapid, turgor-mediated reduction of buoyancy together with gas vesicle formation thus represents an adaptation to the pronounced diurnal variations in light intensity and the limitation of growth by inorganic nutrients as they occur during summer stratification in the surface layer of eutrophic lakes. In some instances (e.g., *Microcystis aeruginosa*) diurnal migrations are mediated by an increase of carbohydrate ballast alone and gas vesicles do not collapse even at maximum turgor pressure (Kromkamp and Mur, 1984; Thomas and Walsby, 1985).

In contrast, gas vesicles of red-colored *Oscillatoria aghardii* and of phototrophic sulfur bacteria are mechanically stronger and do not collapse even at maximum cell turgor pressure. A decrease in the cellular gas vesicle content is therefore the result of their dilution during growth and division of the cells, and thus proceeds rather slowly (Overmann et al., 1991b; Overmann and Pfennig, 1992). Bacteria of this category mostly colonize the low-light environments shortly above or within the chemocline of stratified lakes where photosynthetic rates typically are strongly limited by light and hydrostatic pressure is high. Gas vesicles in green sulfur bacteria are rigid enough to persist at hydrostatic pressures down to depths of 38 m (Overmann et al., 1991b). The cyanobacterium

Trichodesmium contains extremely stable gas vesicles (mean crit ical collapse pressures up to 3.7 MPa, corresponding to a depth of 370 m; Walsby, 1978). The differences in strength of gas vesicles formed by different species is related to their shape (especially the diameter) and the primary structure of the GvpC protein of their sheath (Walsby, 1994).

In addition to the formation of gas vesicles, a new type of buoyant density regulation was detected in *Pelodictyon phaeoclathratiforme*. Cells of this species form large extracellular slime layers during the stationary phase which leads to an increase of the cellular volume by a factor of three (Overmann et al., 1991b).

Advantages of the Vertical Movement by Flagella and by Gas Vesicles

Theoretically, motility based on flagellar movement and vertical migration by means of gas vesicle formation have different advantages under natural conditions. Movement by flagella requires a permanent, (albeit sometimes low) fraction of metabolic energy (proton-motive force), whereas gas vesicle synthesis represents an initial one-time investment of a higher amount of metabolic energy. Once formed, gas vesicles keep bacterial cells in their habitat without any further demand for energy. The purple sulfur bacterium *Lamprobacter modestohalophilus* is capable of both flagella and gas vesicle formation. Motile cells are usually devoid of gas vacuoles and initially dominate during growth in fresh media. Later, cells become immotile and form gas vesicles and slime capsules (Gorlenko et al., 1979). In a very similar manner, cells of *Ectothiorhodospira vacuolata* are flagellated at low sulfide concentrations and light inte nsities, and become immotile and form gas vesicles in stationary phase (Imhoff et al., 1981). This supports the view that flagellar movement of purple sulfur and purple nonsulfur bacteria is favored under conditions of continuous energy supply, while gas vesicle formation represents an adaptation to conditions of starvation. Within one lake ecosystem, vertical migration of a flagellated species (*Chromatium minus*) was observed while the gas-vacuolated *Amoebobacter* did not change its vertical position (Pedrós-Alió and Sala, 1990).

A minimum quantum requirement of flagellar motility can be estimated from data in the literature. A vertical migration over a distance of 2 m (the maximum amplitude of vertical migration observed in nature) during 6 hours corresponds to a swimming speed of 93 $\mu m \cdot s^{-1}$. At a similar speed of 100 $\mu m \cdot s^{-1}$ the frequency of flagellar rotation is > 100 s^{-1} in *Rhodobacter sphaeroides* and requires between 200 and 1000 H^+ per rotation (Armitage et al., 1995). This yields a proton translocation rate of ~6 × 10^4 $H^+ \cdot s^{-1}$ at a swimming velocity of 100 $\mu m \cdot s^{-1}$. Based on an absorbing cross sectional area of the cell of 1 μm^2, an absorption of 36% of the incident light (see Efficiency of light harvesting), a ratio of protons translocated to electrons transferred (H^+/e^- ratio) of 2 (see Conversio n of light into chemical energy), and assuming that each photon absorbed leads to transport of an electron, the proton translocation rate of 6 × 10^4 $H^+ \cdot s^{-1}$ would be reached at an underwater irradiance of 0.2 µmol quanta$\cdot m^{-2} \cdot s^{-1}$. However, all available quanta would be required just for motility at this irradiance and no vertical migration would be possible during the night. Therefore motility by flagella will be of competitive advantage only at significantly higher irradiances. In many lakes, underwater irradiances in layers of phototrophic sulfur bacteria are ≤1 µmol quanta$\cdot m^{-2} \cdot s^{-1}$ (Overmann and Tilzer, 1989a; Overmann et al., 1999a). Under these conditions, purple sulfur bacteria harboring gas vesicles dominate over flagellated forms in the chemocline community (Fig. 4). At least in some lakes, gas vesicles appear to be of selective advantage also at higher underwater irradiances (Overmann et al., 1991b; Overmann and Pfennig, 1992).

Interestingly, the extremely low-light adapted *Chlorobium phaeobacteroides* strain MN1 isolated from the chemocline of the Black Sea was not capable of gas vesicle formation. The green sulfur bacterial layer is located at an 80-m depth and with respect to light intensity represents the lower limit for growth of a phototrophic organism (see The family Chlorobiaceae). The isolated strain exhibits an extremely low maintenance energy requirement. It therefore appears that gas vesicle formation is too energy demanding at the very low light intensities available at an 80-m depth in the Black Sea.

Carbon Metabolism of Phototrophic Prokaryotes

In the natural environment, the principal carbon source of phototrophic bacteria in many instances is CO_2 (Madigan et al., 1989; Sinninghe Damsté et al., 1993; Takahashi et al., 1990). In *Cyanobacteria*, *Chromatiaceae*, *Ectothiorhodospiraceae* and purple nonsulfur bacteria, CO_2 is assimilated by the reductive pentose phosphate or Calvin cycle. Employing this cycle, the formation of one molecule of glyceraldehyde-3-phosphate requires 6 $NAD(P)H+H^+$ and 9 ATP. By comparison, the reductive tricarboxylic acid cycle used for CO_2-assimilation by green sulfur bacteria requires 4 $NADH+H^+$, 2 reduced ferredoxins, and only 5 ATP. As two of the reactions of the reductive tricarboxylic acid cycle (the α-oxoglutarate synthase and pyruvate synthase rea ctions) require reduced ferredoxin as electron donor, this pathway of CO_2 fixation can only proceed under strongly reducing conditions. Furthermore, reduced ferredoxin is a primary product of the light reaction only in FeS-type reaction centers. Ultimately, the lower demand for ATP is possible because of the adapatation of green sulfur bacteria to the strongly reducing conditions of their natural environment. CO_2-fixation by the hydroxypropionate cycle in *Chloroflexus aurantiacus* requires 8 ATP per glyceraldehyde-3-phosphate and therefore is energetically less favorable than in green sulfur bacteria.

Organic carbon as it is present in canonical microbial biomass ($<C_4H_8O_2N>$; Harder and van Dijken, 1976) is considerably more reduced than CO_2. Given the high energy demand of autotrophic growth, the capability for assimilation of organic carbon compounds is of selective advantage especially if natural populations are limited by light or by low concentrations of electron-donating substrates, as is typically the case for phototrophic sulfur bacteria. At limiting concentrations of sulfide or thiosulfate, the cell yield of green sulfur bacteria is increased three times if acetate is available as an additional carbon source (Overmann and Pfennig, 1989b). Acetate represents one of the most important intermediates of anaerobic degradation of organic matter (Wu et al., 1997). That almost all anoxygenic phototrophic bacteria (with the exception of *Rhodopila globiformis*; Imhoff and Trüper, 1989) are capable of acetate assimilation is therefore not surprising. In most phototrophic *Proteobacteria*, acetate is assimilated by acetyl-CoA synthetase and the enzymes of the glyoxylate cycle. In green sulfur bacteria, the ferredoxin-dependent pyruvate synthetase, PEP synthetase, and reactions of the reductive tricarboxylic acid cycle serve this purpose. The capacity for organotrophic growth seems to correlate with the presence of α-oxoglutarate dehydrogenase. The latter is a key enzyme for the complete oxidation of the carbon substrates in the tricarboxylic acid cycle (Kondratieva, 1979), whereas a complete cycle is not needed for the photoassimilation during the presence of inorganic electron donors. The range of carbon substrates utilized and the capacity for photoorganotrophy or chemoorganotrophy varies considerably among the different groups of phototrophic pr okaryotes (Pfennig and Trüper, 1989).

Organic carbon compounds not only are assimilated but also can serve as photosynthetic electron donors in purple nonsulfur bacteria, some *Chromatiaceae* and *Ectothiorhodospiraceae*, all *Heliobacteriaceae*, and members of the *Chloroflexus* subdivision.

Green sulfur bacteria are the least versatile of all phototrophic prokaryotes. All known species are obligately photolithotrophic and assimilate only very few simple organic carbon compounds (acetate, propionate, pyruvate). Few strains have been shown to assimilate fructose or glutamate. Whereas green sulfur bacteria have a higher growth affinity for sulfide than purple sulfur bacteria, acetate seems to be used by purple sulfur bacteria at an affinity 30 times higher than in green sulfur bacteria (Veldhuis and van Gemerden, 1986). In addition, uptake of acetate in *Chlorobium phaeobacteroides* is inhibited by light (Hofman et al., 1985).

Based on their metabolic flexibility, two groups can be distinguished among the *Chromatiaceae*. Several species (*Chromatium okenii*, *Chr. weissii*, *Chr. warmingii*, *Chr. buderi*, *Chr. tepidum*, *Thiospirillum jenense*, *Lamprocystis roseopersicina*, *Thiodictyon elegans*, *Thiodictyon bacillosum*, *Thiocapsa pfennigii*, *Thiopedia rosea*) are obligately phototrophic, strictly anaerobic and photoassimilate acetate and pyruvate only in the presence of CO_2 and sulfide. Assimilatory sulfate reduction is absent in these species (Pfennig and Trüper, 1989). However, particularly those species with limited metabolic flexibility form dense blooms under natural conditions (see Coexistence of phototrophic sulfur bacteria). The second physiological group within the *Chromatiaceae* comprises the small *Chromatium* species (*Chr. gracile*, *Chr. minus*, *Chr. minutissimum*), *Allochromatium vinosum*, *Lamprobacter modestohalophilus*, as well as *Thiocystis* spp., *Thiocapsa*. Most of these species use thiosulfate as electron donor and a wide range of organic carbon compounds including glucose, fructose, glycerol, fumarate, malate, succinate, formate, propionate, and butyrate for photoassimilation, and often are capable of assimilatory sulfate reduction. In some species (especially *Allochromatium vinosum*), these organic carbon substrates also serve as electron-donor for phototrophic or chemotrophic growth.

Most *Ectothiorhodospiraceae* species are capable of photoorganotrophic growth, with *Ectothiorhodospira halophila* and *Ectothiorhodospira halochloris* being the exceptions. The spectrum of electron-donating carbon substrates for photoorganotrophic growth resembles that found in the versatile *Chromatium* species (Pfennig and Trüper, 1989). Assimilation of acetate and propionate proceeds by carboxylation and therefore depends on the presence of CO_2.

Chloroflexus aurantiacus grows preferably by photoorganoheterotrophy (Pierson and Castenholz, 1995). The carbon substrates utilized comprise acetate, pyruvate, lactate, butyrate, C_4-dicarboxylic acids, some alcohols, sugars and amino acids (glutamate, aspartate). This versatility has been seen as the major cause for the profuse growth of *Chloroflexus* in microbial mats where accompanying microorganisms, especially cyanobacteria, may provide the required carbon substrates (Sirevåg, 1995). However, high rates of formation of low-molecular-weight organic carbon substrates by the anaerobic food chain have also been observed in other stratified systems, where the dominating anoxygenic phototrophs could utilize only a narrow range of carbon substrates (Overmann, 1997; Overmann et al., 1996). The refore, the presence of low-molecular-weight organic carbon substrates is not necessarily the most selective factor in the natural environment.

Slow photolithoautotrophic growth with H_2S or H_2 as electron-donating substrates has been shown in laboratory cultures of *Chloroflexus aurantiacus* and in hot spring populations (Pierson and Castenholz, 1995). Carbon fixation proceeds by carboxylation of acetyl-CoA and via

hydroxypropionyl-CoA as an intermediate and yields glyoxylate as the net product (hydroxypropionate cycle; Holo, 1989; Strauß and Fuchs, 1993; Eisenreich et al., 1993). So far this cycle has not been found in any other member of the Bacteria. Glyoxylate is further assimilated into cell material with tartronate semialdehyde and 3-phosphoglycerate as intermediates (Menendez et al., 1999).

The highest metabolic versatility is found in phototrophic α- and β-Proteobacteria (purple nonsulfur bacteria). All representatives grow photoorganoheterotrophically and (with the exception of *Blastochloris viridis*) photolithoautotrophically with H_2 in the light. In addition to the substrates used by versatile purple sulfur bacteria, the spectrum of substrates that can serve as electron donors comprise long-chain fatty acids (like pelargonate), amino acids (aspartate, arginine, glutamate), sugar alcohols (sorbitol, mannitol), or aromatic compounds (benzoate; Imhoff and Trüper, 1989). With the exception of *Rubrivivax gelatinosus*, none of the purple nonsulfur bacteria is capable of degradation of polymers and therefore depends on the anaerobic food chain for the supply of electron-donating substrates required for growth. This dependence and the competition with chemotrophs for the carbon substr ates might be the major reason why dense blooms of purple nonsulfur bacteria do not occur under natural conditions (see Habitats of phototrophic prokaryotes). Some species are capable of also using reduced sulfur compounds as electron donors. However, most species oxidize sulfide to elemental sulfur only (Hansen and van Gemerden, 1972).

In *Heliobacteriaceae*, only a limited number of carbon substrates can serve as photosynthetic electron donor including pyruvate, ethanol, lactate, acetate, and butyrate. High levels of sulfide are inhibitory (Madigan, 1992; Madigan and Ormerod, 1995).

Cyanobacteria are obligate autotrophs par excellence; however, small molecular weight organic compounds such as acetate, sugars and amino acids are assimilated. In the case of amino acids, the presence of various efficient uptake systems has been interpreted as a means of recovery of leaked organic nitrogen, rather than a true chemotrophic capability (Montesinos et al., 1997). Certain strains of cyanobacteria can grow facultatively as chemoheterotrophs in the dark (Rippka et al., 1979), but even under these conditions all of the photosynthetic machinery is synthesized. This lack of regulation implies that chemotrophy has played no significant evolutionary role in these organisms.

Chemotrophic Growth with O_2

Ecophysiology of Chemotrophic Growth

In lakes, purple sulfur and green sulfur bacteria are confined to environments where light reaches sulfide-containing water layers. The physiological properties restrict the distribution of these bacteria in the pelagic habitat (Pfennig, 1978). Dense accumulations of anoxygenic phototrophic bacteria, which apparently are growing chemotrophically, are only known for *Chloroflexus* (see Habitats of phototrophic prokaryotes). Although populations of other anoxygenic phototrophic bacteria do not seem to grow permanently by chemotrophy, the ability of many strains to shift to an aerobic chemotrophic mode of growth is of selective advantage in environments like intertidal sediments.

Green sulfur bacteria and *Heliobacteriaceae* are obligate anaerobes. Under oxic conditions, the reaction of reduced ferredoxin of the type I reaction center with molecular oxygen would create superoxide and other activated oxygen species. *Heliobacteriaceae* are rapidly damaged by exposure to molecular oxygen. This has been attributed not only to the formation of toxic oxygen radicals but also the destruction of the unsaturated fatty acids present in the cell membrane by activated oxygen species (Madigan and Ormerod, 1995). In green sulfur bacteria, it has been observed that the energy transfer from light-harvesting bacteriochlorophylls c/d/e to bacteriochlorophyll *a* drops by a factor of 10 after an increase in redox potential due to the quenching by chlorobium quinone. This mechanism may protect the cells during brief anoxic/oxic transitions. (see The family Chlorobiaceae, Physiology).

All other groups of phototrophic prokaryotes comprise species that not only generate metabolic energy by photosynthesis but are also capable of chemosynthesis with O_2.

Chloroflexus aurantiacus is capable of growth as an aerobic heterotroph. During phototrophic growth, β-carotene, γ-carotene, and hydroxy-γ-carotene-glucoside are the major carotenoids, whereas echinenone and myxobactone predominate in aerobically grown cells (Pierson and Castenholz, 1995). Unlike in purple nonsulfur or purple sulfur bacteria, synthesis of some carotenoids by *C. aurantiacus* is greatly enhanced under aerobic conditions (Pierson and Castenholz, 1974). The expression of the chlorosome CsmA protein is transcriptionally or posttranscriptionally regulated by oxygen (Theroux et al., 1990).

Almost all known species of phototrophic α- and β-Proteobacteria (purple nonsulfur bacteria) are capable of microaerophilic or aerobic chemoorganoheterotrophic growth with oxygen as terminal electron acceptor. Of the purple sulfur bacteria, *Ectothiorhodospira* species, and eight small-celled species of the *Chromatiaceae* (*Thiocapsa rosea*; *Chromatium gracile*; *Chr. minus*; *Allochromatium vinosum*; *Thiocystis violascens*; *Thiocapsa roseopersicina*; *Thiocystis violacea*; *Thiorhodovibrio winogradskyi*) can grow by chemolithotrophy, oxidizing sulfide or thiosulfate with molecular oxygen (De Wit and van Gemerden, 1987b; Kämpf and Pfennig, 1980; Overmann a nd Pfennig, 1992). Only few species grow also chemoorganotrophically with organic carbon substrates as electron donor of respiration. The group of facultatively chemotrophic *Chromatiaceae* includes typical inhabitants of benthic microbial mats like *Thiocapsa roseopersicina* and *Thiorhodovibrio winogradskyi*. This is not surprising considering the pronounced oxic/anoxic fluctuations in this type of habitat. The cells of purple sulfur bacteria in benthic systems are often immotile and form aggregates together with sand grains, apparently as an adaptation to the hydrodynamic instability of the habitat (van den Ende et al., 1996). At the same time, however, immotile cells are exposed to strong diurnal variations in oxygen concentrations. The growth affinities for sulfide are lower for chemotrophically growing *Thiocapsa roseopersicina* than for colorless sulfur bacteria, which may explain that no natural populations of purple sulfur bacteria are known that grow permanently by chemotrophy (see Interactions between phototrophic sulfur bacteria and chemotrophic bacteria).

When grown anaerobically in the light, facultatively chemotrophic species of the purple nonsulfur and purple sulfur bacteria contain a potentially active repiratory system and exhibit ≥50% of the respiratory activity of chemotrophically growing cells (De Wit and van Gemerden, 1987a; Kämpf and Pfennig, 1980; Overmann and Pfennig, 1992; Pfennig, 1978). In cells that still contain bacteriochlorophyll, respiration is inhibited by light. This indicates that respiration and photosynthesis are coupled (e.g., by the membrane potential or common redox carriers; Richaud et al., 1986). An example is the soluble cytochrome c_2 which has a dual function in *Rhodobacter*

sphaeroides where it is needed for electron transfer from the cytochrome bc_1 complex to the reaction center during ph otosynthesis, and to the cytochrome c oxidase during respiration with molecular oxygen. During photosynthetic growth, expression of cytochrome c_2 is increased. At limiting concentrations of electron donating substrate, photosynthesis is preferred over respiration as long as the intracellular bacteriochlorophyll content is maintained at a sufficiently high level (4–7 µg bacteriochlorophyll a·mg $protein_{-1}$ in *Thiocapsa roseopersicina* at light saturation; De Wit and van Gemerden, 1990a).

Growth continues after a shift to microoxic or aerobic conditions. Under oxic conditions the synthesis of pigments and of pigment-binding proteins of the photosynthetic apparatus ceases. The number of intracellular membrane vesicles is reduced dramatically and the composition of membrane lipids is altered. The pigment content in purple sulfur bacteria is inversely related to the ambient oxygen concentration (Kämpf and Pfennig, 1986). At 25% air saturation (52 µM) of oxygen, pigment synthesis in *Thiocapsa roseopersicina* is completely repressed and cells become colorless (De Wit and van Gemerden, 1987b). In continuous cultures of purple sulfur bacteria, active degradation has not been observed and intracellular bacteriochlorophyll concentrations follow the washout curve. Thus bacteriochlorophyll does not seem to be actively degraded but is diluted out by cell division (De Wi t and van Gemerden, 1987b). Concomitantly, the activities of respiratory enzymes (NADH dehydrogenase, cytochrome c oxidases) are increased in chemotrophically grown cells. When the cells of *Thiocapsa roseopersicina* become colorless, they use only one third of the electron donor for reduction of CO_2. The remaining two thirds are used for energy generation and respired. Correspondingly, the protein yield reaches one third of that of phototrophically grown cells (De Wit and van Gemerden, 1987b; De Wit and van Gemerden, 1990b).

In aerobic phototrophic bacteria, aerobic growth is stimulated by light that is absorbed by bacteriochlorophyll *a*. This stimulation is only transient, however, since bacteriochlorophyll synthesis is repressed even by low light intensities (Yurkov and van Gemerden, 1993) thus leading to a loss of the photosynthetic apparatus under continuous illumination.

Respiration in *cyanobacteria* involves a full respiratory chain including a cytochrome aa_3 terminal oxidase. Monomeric sugars are degraded using the oxidative pentose phosphate cycle. A complete tricarboxylic acid cycle has never been shown for any cyanobacterium. The NADPH formed in sugar catabolism is fed to the membrane-bound electron transport chain at the level of plastoquinone. This is in contrast to green chloroplasts, in which plastoquinol is autoxidized (Peltier and Schmidt, 1991). The respiratory electron transport chain of cyanobacteria is located in both the plasma and the thylakoidal membrane, and it shares many functional components with photosynthetic electron transport. The role of exogenous respiration of organic substrates is probably minor under natural conditions. Under anoxia, the known electron acceptor alternatives to oxygen for cyanobacterial chemoorganotrophy are some organic compounds and elemental sulfur. Fermentation seems to be a relatively widespread ability in benthic and bloom-forming cyanobacteria, but it is not universal (Moezelaar and Stal, 1994).

Genetic Regulation by O_2

A shift from anoxic to oxic growth conditions requires the expression of new proteins and cofactors. On the genetic level the formation of the photosynthetic apparatus and the intracytoplasmic membrane system is regulated by two main environmental variables, light intensity (see Response

to changes in light intensity and quality) and molecular oxygen. The two factors act independently of one another and are involved in different mechanism of regulation of bacteriochlorophyll synthesis (Arnheim and Oelze, 1983). Compared to light, molecular oxygen acts as a stronger repressor, however. Although oxygen is a major factor controlling the formation of the photosynthetic apparatus in most of the facultatively phototrophic *Proteobacteria*, *Rhodovulum sulfidophilum* and *Rhodocista centenaria* are exceptional in that these species form the photosynthetic apparatus under both aerobic and anaerobic conditions (Hansen and Veldkamp, 1973; Nickens et al., 1996). Photopigment synthesis is not repressed by O_2 in *Rhodocista centenaria*.

The regulation of bacteriochlorophyll synthesis in purple nonsulfur bacteria is complex. The cells synthesize very little bacteriochlorophyll, probably because of the inhibition of bacteriochlorophyll biosynthesis enzymes (the δ–aminolevulinic acid synthesis and enzymes for the conversion of coproporphyrin; Oelze, 1992) by O_2. Oxygen does not seem to exert an effective transcriptional control. Under oxic conditions the transcription of bacteriochlorophyll synthesis genes decreases 2-fold, while that of light-harvesting I and reaction-center genes decreases by a factor of 30–100 (Bauer, 1995). The tetrapyrrole synthesis pathway has four different branches (leading to heme, bacteriochlorophyll, siroheme and vitamin B_{12}). While the bacteriochlorophyll content is drastically reduced in the presence of oxygen (Arnheim and Oelze, 1983), heme synthesis remains unaffect ed (Lascelles, 1978). The intracellular activity of δ-aminolevulinic acid synthase, the key enzyme of tetrapyrrol synthesis in α-Proteobacteria, is reduced in the presence of oxygen. Regulation by oxygen may occur also during some later steps of tetrapyrrole synthesis. It appears that oxygen inhibits magnesium chelatase, thereby increasing the protoporphyrin IX pool, which in turn leads to increased formation of heme. Feedback inhibition of δ-aminolevulinate synthase by heme would then slow down the synthesis of intermediates but still guarantee the amount needed for heme biosynthesis (Beale, 1995; Biel, 1995; Rebeiz and Lascelles, 1982).

After return to anoxic conditions the synthesis of the photosynthetic apparatus and intracellular membranes occurs in a light-independent manner. Anoxygenic photosynthetic bacteria contain a distinct light-independent protochlorophyllide reductase, composed of probably three subunits (BchN, BchB, and BchL). In angiosperms, the reduction of the fourth ring of the Mg-tetrapyrrole intermediate by NADPH-protochlorophyllide oxidoreductase is a light-dependent step in the chlorophyll biosynthetic pathway. This protein represents one of the only two enzymatic transformations known to require light (Suzuki and Bauer, 1995). Cyanobacteria, green algae and gymnosperms contain both, the light-dependent and light-independent protochlorophyllide reductase. The capacity to synthesize (bacterio)chlorophyll in the dark is of significance for the competitive success of *Chromatiaceae* in intertidal microbial mats. During anoxic conditions in the dark, *Thiocapsa roseopersicina* can synthesize bacteriochlorophyll *a* at maximum rate. Under the fluctuating conditions as they are observed in benthic microbial mats (oxic light, anoxic dark phase), purple sulfur bacteria therefore can maintain a photosynthetic mode of growth as long as bacteriochlorophyll synthesis during the night compensates for the wash out of pigments during the day (De Wit and van Gemerden, 1990b).

A multicomponent regulatory cascade controls the coordinate expression of the light-harvesting and reaction center *puf*, *puh*, and *puc* genes and involve various transcription factors (Bauer, 1995; Bauer and Bird, 1996). In *Rhodobacter capsulatus*, a redox-sensitive repressor (CrtJ) binds under oxic conditions to a conserved palindrome sequence in promotors of bacteriochlorophyll, carotenoid, and light-harvesting complex II genes. A second system for the regulation of the *puf*, *puh*, and *puc* operons probably consists of three components, a membrane-spanning sensor kinase (RegB), a soluble response regulator (RegA), and a hypothetical activator of the nonspecific

alternative sigma factor σ^P (RegX). A decrease in oxygen tension causes autophos phorylation of the membrane-spanning sensor kinase RegB, which then phosphorylates the cytoplasmic response regulator RegA. The latter acts as intermediate and probably transfers its phosphate to a putative third DNA-binding component that activates gene expression. The RegA-RegB system also is involved in regulation of the expression of cytochrome c_2 and the Calvin cycle CO_2 fixation genes and therefore is of general significance for the regulation of cellular metabolism.

The transcripts of the photosynthetic gene cluster exceed 10 kb and extend from pigment biosynthesis genes across promoter regions and into the genes for light-harvesting complex I and reaction center proteins. In *Rhodobacter capsulatus*, transcription of the genes coding structural polypeptides of the reaction center and light-harvesting complex I are not the only peptides initiated at their respective promotors. The transcripts of the bacteriochlorophyll biosynthesis *bchCA* operon extends through the promoter and coding sequences of the downstream *puf BALM* operon, and the transcript of the carotenoid biosynthesis *crtEF* operon extends through both (Wellington et al., 1992). Similarly, the *bchFBKHLM-F1696* and *puhA* operons are transcriptionally linked. The linkage of operons of different components of the phot osynthetic apparatus in such superoperons also has been detected in other species of purple nonsulfur bacteria and may play a significant role in the adaptation of cells to changes in environmental oxygen tension. According to a model (Wellington et al., 1992), the presence of superoperons ensures a rapid physiological response to a decrease in oxygen tension. In the presence of oxygen, a basal level of light-harvesting I and reaction center polypeptides is constantly formed and incorporated into the membrane, but these polypeptides disappear again in the absence of bacteriochlorophyll (Dierstein, 1984; Drews and Golecki, 1995) due to degradation. After a shift from oxic to anoxic conditions, the presence of a basal level of structural polypeptides considerably shortens the lag time for the change from aerobic respiratory to anaerobic photosynthetic growth. During this lag ph ase, the cellular amount of structural polypeptides of the photosynthetic apparatus is further increased by increasing the transcription rate of the *puf* and *puh* genes.

Oxygen does not only regulate the transcription of photosynthesis genes but also later steps in gene expression. Posttranscriptional regulation involves mRNA processing (mRNA degradation) and possibly some later steps (Rödig J. et al., 1999).

In most bacteria, the formation of multiple sigma factors is a prerequisite for the coordination of the regulation of a large number of genes in response to changes in environmental conditions. Sigma factors are dissociable subunits that confer promoter specificity on eubacterial core RNA polymerase and are required for transcription initiation. In phototrophic bacteria, the diversity of sigma factors of the σ^{70} family as they are present in the different phylogenetic groups appears to be correlated with their metabolic flexibility. In the unicellular cyanobacteria *Synechococcus* sp. and *Synechocystis* sp., nine different sigma factors (one member of group 1, four members of group 2, and four members of group 3) have been found, whereas one group 1 and three group 2 sigma factors have been found in *Chloroflexus* spp. In contrast to most other bacteria, the green sulfur bacterium *Chlorobium tepidum* contains only one group 1, but no alternative group 2 sigma factor (Gruber and Bryant, 1998). In *Chloroflexus*, one group 2 σ^{70} factor (SigB) is transcribed at fourfold higher levels during aerobic growth and therefore appears to be involved in the shift in metabolism. It has been proposed that SigB is involved in regulation of pigment synthesis (Gruber and Bryant, 1998).

Significance of Anoxygenic Photosynthesis for the Pelagic Carbon and Sulfur Cycles

The carbon fixation of phototrophic sulfur bacteria has been determined in a wide range of habitats, mostly inland lakes (Overmann, 1997, van Gemerden and Mas, 1995). The theoretical maximum of primary production by phototrophic sulfur bacteria has been estimated to be 10,000 mg $C \cdot m^{-2} \cdot d_{-1}$. Purple and green sulfur bacteria can contribute up to 83% of total primary productivity in these environments. This high number notwithstanding, anoxygenic primary production only represents a net input of organic carbon to the food web if 1) the anaerobic food chain is fueled by additional allochthonous carbon from outside and 2) aerobic grazers have access to the biomass of phototrophic sulfur bacteria. Based on recent experimental evidence, these conditions are met at least in some aquatic ecosystems (Overmann, 1997).

With the exception of geothermal springs, the sulfide required by phototrophic sulfur bacteria for CO_2-assimilation originates from sulfate or sulfur reduction during the terminal degradation of organic matter. This organic matter cannot be provided solely by anoxygenic phototrophic bacteria, since growth (hence accumulation of reduced carbon) constantly diverts electrons from their cycling between anoxygenic phototrophic bacteria and sulfate-reducing bacteria. At least part of the sulfide formation is therefore fueled by carbon that has already been fixed by oxygenic photosynthetic organisms within or outside the ecosystem. Consequently anoxygenic photosynthesis represents not new, but secondary primary production. A complete degradation of the carbon fixed by phototrophic sulfur bacteria in the anaerobic food chain (and thus an efficient recycling of electrons) in an anoxygenic primary production has been estimated to exceed oxygenic photosynthesis by as much as ten times (Overmann, 1997). In reality, anoxygenic photosynthesis surpasses that of phytoplankton mostly in oligotrophic lakes. In many oligotrophic lakes, the input of allochthonous carbon derived from terrestrial sources in the watershed is significant (Rau, 1980; Sorokin, 1970). In an oligotrophic saline meromictic lake (Mahoney Lake, B.C., Canada), purple sulfur bacteria together with the anaerobic food chain efficiently converted allochthonous organic carbon into easily degradable bacterial biomass (Overmann, 1997). It appears likely that phototrophic sulfur bacteria have this ecological function also in other aquatic ecosystems.

The presence of hydrogen sulfide in layers of phototrophic sulfur bacteria may prevent their biomass from entering the grazing food chain. This has been substantiated by stable carbon and sulfur isotope data, which indicated that phototrophic sulfur bacteria are not consumed to a significant extent by higher organisms (Fry, 1986). In addition, a quantitative analysis of loss processes conducted in a few lakes indicates that predation must be of minor significance (Mas et al., 1990; van Gemerden and Mas, 1995). In contrast, recent investigations have revealed that at least in one lake ecosystem, a major fraction of purple sulfur bacterial biomass enters the aerobic food chain via rotifers and calanoid copepods (Overmann et al., 1999b; Overmann et al., 1999c). The key environmental factors that caused this efficient link betw een anoxic and oxic water layers were the autumnal upwelling of phototrophic bacteria into oxic water layers by mixing currents, and the formation of gas vesicles and large cell aggregates by the dominant species, *Amoebobacter purpureus*.

Sulfide formation by sulfate- and sulfur-reducing bacteria and sulfide oxidation back to sulfur and sulfate occur at comparable rates in several lakes (Overmann et al., 1996; Parkin and Brock, 1981). This leads to a closed sulfur cycle and a detoxification of sulfide without concomitant depletion of oxygen (Pfennig, 1978).

The significance of phototrophic sulfur bacteria for the oxidation of sulfide in stratified environments is critically dependent on their cell density rather than the absolute biomass per

surface area of the ecosystem (Jørgensen, 1982). Dense populations in laminated microbial mats can account for 100% of the total sulfide oxidation in those systems, whereas some dilute pelagic populations oxidize only very small amounts (e.g., 4% in the Black Sea) of the sulfide diffusing from below into the chemocline (Overmann et al., 1991a; Overmann et al., 1996).

No information on the ecological significance of aerobic phototrophic bacteria is available to date.

Interactions with Other Microorganisms

Competition for Light

Blue light prevails in very clear open oceans (Fig. 6) where marine *Synechococcus* cells thrive under conditions of low photon flux (~10 µmol quanta·m^{-2}·s^{-1}; Carr and Mann, 1994). Two ecotypes of the marine *Synechococcus* exist which differ in the intracellular ratio of phycourobilin to phycoerythrobilin (Waterbury et al., 1986). Two subpopulations are distinguished according to the predominant chromophore associated with the phycoerythrin. Phycourobilin-rich strains are characteristic of the open oceans whereas strains with a lower PUB content predominate in shelf waters (Olson et al., 1990a). Compared to PEB-containing antennae (absorption maximum, ~550 nm), incorporation of PUB (absorption maximum, ~495 nm) increases the efficiency of light absorption significantly in deeper water lay ers of oligotrophic oceans.

Similarly, coexisting and phylogenetically closely related but genetically distinct populations of *Prochlorococcus* are adapted for growth at different light intensities, which results in their broad depth distribution (Moore et al., 1998). The low-light-adapted ecotype has a higher intracellular content of chlorophylls a and b, a higher chlorophyll b/a ratio, and exhibits a higher maximum quantum yield reaching the theoretical maximum of 0.125 mol C·(mol quanta)$^{-1}$. Its properties enable this ecotype to colonize very low water layers. It has been suggested that the distribution of different ecotypes in the same water column would result in greater integrated production than could be achieved by a single ecotype (Moore et al., 1998).

Based on the specific physiological properties of oxygenic and anoxygenic phototrophic bacteria, multilayered microbial communities frequently develop in stratified pelagic and in benthic (Fig. 5A, B) habitats. Cyanobacteria, eukaryotic algae and even plants (Lemna) form the topmost layers overlying populations of *Chromatiaceae* and green sulfur bacteria (Dubinina and Gorlenko, 1975; Caldwell and Tiedje, 1975; Pfennig, 1978; Camacho et al., 1996; Pierson et al., 1990; Pierson et al., 1990).

Phototrophic sulfur bacteria require the simultaneous presence of light and sulfide, which usually restricts their occurrence to layers well below the surface of lakes and sediments. As a consequence of the absorption of light in the overlying water, the light energy available to phototrophic sulfur bacteria in most pelagic environments is rather low (0.02–10% of surface light intensity; van Gemerden and Mas, 1995; Parkin and Brock, 1980b, Camacho et al., 1996). Similar values have been determined for purple layers in benthic microbial mats (Kühl and Jørgensen, 1992; Pierson et al., 1990; Garcia-Pichel et al., 1994c). A tight correlation between anoxygenic photosynthesis and the amount of light reaching phototrophic sulfur bacteria strongly suggests that light i s the main environmental variable controlling the anoxygenic photosynthesis (van Gemerden and Mas, 1995). Therefore, a selective pressure for efficient light harvesting and maximum

quantum yield exists in anoxygenic phototrophs. The same holds true for a few niche-specialized, deep-dwelling cyanobacteria.

The ecological niches of green sulfur bacteria and *Chromatiaceae* show considerable overlap because both groups grow preferably or exclusively by photolithotrophic metabolism, using ambient sulfide as electron-donating substrate. Different species of the same group should be even more competitive. Besides differences in maintenance energy demand, in adaptation to low light intensities and metabolic flexibility, another important factor determining the species composition of phototrophic sulfur bacteria in their natural habitats is the spectral composition of underwater light. In the overlying layers, light is absorbed by water itself, dissolved yellow substance (gilvin), phytoplankton and inanimate particulates. The limited wavelength range available at great depth selects for species of anoxygenic phototrophic bacteria with complementary absorption spectra. In many lacustrine habitats, light absorption by phytoplankton exceeds that of gilvin or water itself (Kirk, 1983), and light of the blue green to green wavelength range reaches layers of phototrophic sulfur bacteria. Those *Chromatiaceae* which contain the carotenoid okenone (Fig. 7) dominated in 63% of the natural communities studied (van Gemerden and Mas, 1995). It was proposed that energy transfer from carotenoid antenna pigments to the reaction center is more efficient in okenone-forming strains than in other purple sulfur bacteria (Guerrero et al., 1986). In addition, the capability of gas vesicle formation, and the different kinetics of sulfide oxidation (see Coexistence of phototrophic sulfur bacteria) appear to be of selective value for the colonization of pelagic habitats. Below accumulations of purple sulfur bacteria, the green-colored forms of the green sulfur bacteria dominate because of their superior capability to harvest the light reaching them, which has its spectru m shifted to a maximum intensity at 420–450 nm (Table 2) (Montesinos et al., 1997). In contrast, the brown-colored forms of the green sulfur bacteria dominate in lakes where the chemocline is located at depths greater than 9 m and in eutrophic lakes with a pronounced light absorption in the oxic zone.

A similar niche separation occurs in the phototrophic consortia (see The family Chlorobiaceae, Interactions between phototrophic sulfur bacteria and chemotrophic bacteria), which encompass green-colored or brown-colored epibionts (Overmann et al., 1999b). The ecological niche of the brown-colored green sulfur bacteria may be attributed to their use of significantly lower light intensities than purple sulfur bacteria for phototrophic growth and to their lower maintenance energy requirements (see Light absorption and light energy transfer in prokaryotes, Quantum yield, The family Chlorobiaceae). An extremely low-light adapted strain of the green sulfur bacterium *Chlorobium phaeobacteroides* has been isolated from the chemocline of the Black Sea located at an 80-m depth (Overmann et al., 1991a). This isolate (strain MN1) could grow at light intensities as low as 0.25 µmol quanta·m^{-2}·s^{-1}.

In sedimentary environments with their particular optical properties (Fig. 6), the irradiance reaching anoxygenic phototrophic bacteria may be reduced to ←1% of the surface value for light in the visible region, while >10% of the near infrared light is still available (Kühl and Jørgensen, 1992; see Light energy and the spectral distribution of radiation). As a consequence, the long wavelength Q_y bands of bacteriochlorophylls are significant for light-harvesting in sediments, whereas light absorption of anoxygenic phototrophic bacteria in lakes is mediated by carotenoids and the Soret bands of bacteriochlorophylls. In microbial mats, the spectral quality of the scalar irradiance is strongly modified as it penetrates. The presence of populations of phototrophic microorganisms impose strong absorption signatures on the spectrum of the scalar irradiance (Jørgensen and Des Marais, 1988; Pierson et al., 1987). As a result of vertical niche separation, benthic microbial mats can consist of up to five distinctly colored layers that are formed (from the top) by diatoms and cyanobacteria, cyanobacteria alone, purple sulfur bacteria with

bacteriochlorophyll a, purple sulfur bacteria with bacteriochlorophyll b, and green sulfur bacteria (Nicholson et al., 1987). In this vertical sequence different wavelength bands of red and infrared light (compare Table 2, Fig. 7) are successively absorbed by the different microbial layers (Pierson et al., 1990). Distinct blooms of bacteriochlorophyll *b*-containing anoxygenic phototrophic bacteria have been observed only in benthic habitats. Employing this pigment, the phototrophic Proteobacteria *Blastochloris viridis*, *Blastochloris sulfoviridis*, *Thiocapsa pfennigii*, *Halorhodospira halochloris*, *Halorhodospira abdelmalekii* harvest light of a wavelength range (1020–1035 nm), which cannot be exploited by any other photosynthetic organism.

Until recently, no strain of anoxygenic photosynthetic bacteria was known that could absorb light in the wavelength range between 900 and 1020 nm. Because of the prevalence of infrared radiation in the anoxic layers of microbial mats and the strong competition for this wavelength region, bacteria containing other types of photosynthetic antenna complexes would have a high selective advantage. Recently, the α-Proteobacterium *Rhodospira trueperi* was isolated, which contains bacteriochlorophyll *b* in a light-harvesting complex with a maximum absorption at 986 nm (Pfennig et al., 1997). Employing a selective enrichment strategy, the α-Proteobacterium *Roseospirillum parvum* could be isolated which harbors another new type of photosynthetic antenna complex. Here, bacteriochlorophyll *a* is the light-harvesting pigment and in vivo exhibits an absorption maximum at 9 11 nm (Glaeser and Overmann, 1999, Fig. 7). Both isolates originate from benthic microbial mats, indicating that the diversity of pigment-protein complexes in *Proteobacteria* is higher than previously assumed. The variation in the in vivo absorption spectra of the same pigment must be the result of differences in binding to light-harvesting proteins. In contrast, changes in the absorption spectra of the light-harvesting complex of green sulfur bacteria are the result of chemical alterations (e.g., methylation) of the pigment molecules (Bobe et al., 1990) because pigment-pigment interactions dominate in the chlorosomes (see Light absorption and light energy transfer in prokaryotes).

Because methanogenesis is the predominant pathway of terminal degradation in rice fields, *Heliobacteriaceae* probably compete with the photoheterotrophic purple nonsulfur bacteria in their natural environment (Madigan and Ormerod, 1995). Owing to the presence of bacteriochlorophyll g, *Heliobacteriaceae* take advantage of a wavelength region of the electromagnetic spectrum, which is not absorbed by other phototrophic bacteria. As a result of the small and fixed size of the photosynthetic antenna (see Light absorption and light energy transfer in Prokaryotes), these bacteria are adapted to higher light intensities than other anoxygenic phototrophic bacteria (~1,000 µmol quanta·m^{-2}·s^{-1}).

In addition to the capacity of absorbing light in the long wavelength range, metabolic flexibility is of highly selective value for the colonization of benthic habitats with their high fluctuations in oxygen and sulfide concentrations (see Chemotrophic growth with O_2).

However, the composition of communities of phototrophic sulfur bacteria is not solely determined by competition. The simultanous presence of green sulfur bacteria and *Chromatiaceae* possibly is also based on syntrophic interactions (see Coexistence of phototrophic sulfur bacteria).

Coexistence of Phototrophic Bacteria

Within the *Chromatiacea* the small-celled genus *Chromatium* species exhibit a considerably greater metabolic flexibility than the large-celled species (see Carbon metabolism; Chemotrophic growth with O_2). In addition, small-celled species like *Allochromatium vinosum* have a higher growth

affinity for sulfide. Based on these pure culture data, it is therefore unexpected that large-celled forms in fact dominate in natural ecosystems. The large-celled *Chromatium weissei* oxidizes sulfide twice as fast as the small-celled *Allochromatium vinosum*. Whereas the former preferentially oxidizes sulfide to zero-valent sulfur, the latter oxidizes a larger fraction directly to sulfate. Under fluctuating conditions as they occur in the chemocline of lakes, *Chromatium weissei* is capable of rapidly oxidizing sulfide at the onset of illumination, thereby accumulating zero-valent sulfur. During the remaining light period and because of its higher affinity for sulfide, *Allochromatium vinosum* utilizes most of the sulfide. Continuous cocultures of both species have thus been established by illumination in light-dark cycles (van Gemerden, 1974).

Furthermore, stable coexistence of two organisms is feasible in the presence of two substrates for which the two competitors have complementary affinities. Stable syntrophic interactions can be established in laboratory cocultures of purple sulfur (*Allochromatium vinosum*) and green sulfur bacteria (*Chlorobium limicola* f.sp. thiosulfatophilum; van Gemerden and Mas, 1995). Because of its higher affinity, the green sulfur bacterium oxidizes sulfide to zero-valent sulfur. The extracellular sulfur is mobilized as polysulfide, which can be used instantaneously as electron donor of the purple sulfur bacterium. The presence of sulfide inhibits the green sulfur bacterium from using polysulfide (see The family Chlorobiaceae, Interactions with different groups of phototrophic bacteria). Sulfide and polysulfide thus are the mutual substrates for the two different phototrophic sulfur bacteria.

Purple and green sulfur bacteria also have complementary affinities for sulfide and acetate (see Carbon metabolism). Accordingly, stable continuous cocultures of *Chlorobium phaeobacteroides* and *Thiocapsa roseopersicina* can be established (Veldhuis and van Gemerden, 1986).

Interactions Between Phototrophic Sulfur Bacteria and Chemotrophic Bacteria

A considerable number of strains of *Chromatiacae* is capable of switching to a chemolithotrophic growth mode after prolonged incubation in the presence of molecular oxygen (see Chemotrophic growth with O_2). Under these conditions, purple sulfur bacteria compete with colorless sulfur bacteria like *Thiobacillus* spp. Compared to thiobacilli, the purple sulfur bacterium *Thiocapsa roseopersicina* attains a higher growth yield under chemolithotrophic conditions (De Wit and van Gemerden, 1987a). However, the growth affinity for sulfide of the colorless sulfur bacteria is up to 47 times higher than that of *Chromatiacae* (De Wit and van Gemerden, 1987b; van Gemerden and Mas, 1995). Therefore *Chromatiacae* growing exclusively by chemolithotrophy would be rapidly outcompeted by colorless sulfur bacteria.

Culture experiments indicate that *Thiocapsa roseopersicina*, a typical inhabitant of laminated microbial mats in temperate environments, can replenish its photosynthetic pigments during anoxic periods in the dark, thereby maintaining a phototrophic growth mode also during the subsequent oxic light period (De Wit and van Gemerden, 1990b). Based on microelectrode measurements, purple sulfur bacteria in marine microbial mats of the North Sea barrier islands are exposed to oxygen during most of the day, whereas anoxic conditions prevail during the night (De Wit et al., 1989). Thus, the anoxygenic phototrophs cannot grow during the night and face competition for sulfide by colorless sulfur bacteria during the day. Because of their higher affinity for sulfide, the latter would be expected to outcompete phototrophically growing purple sulfur bacteria. In cocultures of *Thiocapsa roseopersicina* and *Thiobacillus thioparus*, sulfide is indeed entirely used by the colorless sulfur bacterium in the presence of oxygen. If oxygen concentrations are limiting, however, sulfide is oxidized incompletely by the chemolithotroph and soluble zero-valent sulfur

formed (either as polysulfide or polythionates) that in turn is used by the purple sulfur bacterium for phototrophic growth (van den Ende et al., 1996). Both diurnal fluctuations between oxic light and anoxic dark periods and syntrophism based on sulfur compounds may permit a stable coexistence of these groups and explain their simultaneous presence in natural microbial mats.

Stable associations can be established between green sulfur bacteria and sulfur- or sulfate-reducing bacteria (see The family Chlorobiaceae, Interactions with chemotrophic bacteria). These associations are based on a cycling of sulfur compounds but not carbon (see Significance of anoxygenic photosynthesis for the pelagic carbon and sulfur cycles). The simultaneous growth of both types of bacteria is fueled by the oxidation of organic carbon substrates and light. In a similar manner, cocultures of *Chromatiaceae* with sulfate-reducing bacteria have been established in the laboratory (van Gemerden, 1967).

The most spectacular type of association involving phototrophic bacteria is represented by the phototrophic consortia. These consortia consist of green sulfur bacterial epibionts that are arranged in a regular fashion around a central chemotrophic bacterium. A rapid signal transfer exists between the two partners and permits phototrophic consortia to scotophobotactically accumulate at preferred light intensities and wavelengths. In this association, the immotile green sulfur bacteria attain motility like purple sulfur bacteria. The high numbers of phototrophic consortia found in many lakes indicate that this strategy must be of high competitive value under certain environmental conditions.

A commensal relationship may exist between coccoid epibiotic bacteria and the purple sulfur bacterium *Chromatium weissei* (Clarke et al., 1993). This unidentified epibionts attaches to healthy cells but does not form lytic plaques on lawns of host cells like the morphologically similar parasite *Vampirococcus* (see Significance of bacteriophages and parasitic bacteria). Possibly, the epibiont grows chemotrophically on carbon compounds excreted by the purple sulfur bacterium.

A syntrophic interaction between cyanobacteria and sulfate-reducing bacteria appears to exist in microbial mats where both types of microorganisms occur in close spatial proximity, if not intermixed with each other. In these ecosystems, the excretion of organic carbon substrates by cyanobacteria may provide the electron-donating substrates for sulfate-reducing bacteria (Jørgensen and Cohen, 1977; Skyring and Bauld, 1990; Fründ and Cohen, 1992). The glycolate produced by photorespiration (Fründ and Cohen, 1992), as well as the formate, acetate and ethanol produced by glycogen fermentation (Moezelaar and Stal, 1994) most likely are the substrates excreted by cyanobacteria.

Despite a pronounced limitation of sulfate reduction by carbon substrates (Overmann et al., 1996, Overmann, 1997), no close syntrophic relationship was found between purple sulfur and sulfate-reducing bacteria in a meromictic lake. In this specific environment degradation of biomass by the entire anaerobic food chain rather than excretion of small carbon molecules and their direct utilization by sulfate-reducing bacteria provides the electron-donating substrates for sulfate-reducing and sulfur-reducing bacteria.

Symbioses Between Phototrophic Bacteria and Eukaryotes

Only one example is known for an intracellular symbiosis of anoxygenic phototrophic bacteria with an eukaryotic organism. The ciliate *Strombidium purpureum* inhabits the photic zone of sulfide-containing marine sands and harbors 200–700 purple endosymbionts. Symbionts are arranged

along the periphery of the host cell and contain intracellular tubular or vesicular membranes, bacteriochlorophyll *a* and spirilloxanthin (Fenchel and Bernard, 1993a; Fenchel and Bernard, 1993b). The ciliate shows a photosensory behavior, accumulating at wavelength that corresponds to the absorption maxima of the endosymbionts. It has been suggested that the intracytoplasmic purple bacteria increase the efficiency of the fermentative host by using its end products for anoxygenic photosynthesis. Furthermore, respiration of the bacteria may protect the host against oxygen toxicity.

In the course of evolution, *Cyanobacteria* have entered into symbiotic associations with a multitude of organisms (Schenk, 1992). Besides all eukaryotic phototrophs, from microalgae to *Sequoia sempervirens*, which have intracellular cyanobacterial symbioses, the most common extracellular symbioses of nonheterocystous cyanobacteria are in the form of cyanolichens and involve the unicellular genera *Chroococcidiopsis*, *Gloeocapsa* , "*Chroococcus*", and *Gloeothece*, as well as members of the genera *Nostoc*, *Calothrix*, *Scytonema*, *Stigonema*, and *Fischerella* as photobionts. Heterocystous cyanobacteria in the genus *Nostoc* form extracellular symbioses with liverworts and hig her plants (Cycads, duckweed). *Anabaena* enters in symbiosis with water ferns of the genus *Azolla*. *Prochloron* strains, large-celled *Synechocystis* and small-celled *Acaryochloris marina* are known from extracellular symbioses with ascidians in tropical or subtropical marine waters; *Prochloron* is found as ectosymbiont on the marine didemnid ascidian *Lissoclinum patella* (Lewin and Withers, 1975). Extracellular symbioses of the *Pseudanabaena*-like "*Konvophoron*" occur in Mediterranean invertebrates. Finally, intracellular symbioses of nonheterocystous cyanobacteria are known with tropical sponges ("*Aphanocapsa*", *Oscillatoria*, *Synechocystis*, *Proc hloron*), with green algae (*Phormidium*) and dinoflagellates (unidentified). Heterocystous cyanobacteria occur intracellularly in oceanic diatoms of the genera *Hemiaulus* and *Rhizosolenia* (and the cyanobacterium *Richelia intracellularis*). The cyanobacterial symbiont consists of a short cell filament with a terminal heterocyst (Mague et al., 1977). The numbers of filaments varies with host species. *Nostoc* thrives intracellularly in *Trifolium* (clover) and also in the terrestrial non-lichenic fungus *Geosiphon pyriforme*. With the notable exception of lichenic photobionts, many symbiotic cyanobacteria have resisted cultivation in spite of continued efforts.

Significance of Bacteriophages and Parasitic Bacteria

In addition to grazing, light and nutrient limitation, cyanophage infection of cyanobacteria may be a significant factor limiting primary productivity in the marine environment. However, because of inactivation by solar radiation and resistence of the host cells, the role of cyanophages has remained unclear (Bergh et al., 1989; Proctor and Fuhrman, 1990; Suttle et al., 1990; Suttle et al., 1993; Waterbury and Valois, 1993).

Several bacteria have been discovered that attack phototrophic bacteria (Guerrero et al., 1986; Nogales et al., 1997). *Vampirococcus* attaches to the cell surface of *Chromatium* spp. where it divides, forming chains of up to three cells. Concomitantly, the cytoplasm of the host cell appears to be degraded. *Daptobacter* penetrates the cell envelope and divides intracellularly by binary fission. In contrast to *Vampirococcus*, *Daptobacter* has been cultivated in the absence of the host and grows by fermentative metabolism. *Bdellovibrio* has a broad host range, and under laboratory conditions attacks also purple sulfur bacteria. *Bdellovibrio* forms daughter cells by multiple division in the periplasmic space of the host cell. The Gram-negative chemotrophic bacterium *Stenotrophomonas maltophilia* is a non-obligatory parasite of green sulfur bacteria, which causes cell lysis and ghost formation (Nogales et al., 1997). Its host range is not limited to green sulfur bacteria. The presence of parasitic bacteria in water samples becomes evident by the formation of

lytic plaques on lawns of host bacteria (Esteve et al., 1992; Nogales et al., 1997). Up to 94% of the cells of phototrophic sulfur bacteria may be infected by parasitic bacteria in natural samples. Since infection is largely limited to nongrowing cells, the impact of parasitism on populations of phototrophic sulfur bacteria appears to be limited (van Gemerden and Mas, 1995).

Evolutionary Considerations

Porphyrins are found in all organisms from archaebacteria through plants to animals, and are indispensable as prosthetic groups for energy conservation. In contrast, the partially reduced derivates of porphyrins, the (bacterio)chlorophylls, are synthesized by members of only a few bacterial divisions (Fig. 1). This indicates that the capability for synthesis of porphyrins is a very ancient trait, whereas only a few prokaryotes acquired the capability to form photosynthetic pigments. Photosynthesis requires the presence of various complex protein structures and cofactors, and thus the expression of a large number of different genes (see Photosynthetic gene cluster). Previously, it had therefore appeared justified to consider all phototrophic prokaryotes as a monophyletic group only distantly related to nonphototrophic bacteria (Pfennig and Trüper, 1974; Trüper and Pfennig, 1978). Two lines of evidence have been used to recon struct the evolution of photosynthesis.

Fossil Evidence

The oldest fossils of microorganisms have been dated back to the early Archaean (3.8 billion years ago) and may represent remains of cyanobacteria (Awramik, 1992). They consist of chemical fossils and stromatolites that have been detected especially in sedimentary rocks of the Pilbara region, Western Australia, and the Barberton Mountain Land, South Africa. Stromatolites are laminated convex domes and columns of cm to dm size and have been found in 3.5 to 0.8 billion year old rocks. Although scarce in biosynthetic molecular skeletons, the insoluble, high-molecular-weight organic matter (kerogen) contains isotopic evidence for autotrophic carbon fixation. The ratio of stable carbon isotopes ($\delta^{13}C$ values) are in the range of –35.4 to –30.8°/oo, which is typical for CO_2-carbon fixed by the ribulose-1,5-bisphosphate cycle (Hayes et al., 1983). In addition, the se ancient sediments contain laminated domes and columns of cm to dm size, which in analogy to extant stromatolites have been interpreted as organosedimentary structures produced by the trapping, binding, and precipitation activity of filamentous microorganisms, most likely cyanobacteria.

Alternatively, it has been proposed that anoxygenic photosynthetic bacteria and not the oxygenic cyanobacteria formed the oldest stromatolites. Based on the phylogenetic analysis of the 16S rRNA gene sequence (Oyaizu et al., 1987) and the ecophysiology (Ward et al., 1989) of the filamentous green photosynthetic bacterium *Chloroflexus aurantiacus*, similar anoxygenic phototrophic bacteria may be the more likely candidate microorganisms that built the most ancient stromatolites. However, according to analyses of the nucleotide sequences of its reaction center polypeptides and primary sigma factor (see Molecular evidence), *Chloroflexus aurantiacus* does not represent a deep branch of bacterial evolution. Gypsum layers within the supposed stromatolites have been interpreted as indicators of sulfide oxidation by either anoxygenic phototrophs or colorless sulfur-oxidizing bacteria (Awramik, 1992). However, similar structures have been discovered in lacustrine, and thus sulfur-depleted, settings with little input of allochthonous organic carbon (Buick, 1992). Therefore, at least some 2.7 billion year-old stromatolites are more likely to have harbored oxygenic cyanobacteria. Taken together with the fossil evidence, this would indicate that

diversification of the major groups of phototrophic microorganisms did occur during the early Archaean (Awramik, 1992).

Because of the indefinite character of the fossil evidence, 16S rRNA sequences and components of the photosynthetic apparatus of the different photosynthetic prokaryotes have been used to gain additional insight into the evolution of photosynthesis.

Molecular Evidence

Chlorophyll-based photosystems are only found in the Bacteria and chloroplasts, suggesting that this type of energy conversion originated in the bacterial lineage after the divergence of Archaea and Eukarya. So far, photosynthetic species have not been discovered in the very early lineages of the bacterial radiation (e.g., the thermophilic oxygen reducers and *Thermotogales*; Fig. 1). Because most species of these lineages are chemolithotrophic, it has been proposed that chemolithoautotrophy preceded phototrophy during the evolution of the Bacteria (Pace, 1997). This conclusion is supported by the fact that in phylogenetic trees based on protein sequences of elongation factor EF-Tu and the β-subunit of ATP synthase, only the *Aquificales* and *Thermotogales* branch deeper than the majority of the bacterial divisions, while the *Chloroflexus* subdivision does not (Stackebran dt et al., 1996), thus indicating that *Chloroflexus* does not represent the descendant of a more ancient ancestor than other phototrophic bacteria.

At present, five of the known bacterial lineages comprise phototrophic species (Fig. 1, see Taxonomy of phototrophy among prokaryotes). Based on 16S rRNA sequences, extant phototrophic species of different lineages are only very distantly related to each other. Furthermore, one lineage, the *Chloroflexus* subgroup, represents an early branch in the evolution of the Bacteria. Given the complexity of the photosynthetic apparatus, it is unlikely that photosynthesis has evolved more than once during the evolution of the domain Bacteria (Woese, 1987). The phylogenetic analysis indicates that either an early ancestor of most known bacteria had acquired the capacity for photosynthetic growth (Stackebrandt et al., 1988) or, alternatively, that the genes coding the photosynthetic apparatus were transferred laterally between phylogenetically distant bacteria. The evidence for the various scenarios of the evolution of bacterial photosynthesis is discussed in the present section.

Originally, it had been proposed (Oparin, 1938; Gest and Schopf, 1983a) that anaerobic, heterotrophic prokaryotes capable of fermenting hexose sugars were among the earliest life forms and that electron transport and photosynthesis evolved as a response to the depletion of organic nutrients from the primordial soup. Based on one hypothesis (the Granick hypothesis; Granick, 1965), the biosynthetic pathway of photosynthesis pigment molecules may be taken as a recapitulation of evolution such that compounds with shorter biosynthetic pathways reflect the more ancestral state. The synthesis of bacteriochlorophyll requires one additional enzymatic reduction than that of chlorophyll. Because chlorophyll precedes bacteriochlorophyll in the biosynthetic pathway, the former should have existed earlier in nature. It has been proposed (Pierson and Olson, 1989) that a non-oxygenic photosynthetic ancestor containing chlorophyll *a* and the two types of reaction centers evolved prior to the major radiation event of the Bacteria. During the subsequent radiation, oxygen evolution appeared in one line of descent whereas either the quinone or the FeS-type photosystem was lost in other lineages, concomitant with the emergence of the different bacteriochlorophylls. Besides avoiding an a priori lateral gene transfer of the complete photosynthetic gene cluster, this Pierson-Olson hypothesis takes into account the ecological conditions of the early biosphere in which the absence of oxygen and ozone caused a

predominance of radiation in the blue and UV wavelength range, which in turn would render the red-shifted absorption maxima of bacteriochlorophylls of little selective advantage (Boxer, 1992).

As an argument against the Granick and Pierson-Olson hypotheses, several types of phototrophic bacteria that would be expected are apparently missing in nature. As an example, anoxygenic chlorophyll-containing forms have never been found, although it has been argued that the 8-hydroxychlorophyll-containing *Heliobacteriaceae* represents this type inasmuch as bacteriochlorophyll g is easily converted to chlorophyll *a* by oxidation. Bacteriochlorophylls occur in both types of reaction centers, the pheophytin-type (*Proteobacteria*, *Chloroflexus*) and the FeS-type. This could indicate that the presence of bacteriochlorophyll represents a primitive trait. The chlorophyll-first hypothesis postulates that bacteriochlorophyll has replaced chlorophyll independently in at least three different bacterial lineages. Chlorophyll, however, is presently only found in oxygen-evolving organisms of the phylum *Cyanobacteria* whic h, based on 16S rRNA sequence comparison, represents the most recently evolved group of phototrophic bacteria (Woese, 1987, Fig. 1). *Cyanobacteria* contain two different photosystems and thus have the most complex photosynthetic apparatus. In addition, the much higher complexity of the oxygen-evolving PSII of oxygenic phototrophic organisms may imply that it appeared later than the other photosystems during evolution.

As another argument against the Pierson-Olson hypothesis, chlorophyll itself should have been of little selective advantage in Earth's early biosphere and it has been proposed that quinone-iron complexes represented the first photosynthetic unit (Boxer, 1992). In contrast to the complex porphyrin pigments, quinones can form spontaneously from acetyl thioesters (Hartmann, 1992). Furthermore, the discrepancy between the presence of chlorophyll exclusively in the most highly evolved bacteria and its shorter biosynthetic pathway may be explained by the finding that the chlorin reductase, which catalyzes the additional step of the biosynthetic pathway for bacteriochlorophyll, is phylogenetically older than the enzyme (protochlorophyllide reductase) that catalyzes the preceeding step. This enzyme is present in both the chlorophyll- and bacteriochlorophyll-containing bacteria (Burke et al., 1993). An ancien t reductase may have been able to perform both, the reduction of protochlorophyllide and of chlorin, such that bacteriochlorophyll was the photochemically active pigment in the last common ancestor of all extant phototrophic bacteria.

An analysis of the distribution of the different types of reaction centers among the different bacterial phyla and the amino acid sequences of reaction center proteins (Blankenship, 1992) provides an alternative hypothesis for the evolution of photosynthesis, namely the possibility of lateral transfer of photosynthesis genes. Both the pheophytin/quinone and the FeS-type reaction centers are found in phylogenetically distant groups (e.g., a pheophytin/quinone reaction center in *Chloroflexus* and phototrophic members of the α-Proteobacteria). Even more significantly, a phylogenetic analysis of the amino acid sequences of pheophytin-type reaction center polypeptides from the three different bacterial lineages *Chloroflexaceae*, *cyanobacteria* and α-Proteobacteria indicated that the reaction center of *Chloroflexus aurantiacus* is more closely related to that of phototrophic members of the α-Proteobacteria than to the PSII reaction center of cyanobacteria (Blankenship, 1992). Thus the reaction center of *Chloroflexus* must have evolved after (and not prior to) the divergence of the D1/D2 branch from the L/M line of descent. Another essential component of the photosynthetic apparatus of *Chloroflexus* and green sulfur bacteria are the light-harvesting chlorosomes. Based on amino acid sequence comparison of protein constituents, chlorosomes of both groups have a common evolutionary origin (Wagner-Huber et al., 1988). Similarly, a comparison of the amino acid sequences of the group 1 σ^{70} primary sigma factor also has demonstrated a close relationship to the green sulfur bacteria with respect to this component of the central housekeeping function (Gruber and Bryant, 1998). Other features of *Chloroflexus*

aurantiacus appear to be unique (like the lipid and carotenoid composition), or ancient (like the hydroxypropionate pathway of CO_2-fixation). Recently, the activity of the key enzymes of this pathway have been reported for some archaea (Menendez et al., 1999) such that *Chloroflexus aurantiacus* seems to represent a "chimeric" organism.

Based on the most parsimonious assumption that homodimeric reaction centers are ancestral to homodimeric ones, the reaction centers of green sulfur bacteria and *Heliobacteriaceae* would resemble most the reaction center of the ancestor of all extant bacteria. It has been hypothesized (Gruber and Bryant, 1998) that the reaction center of *Chloroflexus aurantiacus* was acquired by a recent lateral gene transfer event that may have replaced a type I reaction center with a type II (FeS) reaction center, whereas other features like primary sigma factor or chlorosomes still reflect the common descent of *Chloroflexus* and the green sulfur bacteria. Alternatively, it has been suggested that transfer of the genetic information of the relatively simple chlorosomes occurred after the evolution of the two classes of reaction centers and that the green sulfur bacteria represent a relatively modern evolutionary invention (Stackebrandt et al., 1996).

The presence of two homologous polypeptides in all known reaction centers would suggest a single gene duplication event in an early ancestor of all phototrophic bacteria. As an additional result of the phylogenetic analysis of the amino acid sequences of pheophytin-type reaction center polypeptides from the three different bacterial lineages (*Chloroflexaceae*, *cyanobacteria* and α-Proteobacteria; Blankenship, 1992), the most likely occurrence of two independent gene duplications is suggested—one leading to the reaction center of PSII in cyanobacteria and green plants (polypeptides D1 and D2) and another to the reaction center of *Chloroflexus* and purple nonsulfur bacteria (polypeptides L and M). Another, third, independent gene duplication has to be assumed during the evolution of the FeS-type reaction center. The reason for the paraphyletic development of the three lineages may be a functional advan tage of dimeric reaction centers over monomeric ones.

Yet another evolutionary scenario for photosynthetic reaction centers (Vermaas, 1994) has been based on the finding that the sixth membrane-spanning region of the heliobacterial (FeS- or PSI-type) reaction center shows a great similarity to the sixth membrane-spanning region of the CP47 antenna polypeptide of (the quinone-type) PSII, and the preceeding N-terminal five hydrophobic regions still show significantly greater similarity to CP47 (and to another PSII antenna protein, CP43) than to the respective portion of PSI. According to this model, an ancestral homodimeric antenna/reaction center complex comprised 11 putative transmembrane regions and contained two quinones and an F_x-type Fe_4S_4 iron-sulfur center. Relatively few modifications may have led to the homodimeric complex of green sulfur bacteria and *Heliobacteriaceae*, whereas a gene duplication event and divergent evolution led to the heterodimeric PSI. As a para llel line of descent, splitting of the ancestral reaction center complex into a reaction center and a separate antenna protein may have occurred. Operon duplication, loss of the FeS, and divergent evolution are assumed to have resulted in two separate lineages. By association with an additional water-splitting enzyme system, PSII was formed. In contrast, the separate antenna polypeptide was lost and replaced by a modified antenna complex (light-harvesting I) during evolution of the reaction center of Proteobacteria and *Chloroflexus*. Significantly, however, this theory does not explain the occurrence of the quinone-type reaction center in these latter two groups, which are phylogenetically very distant. In addition, the combination of a reaction center typical for *Proteobacteria* with an antenna structure characteristic for green sulfur bacteria would still need to be explained by lateral gene transfer of either of the two components.

Based on the obvious discrepancy between the phylogeny of ribosomal RNA and reaction center proteins, the hypothesis of lateral transfer of photosynthesis genes between distantly related

groups of bacteria has been put forward. Lateral gene transfer as yet seems to provide the simplest explanation for the distribution pattern of photosynthesis genes within the bacterial radiation (Blankenship, 1992; Nagashima et al., 1993; Nagashima et al., 1997). Such a lateral gene transfer would encompass reaction center structural genes, genes coding for other electron transfer proteins, and genes needed for the biosynthesis of pigments and cofactors. In purple nonsulfur bacteria the majority of these genes indeed form a single cluster of 46 kb (which does not encompass the genes for the light-harvesting II complex, however; Bauer and Bird, 1996; Wellington et al., 1992; Yildiz et al., 1992). The genetic organization may be taken as evidence for lateral gene transfer as the cluster represents only ~1.3% of the total genome size. It should be mentioned, however, that clustering of most photosynthesis genes may also be due to structural or regulatory constraints. Supporting the latter argument (Yildiz et al., 1992), photosynthesis genes in α-Proteobacteria are transcriptionally coupled in superoperons involving overlapping transcripts. The particular genetic organization is the prerequisite for adaptation of the cells to changing light intensity (see Genetic regulation in response to light) and oxygen tension (see Genetic regulation by O_2). Therefore a selective pressure may exist to retain the linkage order and would make the genetic organization of the photosynthesis genes less suitable for phylogenetic inference. Furthe rmore, the high correlation between the phylogenetic trees for 16S rRNA and cytochrome c in phototrophic members of the α-Proteobacteria has been taken as evidence that a lateral transfer of photosynthesis genes did not occur at least within this phylogenetic group (Woese et al., 1980). Thus, the presence of reaction centers in aerobic bacteriochlorophyll-containing α-Proteobacteria may represent an atavistic trait, and the genes coding the reaction center might have been lost frequently during the evolution of aerobic representatives in this group (Stackebrandt et al., 1996).

Because the pigment composition of the oxygenic photosynthetic 'Prochlorophytes' is very similar to that of green plant chloroplasts, and like the latter 'Prochlorophytes' have appressed thylakoid membranes, it has been proposed that the chloroplasts of green plants evolved from an endosymbiotic 'prochlorophyte' (van Valen and Maiorana, 1980; Lewin, 1981). In contrast to the other oxygenic phototrophs, *Prochlorococcus* contains divinyl isomers of chlorophylls a and b, and α- instead of β-carotene (Chrisholm et al., 1992; Goericke and Repeta, 1992). However, based on sequence comparison of 16S rRNA (Urbach et al., 1992) and the *rpoC1* (Palenik and Haselkorn, 1992) genes, the three known prochlorophyte lineages (*Prochloron*, *Prochlorothrix*, and *Prochlorococcus*) are no direct ancestors of chloroplasts. In addition, these analyses revealed that 'Prochlorophytes' most likely are of polyphyletic origin and that the use of chlorophyll *b* as additional light-harvesting pigments must have developed at least four times during evolution. In this case, too, a horizontal transfer of the respective biosynthesis genes could be invoked to explain the distribution pattern of chlorophyll *b* among the different members of the cyanobacterial division (Palenik and Haselkorn, 1992). Immunological studies and differences in the chlorophyll a/ chlorophyll *b* ratio of the antennae isolated from different 'Prochlorophytes' indicate that the capacity to bind chlorophyll *b* arose several times and independently from the cyanobacterial ancestors, and thus confirm the results of s equence comparisons of the *16S rRNA* and *rpoC1* genes.

Literature Cited

Alberti M, Burke DH, Hearst JE.; 1995. *Structure and sequence of the photosynthesis gene cluster In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic photosynthetic bacteria* Kluwer Academic Publishers Dordrecht, Boston, London, , pp. 1083–1106

Amesz J.; 1995. *The antenna-reaction center complex of Heliobacteria* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 687–697

K Anagnostidis, J Komárek.; 1988. *Modern approach to the classification system of the cyanophytes. 3. Oscillatoriales* **Arch Hydrobiol Suppl 80 Algol. Studies**, vol. 53, pp. 327–472 PubMed

A Angerhofer, RJ Cogdell, MF Hipkins.; 1986. *A spectral characterization of the light-harvesting pigment-protein complexes fromRhodopseudomonas acidophila* **Biochim Biohys Acta**, vol. 848, pp. 333–341 PubMed

Armitage JP, Kelly DJ, Sockett RE.; 1995. *Flagellate motility, behavioral responses and active transport in purple non-sulfur bacteria* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.) *Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 1005–1028

J P Armitage.; 1997. *Behavioral resposnes of bacteria to light and oxygen* **Arch Microbiol**, vol. 168, pp. 249–261 PubMed

Arnheim K, Oelze J.; 1983. *Differences in the control of bacteriochlorophyll formation by light and oxygen* **Arch Microbiol**, vol. 135, pp. 299–304 PubMed

Awramik, S.M.; 1992. *The oldest records of photosynthesis* **Photosynth Res**, vol. 33, pp. 75–89 PubMed

Barry BA, Boerner RJ, de Paula JC.; 1994. *The use of cyanobacteria in the study of the structure and function of photosystem II* *In:* Bryant DA (Eds.)*The molecular biology of cyanobacteria* Kluwer Academic Publishers Dordrecht, Boston, London, , pp. 217–257

Bauer CE, Bollivar DW, Suzuki JY.; 1993. *Genetic analyses of photopigment biosynthesis in eubacteria: a guiding light for algae and plants* **J Bacteriol**, vol. 175, pp. 3919–3925 PubMed

Bauer CE.; 1995. *Regulation of photosynthesis gene expression* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 1221–1234

Bauer CE, Bird TH.; 1996. *Regulatory circuits controlling photosynthesis gene expression* **Cell**, vol. 85, pp. 5–8 PubMed

Beale SI.; 1995. *Biosynthesis and structures of porphyrins and hemes* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 153–177

B. M. Bebout, F Garcia-Pichel; 1995. *UVB-induced vertical migrations of cyanobacteria in a microbial mat* **Appl Environm Microbiol**, vol. 61, pp. 4215–4222 PubMed

Beck H, Hegeman GD, White D.; 1990. *Fatty acid and lipopolysaccharide analyses of three*

Heliobacterium spp. **FEMS Microbiol Lett**, vol. 69, pp. 229–232 PubMed

Beer-Romero P, Favinger JL, Gest H.; 1988. *Distinctive properties of bacilliform photosynthetic heliobacteria* **FEMS Microbiol Lett**, vol. 49, pp. 451–454 PubMed

Bergh Ø, Børsheim KY, Bratbak G, Heldal M.; 1989. *High abundance of viruses found in aquatic environments* **Nature**, vol. 340, pp. 467–468 PubMed

Biebl H, Drews G.; 1969. *Das in vivo Spektrum als taxonomisches Merkmal bei Untersuchungen zur Verbreitung der Athiorhodaceae* **Zbl Bakt Abt II**, vol. 123, pp. 425–452 PubMed

Biedermann M, Drews G, Marx R, Schröder J.; 1967. *Der Einfluß des Sauerstoffpartialdruckes und der Antibiotica Actinomycin und Puromycin auf das Wachstum, die Synthese von Bacteriochlorophyll und die Thylakoidmorphogenese inDunkelkulturen von Rhodospirillum rubrum* **Arch Mikrobiol**, vol. 56, pp. 133–147 PubMed

Biel AJ.; 1986. *Control of bacteriochlorophyll accumulation by light in Rhodobacter capsulatus* **J Bacteriol**, vol. 168, pp. 655–659 PubMed

Biel AJ.; 1995. *Genetic analysis and regulation of bacteriochlorophyll biosynthesis In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 1125–1134

Blankenship, R.E.; 1992. *Origin and early evolution of photosynthesis* **Photosynth Res**, vol. 33, pp. 91–111 PubMed

Blankenship RE, Olson JM, Miller M.; 1995. *Antenna complexes from green photosynthetic bacteria In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic photosynthetic bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 399–435

Bobe FW, Pfennig N, Swanson KL, Smith KM.; 1990. *Red shift of absorption maxima in Chlorobiaceae through enzymic methylation of their antenna bacteriochlorophylls* **Biochemistry**, vol. 29, pp. 4340–4348 PubMed

Bowyer JR, Hunter CN, Ohnishi T, Niederman RA.; 1985. *Photosynthetic membrane development in Rhodopseudomonas sphaeroides* **J Biol Chem**, vol. 260, pp. 3295–3304 PubMed

Boxer, S.G.; 1992. *Some speculations concerning the evolution of photosynthetic function* **Photosynth Res**, vol. 33, pp. 113–119 PubMed

Brockmann H, Lipinski A.; 1983. *Bacteriochlorophyll g. A new bacteriochlorophyll from Heliobacterium chlorum* **Arch Microbiol**, vol. 136, pp. 17–19 PubMed

Brune DC.; 1989. *Sulfur oxidation by phototrophic bacteria* **Biochim Biophys Acta**, vol. 975, pp. 189–221 PubMed

D A Bryant.; 1982. *Phycoerythrocyanin and phycoerythrin: properties and occurrence in*

cyanobacteria **J Gen Microbiol**, vol. 128, pp. 835–844 PubMed

B Büdel, U Karsten, F Garcia-Pichel.; 1997. *Ultraviolet-absorbing scytonemin and mycosporine-like amino acids in exposed. rock-inhabiting cyanobacterial lichens* **Oecologia**, vol. 112, pp. 165–172 PubMed

Buick, R.; 1992. *The antiquity of oxygenic photosynthesis: evidence from stromatolites in sulphate-deficient Archaean lakes* **Science**, vol. 255, pp. 74–77 PubMed

Burke, DH, Hearst, JE, Sidow, A.; 1993. *Early evolution of photosynthesis:Clues from nitrogenase and chlorophyll iron proteins* **Proc Natl Acad Sci USA**, vol. 90, pp. 7134–7138 PubMed

Caldwell DE, Tiedje JM.; 1975. *The structure of anaerobic bacterial communities in the hypolimnia of several Michigan lakes* **Can J Microbiol**, vol. 21, pp. 377–385 PubMed

A Camacho, F Garcia-Pichel, E Vicente, R W Castenholz.; 1996. *Adaptation to sulfide and to the underwater light field in three cyanobacterial isolates from lakeArcas (Spain)* **FEMS Microbiol Ecol**, vol. 21, pp. 293–301 PubMed

R. E. Cameron.; 1966. *Desert Algae: soil crusts and diaphanous substrata as algal habitats* **Jet Propulsion Lab. Tech. Rep.**, vol. 32–971, pp. 1–41 PubMed

Campbell L, Vaulot D.; 1993. *Photosynthetic picoplankton community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA)* **Deep Sea Res**, vol. 40, pp. 2043–2060 PubMed

Campbell L, Nolla HA, Vaulot D.; 1994. *The importance of Prochlorococcus to community structure in the central North Pacific Ocean* **Limnol Oceanogr**, vol. 39, pp. 954–961 PubMed

D G Capone, J P Zehr, H W Paerl, B Bergman, E J Carpenter.; 1977. *Trichodesmium, a globally significant cyanobacterium* **Science**, vol. 276, pp. 1221–1229 PubMed

Carr NG, Mann NH.; 1994. *The oceanic cyanobacterial picoplankton* *In:* Bryant DA (Eds.)*The Molecular Biology of Cyanobacteria* Kluwer Academic Publishers Dordrecht, Boston, London, , pp. 27–48

R W Castenholz.; 1982. *Motility and Taxes* *In:* N G Carr, B A Whitton (Eds.)*The biology of cyanobacteria* Blackwell Scientific Publications Oxford, , pp. 413–440

R W Castenholz, H C Utkilen.; 1984. *Physiology of sulfide tolerance in a thermophilic Oscillatoria* **Arch Microbiol**, vol. 138, pp. 299–305 PubMed

R W Castenholz.; 1989. *Oxygenic Photosynthetic Bacteria* *In:* J T Staley, M P Bryant, N Pfennig, J G Holt (Eds.)*Bergey's Manual of Systematic Bacteriology* Williams & Wilkins Baltimore, , pp. 1710–1806

R W Castenholz, J Bauld, B B Jørgensen.; 1990. *Anoxygenic microbial mats of hot springs: thermophilic Chlorobium sp.* **FEMS Microbio Ecol**, vol. 74, pp. 325–336 PubMed

R W Castenholz.; 1992. *Species usage, concept and evolution in the cyanobacteria (Blue-green algae)* **J Phycol**, vol. 28, pp. 735–745 PubMed

Castenholz RW, Pierson BK.; 1995. *Ecology of thermophilic anoxygenic phototrophs In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 87–103

R W Castenholz, F Garcia-Pichel.; 1999. *Cyanobacterial responses to UV-radiation In:* B A Whitton, M Potts (Eds.)*Ecology of cyanobacteria: their diversity in time and space* Kluwer Academic Publications Dordrecht, , pp.

Chisholm SW, Olson RJ, Zettler ER, Goericke R, Waterbury JB, Welschmeyer NA.; 1988. *A novel free-living prochlorophyte abundant in the oceanic euphotic zone* **Nature**, vol. 334, pp. 340–343 PubMed

Chisholm SW, Frankel SL, Goericke R, Olson RJ, Palenik B, Waterbury JB, West-Johnsrud L, Zettler ER.; 1992. *Prochlorococcus marinus nov. gen. nov. sp.: an oxyphototrophic marine prokaryote containing divinyl chlorophyll a and b* **Arch Microbiol**, vol. 157, pp. 297–300 PubMed

Clarke KJ, Finlay BJ, Vicente E, Lloréns H, Miracle MR.; 1993. *The complex life-cycle of a polymorphic prokaryote epibiont of the photosynthetic bacterium Chromatium weissei* **Arch Microbiol**, vol. 159, pp. 498–505 PubMed

Cohen Y, Jørgensen BB, Padan E, Shilo M.; 1975. *Sulphide-dependent anoxygenic photosynthesis in the cyanobacterium Oscillatoria limnetica* **Nature**, vol. 257, pp. 489–492 PubMed

Y Cohen, B B Jørgensen, N P Revsbech, R Poplawski.; 1986. *Adaptation to hydrogen sulfide of oxygenic and anoxygenic photosynthesis among cyanobacteria* **Appl. Environ. Microbiol**, vol. 51, pp. 398–407 PubMed

Coolen MJL, Overmann J.; 1998. *Analysis of subfossil molecular remains of purple sulfur bacteria in a lake sediment* **Appl Environ Microbiol**, vol. 64, pp. 4513–4521 PubMed

De Wit R, van Gemerden H.; 1987a. *Chemolithotrophic growth of the phototrophic sulfur bacterium Thiocapsa roseopersicina* **FEMS Microbiol Ecol**, vol. 45, pp. 117–126 PubMed

De Wit R, van Gemerden H.; 1987b. *Oxidation of sulfide to thiosulfate by Microcholeus chtonoplastes* **FEMS Microbiol Ecol**, vol. 45, pp. 7–13 PubMed

De Wit R, van Boekel WHM, van Gemerden H.; 1988. *Growth of the cyanobacterium Microcoleus chtonoplastes on sulfide* **FEMS Microbiol Ecol**, vol. 53, pp. 203–209 PubMed

De Wit R, Jonkers HM, van den Ende FP, van Gemerden H.; 1989. *In situ fluctuations of oxygen and sulphide in marine microbial sediment ecosystems* **Neth J Sea Res**, vol. 23, pp. 271–281 PubMed

De Wit R, van Gemerden H.; 1990a. *Growth and metabolism of the purple sulfur bacterium*

Thiocapsa roseopersicina under combined light/dark and oxic/anoxic regimens **Arch Microbiol**, vol. 154, pp. 459–464 PubMed

De Wit R, van Gemerden H.; 1990b. *Growth of the phototrophic purple sulfur bacterium Thiocapsa roseopersicina under oxic/anoxic regimens in the light* **FEMS Microbiol Ecol**, vol. 73, pp. 69–76 PubMed

Dierstein R.; 1984. *Synthesis of pigment-binding protein in toluene-treated Rhodopseudomonas capsulata and in cell-free systems.* **Eur J Biochem**, vol. 138, pp. 509–518 PubMed

Dietrich, G, Kalle, K, Krauss, W, Siedler, G.; 1975. *Allgemeine Meereskunde* Gebrüder Bornträger Berlin, Stuttgart, , pp. 593

Drews G, Golecki JR.; 1995. *Structure, molecular organization, and biosynthesis of membranes of purple bacteria In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 231–257

Dubinina GA, Gorlenko VM.; 1975. *New filamentous photosynthetic green bacteria containing gas vacuoles* **Mikrobiologiya**, vol. 44, pp. 511–517 PubMed

J W Eaton, B Moss.; 1966. *The estimation of numbers and pigment content in epipelic algal populations* **Limnol Ocean**, vol. 11, pp. 584–594 PubMed

M Ehling-Schulz, W Bilger, S Scherer.; 1997. *UVB induced synthesis of photoprotective pigments and extracellular polysaccharides in the terrestrial cyanobacterium Nostoc commune* **J Bacteriol**, vol. 179, pp. 1940–1945 PubMed

Eichler B, Pfennig N.; 1986. *Characterization of a new platelet-forming purple sulfur bacterium Amoebobacter pedioformis sp. nov.* **Arch Microbiol**, vol. 146, pp. 295–300 PubMed

Eisenreich W, Strauß G, Werz U, Fuchs G, Bacher A.; 1993. *Retrobiosynthetic analysis of carbon fixation in the phototrophic eubacterium Chloroflexus aurantiacus* **Eur J Biochem**, vol. 215, pp. 619–632 PubMed

Esteve I, Gaju N, Mir J, Guerrero R.; 1992. *Comparison of techniques to determine the abundance of predatory bacteria attacking Chromatiaceae* **FEMS Microbiol Ecol**, vol. 86, pp. 205–211 PubMed

Evans WR, Fleischman DE, Calvert HE, Pyati PV, Alter GM, Rao NSS.; 1990. *Bacteriochlorophyll and photosynthetic reaction centers in Rhizobium strain BTA:1* **Appl Environ Microbiol**, vol. 56, pp. 3445–3449 PubMed

Fenchel T, Bernard C.; 1993a. *A purple protist* **Nature**, vol. 362, pp. 300 PubMed

Fenchel T, Bernard C.; 1993b. *Endosymbiotic purple non-sulphur bacteria in an anaerobic ciliated protozoon* **FEMS Microbiol Lett**, vol. 110, pp. 21–25 PubMed

Ferguson SJ, Jackson JB, McEwan AG.; 1987. *Anaerobic respiration in the Rhodospirillaceae: characterization of pathways and evaluation of roles in redox balancing during photosynthesis* **FEMS Microbiol Rev**, vol. 46, pp. 117–143 PubMed

A Fernández-González, I M Martínez-Pérez, A Vioque.; 1998. *Characterization of two carotenoid gene promoters in the cyanobacterium Synechocystis sp PCC6803* **Biochim Biophys Acta**, vol. 1443, pp. 343–351 PubMed

Ferris MJ, Ruff-Roberts AL, Kopczynski ED, Bateson MM, Ward DM.; 1996. *Enrichment culture and microscopy conceal diverse thermophilic Synechococcus populations in a single hot spring microbial mat habitat* **Appl Environ Microbiol**, vol. 62, pp. 1045–1050 PubMed

Fleischman DE, Evans WR, Miller IM.; 1995. *Bacteriochlorophyll-containing Rhizobium species* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 123–136

Foy RH. Gibson CE.; 1982. *Photosynthetic characteristics of planktonic blue-green algae: changes in photosynthetic capacity and pigmentation of Oscillatoria redekei Van Goor under high and low light* **Br Phycol**, vol. 17, pp. 183–193 PubMed

Fröstl JM, Overmann J.; 1998. *Physiology and tactic response of the phototrophic consortium "Chlorochromatium aggregatum"* **Arch Microbiol**, vol. 169, pp. 129–135 PubMed

Fründ C, Cohen Y.; 1992. *Diurnal cycles of sulfate reduction under oxic conditions in cyanobacterial mats* **Appl Environ Microbiol**, vol. 58, pp. 70–77 PubMed

E I Friedmann, R Ocampo.; 1976. *Endolithic blue-green algae in the Dry valleys: primary producers in the Anctarctic Desert Ecosystem* **Science**, vol. 193, pp. 1247–1249 PubMed

E I Friedmann.; 1982. *Endolithic microorganims in the Antactc Cold Desert* **Science**, vol. 215, pp. 1045–1053 PubMed

F E Fritsch.; 1922. *The terrestrial algae* **J Ecol**, vol. 10, pp. 220–236 PubMed

Fry B.; 1986. *Sources of carbon and sulfur nutrition for consumers in three meromictic lakes of New York state* **Limnol Oceanogr**, vol. 31, pp. 79–88 PubMed

Göbel F.; 1978. *Quantum efficiencies of growth* *In:* Clayton RK, Sistrom WR (Eds.)*The photosynthetic bacteria* Plenum Press New York, , pp. 907–925

E A Galinski.; 1995. *Osmoadaptation in bacteria* **Adv Microb Physiol**, vol. 37, pp. 274–328 PubMed

Gantt E.; 1994. *Supramolecular membrane organization* *In:* Bryant DA (Eds.)*The Molecular Biology of Cyanobacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 119–138

F Garcia-Pichel, R W Castenholz.; 1990. *Comparative anoxygenic photosynthetic capacity in 7*

strains of a thermophilic cyanobacterium **Arch Microbiol**, vol. 153, pp. 344–355 PubMed

F Garcia-Pichel, M Mechling, R W Castenholz.; 1994a. *Diel migrations of microorganisms within a benthic, hypersaline mat community* **Appl Environ Microbiol**, vol. 60, pp. 1500–1511 PubMed

F. Garcia-Pichel.; 1994b. *A model for internal self-shading in planktonic microorganisms and its implications for the usefulness of sunscreens* **Limnol Ocean**, vol. 39, pp. 1704–1717 PubMed

F Garcia-Pichel, R W Castenholz.; 1994c. *On the significance of solar ultraviolet radiation for the ecology of microbial mats* *In:* L J Stal, P Caumette (Eds.)*Microbial mats. Structure, development and environmental significance* Springer-Verlag Heidelberg, , pp. 77–84

F Garcia-Pichel.; 1995. *A scalar irradiance fiber-optic microprobe for the measurement of ultraviolet radiation at high spatial resolution* **Photochem Photobiol**, vol. 61, pp. 248–254 PubMed

F Garcia-Pichel, J Belnap.; 1996. *Microenvironments and microscale productivity of cyanobacterial desert crusts* **J Phycol**, vol. 32, pp. 774–782 PubMed

F Garcia-Pichel, L Prufert-Bebout, G Muyzer.; 1996. *Phenotypic and phylogenetic analyses show Microcoleus chthonoplastes to be a cosmopolitan cyanobacterium* **Appl Environ Microbiol**, vol. 62, pp. 3284–3291 PubMed

F Garcia-Pichel, B Bebout; 1996. *The penetration of ultraviolet radiation into shallow water sediments: high exposure for photosynthetic communities* **Mar. Ecol. Prog. Ser.**, vol. 131, pp. 257–262 PubMed

F Garcia-Pichel, U Nübel, G Muyzer.; 1998. *The phylogeny of unicellular, extremely halotolerant cyanobacteria* **Arch Microbiol**, vol. 169, pp. 469–482 PubMed

F Garcia-Pichel.; 1999. *Cyanobacteria* *In:* J Lederberg (Eds.)*Encyclopedia of Microbiology* Academic Press San Diego,

F. Garcia-Pichel, R.W. Castenholz.; 1999. *Photomovements of microroganisms in sediments and soils* *In:* D-P Häder (Eds.)*Photomovements* Elsevier Amsterdam,

Gates DM.; 1962. *Energy exchange in the biosphere* Harper & Row New York, , pp. 151

L Geitler.; 1932. *Cyanophyceae* Akademische Verlagsgesellschaft Leipzig, , pp. 1035

Gest H, Schopf JW.; 1983a. *Biochemical evolution of anaerobic energy conversion: the transition from fermentation to anoxygenic photosynthesis* *In:* Schopf JW (Eds.)*Earth's Earliest Biosphere* Princeton University Press Princeton, NJ, pp. 135–148

Gest H, Favinger JL.; 1983b. *Heliobacterium chlorum: an anoxygenic brownish-green photosynthetic bacterium containing a new form of bacteriochlorophyll* **Arch Microbiol**, vol. 136, pp. 11–16 PubMed

Gest H.; 1993. *Photosynthetic and quasi-photosynthetic bacteria* **FEMS Microbiol Lett**, vol. 112, pp. 1–6 PubMed

S J Giovanonni, S Turner, G J Olsen, S Barns, D J Lane, N R Pace.; 1988. *Evolutionary relatiosnhips among cyanobacteria and green chloroplasts* **J Bacteriol**, vol. 170, pp. 3548–3592 PubMed

Glaeser J, Overmann J.; 1999. *Selective enrichment and characterization of Roseospirillum parvum, gen. nov. and sp. nov., a new purple nonsulfur bacterium with unusual light absorption properties* **Arch Microbiol**, vol. 171, pp. 405–416 PubMed

Goericke, R, Repeta, DJ.; 1992. *The pigments of Prochlorococcus marinus: The presence of divinyl chlorophyll a and b in a marine procaryote* **Limnol Oceanogr**, vol. 57, pp. 425–433 PubMed

Goericke R, Welschmeyer NA.; 1993. *The marine prochlorophyte Prochlorococcus contributes significantly to phytoplankton biomass and primary production in the Sargasso Sea* **Deep-Sea Res**, vol. 40, pp. 2283–2294 PubMed

Golbeck JH.; 1994. *Photosystem I in cyanobacteria In:* Bryant DA (Eds.)*The molecular biology of cyanobacteria* Kluwer Academic Publishers Dordrecht, Boston, London, , pp. 319–360

S S Golden.; 1994. *Light responsive gene expression and the biochemistry of photosystem II reaction center In:* D A Bryant (Eds.)*The molecular biology of cyanobacteria* Kluwer Academic Press Dordrecht, , pp. 693–714

Golecki JR, Oelze J.; 1987. *Quantitative relationship between bacteriochlorophyll content, cytoplasmic membrane structure and chlorosome size in Chloroflexus aurantiacus* **Arch Microbiol**, vol. 148, pp. 236–241 PubMed

VM Gorlenko, EN Krasil´nikova, OG Kikina, NY Tatarinova.; 1979. *The new motile purple sulfur bacterium Lamprobacter modestohalophilus nov. gen., nov. sp. with gas vacuoles* **Izv. Akad. Nauk. S.S.S.R. Ser. Biol.**, vol. 5, pp. 755–767 PubMed

Gottschalk G.; 1986. *Bacterial metabolism* Springer New York, , pp. 359

Granick, S.; 1965. *Evolution of heme and chlorophyll In:* Bryson, V, Vogel, HJ (Eds.)*Evolving genes and proteins* Academic Press New York, , pp. 67–88

Guerrero R, Pedrós-Alió C, Esteve I, Mas J, Chase D, Margulis L.; 1986. *Predatory prokaryotes: Predation and primary consumption evolved in bacteria* **Proc Natl Acad Sci USA**, vol. 83, pp. 2138–2142 PubMed

R Guyoneaud, R Matheron, R Baulaigue, K Podeur, A Hirschler, P Caumette.; 1996. *Anoxygenic phototrophic bacteria in eutrophic coastal lagoons of the French Mediterranean and Atlantic Coasts* **Hydrobiologia**, vol. 329, pp. 33–43 PubMed

D-P Häder.; 1987. *Photosensory behavior in prokaryotes* **Microbiol Rev**, vol. 51, pp. 1–21 PubMed

Hansen TA, van Gemerden H.; 1972. *Sulfide utilization by purple nonsulfur bacteria* **Arch Mikrobiol**, vol. 86, pp. 49–56 PubMed

Hansen TA, Veldkamp H.; 1973. *Rhodopseudomonas sulfidophila nov. sp., a new species of the purple nonsulfur bacteria* **Arch Microbiol**, vol. 92, pp. 45–58 PubMed

Harashima K, Shiba T, Totsuka T, Simidu U, Taga N.; 1978. *Occurrence of bacteriochlorophyll a in a strain of an aerobic heterotrophic bacterium* **Agricult Biol Chem Tokyo**, vol. 42, pp. 1627–1628 PubMed

Harder W, van Dijken JP.; 1976. *Theoretical considerations on the relation between energy production and growth of methane-utilizing bacteria* *In:* Schlegel HG, Gottschalk G, Pfennig N (Eds.)*Symposium on microbial production and utilization of gases (H_2, CH4, CO)* E Goltze KG Göttingen, , pp. 403–418

Hartman, H.; 1992. *Conjectures and reveries* **Photosynth Res**, vol. 33, pp. 171–176 PubMed

Hartmann R, Sickinger H-D, Oesterhelt D.; 1980. *Anaerobic growth of halobacteria* **Proc Natl Acad Sci USA**, vol. 77, pp. 3821–3825 PubMed

JM Hayes, IR Kaplan, KW Wedeking.; 1983. *Precambrian organic geochemistry, preservation of the record* *In:* JW Schopf (Eds.)*Earth's Earliest Biosphere* Princeton University Press Princeton, NJ, pp. 93–134

S Heising, L Richter, W Ludwig, B Schink.; 1999. *Chlorobium ferrooxidans sp. nov., a phototrophic green sulfur bacterium that oxidizes ferrous iron in coculture with a "Geospirillum" sp. strain* **Arch Microbiol**, vol. 172, pp. 116–124 PubMed

Hofman PAS, Veldhuis MJW, van Gemerden H.; 1985. *Ecological significance of actetate assimilation by Chlorobium phaeobacteroides* **FEMS Microbiol Ecol**, vol. 31, pp. 271–278 PubMed

Holo H.; 1989. *Chloroflexus aurantiacus secretes 3-hydroxypropionate, a possible intermediate in the assimilation of CO_2 and acetate* **Arch Microbiol**, vol. 151, pp. 252–256 PubMed

Holtin RW, Stam WT, Boele-Bos SA.; 1990. *DNA-DNA reassociation studies with DNA from Prochloron (prochlorophyta) samples of Indo-West Pacific origin* **J Phycol**, vol. 26, pp. 358–361 PubMed

Hugenholtz, P, Pitulle, C, Hershberger, KL, Pace, NR.; 1998. *Novel division level bacterial diversity in a Yellowstone hot spring* **J Bacteriol**, vol. 180, pp. 366–376 PubMed

JF Imhoff, BJ Tindall, WD Grant, HG Trüper.; 1981. *Ectothiorhodospira vacuolata sp. nov., a new phototrophic bacterium from soda lakes* **Arch Microbiol**, vol. 130, pp. 238–242 PubMed

Imhoff JF, Trüper HG.; 1989. *Purple nonsulfur bacteria* *In:* Staley JT, Bryant MP, Pfennig N, Holt JG (Eds.)*Bergey's Manual of Systematic Bacteriology* Williams and Wilkins Baltimore, , pp. 1658–1682

Jørgensen BB, Kuenen JG, Cohen Y.; 1979. *Microbial transformations of sulfur compounds in a stratified lake (Solar Lake, Sinai)* **Limnol Oceanogr**, vol. 24, pp. 799–822 PubMed

Jørgensen BB.; 1982. *Ecology of the bacteria of the sulphur cycle with special reference to anoxic-oxic interface environments* **Phil Trans Royal Soc London B**, vol. 298, pp. 543–561 PubMed

Jørgensen BB, Des Marais DJ.; 1986. *A simple fiber-optic microprobe for high resolution light measurements: applications in marinesediments* **Limnol Oceanogr**, vol. 31, pp. 1374–1383 PubMed

B B Jørgensen, D J Des Marais.; 1988. *Optical properties of benthic photosynthetic communities: fiber-optic studies of cyanobacterial mats* **Limnol Ocean**, vol. 33, pp. 99–113 PubMed

Jannasch HW.; 1989. *Chemosynthetically sustained ecosystems in the deep sea* *In:* Schlegel HG, Bowien B (Eds.)*Autotrophic Bacteria* Springer New York, , pp. 147–166

Jorgensen BB, Cohen Y.; 1977. *Solar Lake (Sinai). 5. The sulfur cycle of the benthic microbial mats* **Limnol Oceanogr**, vol. 22, pp. 657–666 PubMed

Kämpf C, Pfennig N.; 1980. *Capacity of Chromatiaceae for chemotrophic growth. Specific respiration rates of Thiocystis violacea and Chromatium vinosum* **Arch Microbiol**, vol. 127, pp. 125–135 PubMed

Kämpf C, Pfennig N.; 1986. *Chemoautotrophic growth of Thiocystis violacea, Chromatium gracile and C. vinosum in the dark at various O_2-concentrations* **J Basic Microbiol**, vol. 26, pp. 517–531 PubMed

Kühl M, Jørgensen BB.; 1992. *Spectral light measurements in microbenthic phototrophic communities with a fiber-optic microprobe coupled to a sensitive diode array detector* **Limnol Oceanogr**, vol. 37, pp. 1813–1823 PubMed

T Kana, P M Gilbert, R Goericke, N A Welschmeyer.; 1988. *Zeaxanthin and beta-carotene in Synechococcus WH7803 respond differently to irradiation* **Limnol Oceanogr**, vol. 33, pp. 1623–1627 PubMed

O I Keppen, O I Baulina, E N Kondratieva.; 1994. *Oscillochloris trichoides neotype strain DG-6* **Photosynthesis Res**, vol. 41, pp. 29–33 PubMed

Kimble LK, Mandelco L, Woese CR, Madigan MT.; 1995. *Heliobacterium modesticaldum, sp. nov., a thermophilic heliobacterium of hot springs and volcanic soils* **Arch Microbiol**, vol. 163, pp. 259–267 PubMed

Kirk JTO.; 1983. *Light and photosynthesis in aquatic ecosystems* Cambridge University Press Cambridge, , pp. 401

Kok B.; 1973. *Photosynthesis* *In:* Gibbs M, Hollaender A, Kok B, Krampitz LO, San Pietro A (Eds.) *Proceedings of the Workshop on Bio-solar Conversion* National Science Foundation Bethesda, MD

J Komárek, K Anagnostidis.; 1989. *Modern approach to the classification system of cyanophytes. 4. Nostocales* **Arch Hydrobiol Suppl 823, Algol. Studies**, vol. 56, pp. 247–345 PubMed

Kondratieva EN.; 1979. *Interrelation between modes of carbon assimilation and energy production in phototrophic purple and green bacteria* *In:* Quale JR (Eds.)*Microbial Biochemistry* University Park Press Baltimore, , pp. 117–175

Konopka A, Brock TD, Walsby AE.; 1978. *Buoyancy regulation by planktonic blue-green algae in Lake Mendota, Wisconsin* **Arch Hydrobiol**, vol. 83, pp. 524–537 PubMed

Kromkamp JC, Mur LR.; 1984. *Buoyant density changes in the cyanobacterium Microcystis aeruginosa due to changes in the cellular carbohydrate content* **FEMS Microbiol Lett**, vol. 25, pp. 105–109 PubMed

C Krutschel, R W Castenholz.; 1998. *The effect of solar UV and visible irradiance on the vertical movements of cyanobacteria in microbial mats of hypesaline waters* **FEMS Microbiol Ecol**, vol. 27, pp. 53–72 PubMed

Lancaster CRD, Michel H.; 1996. *Three-dimensional structures of photosynthetic reaction centers* **Photosynth Res**, vol. 48, pp. 65–74 PubMed

J Laroche, G M W Vanderstaay, F Partensky, A Ducret, R Aeberssold, R Li, S S Golden, R G Hiller, P M Wrench, A W D Larkum, B R Green.; 1996. *Independent evolution of the Prochlorophyte and green plant Chlorophyll a/b light-harvesting proteins* **Proc Natl Acad Sci (USA)**, vol. 93, pp. 15244–15248 PubMed

Lascelles J.; 1978. *Regulation of pyrrole synthesis* *In:* Clayton RK, Sistrom WR (Eds.)*The Photosynthetic Bacteria* Plenum Press New York, , pp. 795–808

C Lassen, H Plough, B B Jørgensen.; 1992. *A fiber-optic scalar irradinace microsensor: application for spectral light measurements in sediments* **FEMS Microbiol Ecol**, vol. 86, pp. 247–254 PubMed

Lewin RA, Withers NW.; 1975. *Extraordinary pigment composition of a prokaryotic alga* **Nature**, vol. 256, pp. 735–737 PubMed

Lewin, RA.; 1981. *Prochloron and the theory of symbiogenesis* **Ann N Y Acad Sci**, vol. 361, pp. 325–329 PubMed

Liebl U, Mockensturm-Wilson M, Trost JT, Brune DC, Blankenship RE, Vermaas W.; 1993. *Single core polypeptide in the reaction center of the photosynthetic bacterium Heliobacillus mobilis: structural implications and relations to other photosystems* **Proc Natl Acad Sci USA**, vol. 90, pp. 7124–7128 PubMed

Lindholm T, Weppling K, Jensen HS.; 1985. *Stratification and primary production in a small brackish lake studied by close-interval siphon sampling* **Verh Internat Verein Limnol**, vol. 22, pp. 2190–2194 PubMed

Liu H, Nolla HA, Campbell L.; 1997. *Prochlorococcus growth rate and contribution to primary production in the equatorial and subtropical North Pacific Ocean* **Aquat Microb Ecol**, vol. 12, pp. 39–47 PubMed

Loach PA, Parkes-Loach PS.; 1995. *Structure-function relationships in core light-harvesting complexes (LHI) as determined by characterization of the structural subunit and by reconstitution experiments In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 437–471

H Lokstein, C Steglich, W R Hess.; 1999. *Light-harvesting antenna function of phycorerythrin in Prochlorococcus marinus* **Biochim Biophys Acta- Bioenergetics**, vol. 1410, pp. 97–98 PubMed

Madigan MT, Takigiku R, Lee RG, Gest H, Hayes JM.; 1989. *Carbon isotope fractionation by thermophilic phototrophic sulfur bacteria: Evidence for autotrophic growth in natural populations* **Appl Environ Microbiol**, vol. 55, pp. 639–644 PubMed

Madigan MT.; 1992. *The Family Heliobacteriaceae In:* Balows A, Trüper HG, Dworkin M, Harder W, Schleifer KH (Eds.)*The Prokaryotes* Springer New York, , pp. 1982–1992

Madigan MT, Ormerod JG.; 1995. *Taxonomy, physiology and ecology of Heliobacteria In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publisher Dordrecht, The Netherlands, pp. 17–30

Madigan MT, Martinko JM, Parker J.; 1997. *Biology of Microorganisms* Prentice Hall International London, , pp. 986

Mague TH.; 1977. *Ecological aspects of dinitrogen fixation by blue-green algae In:* Hardy RWF, Gibson AH (Eds.)*A treatise on dinitrogen fixation* Wiley New York, , pp. 85–140

Malkin, R.; 1992. *Cytochrome bc_1 and b_6f complexes of photosynthetic membranes* **Photosynth Res**, vol. 33, pp. 121–136 PubMed

Martin JH, Gordon RM, Fitzwater SE.; 1990. *Iron in Antarctic waters* **Nature**, vol. 345, pp. 156–158 PubMed

J Mas, C Pedrós-Alió, R Guerrero.; 1990. *In situ specific loss and growth rates of purple sulfur bacteria in Lake Cisó* **FEMS Microbiol Ecol**, vol. 73, pp. 271–281 PubMed

K Masamoto, K I Furukawa.; 1997. *Accumulation of zeaxanthin in the cell of the cyanobacterium Synechococcus sp strain PCC7942 grown under high irradiance* **J Plant Physiol**, vol. 151, pp. 257–261 PubMed

Matthijs HCP, van der Staay GWM, Mur LR.; 1994. *Prochlorophytes: The 'other' cyanobacteria? In:* Bryant DA (Eds.)*The Molecular Biology of Cyanobacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 49–64

Mauzerall, D.; 1992. *Light, iron, Sam Granick and the origin of life* **Photosynth Res**, vol. 33, pp.

163–170 PubMed

McDermott G, Prince SM, Freer AA, Hawthornthwaite-Lawless AM, Papiz MZ, Cogdell RJ, Isaacs NW.; 1995. *Crystal structure of an integral membrane light-harvesting complex from photosynthetic bacteria* **Nature**, vol. 374, pp. 517–521 PubMed

Menendez C, Bauer Z, Huber H, Gad'on N, Stetter K-O, Fuchs G.; 1999. *Presence of acetyl coenzyme A (CoA) carboxylase and propionyl-CoA carboxylase in autotrophic Crenarchaeota and indication for operation of a 3-hydroxypropionate cycle in autototrophic carbon fixation* **J Bacteriol**, vol. 181, pp. 1088–1098 PubMed

D F Millie, D A Ingram, C P Dionigi.; 1990. *Pigment and photosynthetic responses of Oscillatoria aghardii (Cyanophyta) to photon flux and spectral quality* **J Phycol**, vol. 26, pp. 660–666 PubMed

S Miyachi, K Strassdat, H Miyashita, H Senger.; 1997. *Quantum requirement of photosynthesis in the primarily Chlorophyll d containing prokaryote Acaryochloris marina* **Z Naturforsch C-A**, vol. 52, pp. 636–638 PubMed

H Miyashita, H Ikemoto, N Kurano, K Adachi, M Chihara, S Miyachi.; 1996. *Chlorophyll d as a major pigment* **Nature**, vol. 383, pp. 402–402 PubMed

Moezelaar R, Stal L.J.; 1994. *Anaerobic dark energy generation in the mat-building cyanobacterium Microcoleus chthonoplastes* *In:* Stal LJ, Caumette P (Eds.)*Microbial Mats* Springer New York, , pp. 273–278

M L Montesinos, A Herrero, E Flores.; 1997. *Amino acid transport in taxonomically diverse cyanobacteria and identification of two genes encoding elements of a neutral aminoacid permease putatively involved in recapture of leaked hydrophobic amino acids* **J Bacteriol**, vol. 179, pp. 853–862 PubMed

Moore LR, Rocap G, Chisholm SW.; 1998. *Physiology and molecular phylogeny of coexisting Prochlorococcus ecotypes* **Nature**, vol. 393, pp. 464–467 PubMed

Nagashima KVP, Shimada K, Matsuura K.; 1993. *Phylogenetic analysis of photosynthesis genes of Rhodocyclus gelatinosus: possibility of horizontal gene transfer in purple bacteria* **Photosynth Res**, vol. 36, pp. 185–191 PubMed

Nagashima KVP, Hiraishi A, Shimada K, Matsuura K.; 1997. *Horizontal transfer of genes coding for the photosynthetic reaction centers of purple bacteria* **J Mol Evol**, vol. 45, pp. 131–136 PubMed

B Nelissen, Y van de Peer, A Wilmotte, R de Wachter.; 1995. *An early origin of plastids within the cyanobacterial divergence is sugggested by evolutionary trees based on complete 16S rDNA sequences* **Mol Biol Evol**, vol. 12, pp. 1166–1173 PubMed

D C Nelson, R W Castenholz.; 1982. *Light responses in Beggiatoa* **Arch Microbiol**, vol. 131, pp. 146–155 PubMed

Nicholson JAM, Stolz JF, Pierson BK.; 1987. *Structure of a microbial mat at Great Sippewissett*

Marsh, Cape Cod, Massachusetts **FEMS Microbiol Ecol**, vol. 45, pp. 343–364 PubMed

Nickens D, Fry CJ, Ragatz L, Bauer CE, Gest H.; 1996. *Biotype of the purple nonsulfur photosynthetic bacterium, Rhodospirillum centenum* **Arch Microbiol**, vol. 165, pp. 91–96 PubMed

Nogales B, Guerrero R, Esteve I.; 1997. *A heterotrophic bacterium inhibits growth of several species of the genus Chlorobium* **Arch Microbiol**, vol. 167, pp. 396–399 PubMed

Noguchi T, Hayashi H, Shimada K, Takaichi S, Tasumi M.; 1992. *In vivo states and function of carotenoids in an aerobic photosynthetic bacterium, Erythrobacter longus* **Photosynth Res**, vol. 31, pp. 21–30 PubMed

A Nonnengießer, A Schuster, F Koenig.; 1996. *Carotenoids and reaction center II- D1 protein in light regulation of the photosynthetic apparatus in Aphanocapsa* **Bot Acta**, vol. 109, pp. 115–124 PubMed

U Nübel.; 1999. *Diversität und Salinitätsabhängiges Verhalten benthischer, cyanobakterieller Lebensgemeinschaften. Ph D. Thesis* University of Bremen Bremen, , pp.

Oelze J.; 1992. *Light and oxygen regulation of the synthesis of bacteriochlorophylls a and c in Chloroflexus aurantiacus* **J Bacteriol**, vol. 174, pp. 5021–5026 PubMed

Oesterhelt D, Stoeckenius W.; 1973. *Function of a new photoreceptor membrane* **Proc Natl Acad Sci USA**, vol. 70, pp. 2853–2857 PubMed

Oesterhelt D, Krippahl G.; 1983. *Phototropic growth of halobacteria and its use for isolation of photosynthetically-deficient mutants* **Ann Microbiol (Inst Pasteur)**, vol. 134 B, pp. 137–150 PubMed

Oh-Hama, T.; 1989. *Evolutionary consideration of the two pathways of 5-aminolevulinic acid biosynthesis in organelles and prokaryotes* **Endocytology**, vol. IV, pp. 589–592 PubMed

Oh-hama T, Santander PJ, Stolowich NJ, Scott AI.; 1991. *Bacteriochlorophyll c formation via the C5 pathway of 5-aminolevulinic acid synthesis in Chloroflexus aurantiacus* **FEBS Lett**, vol. 281, pp. 173–176 PubMed

Okamura K, Takamiya K, Nishimura M.; 1985. *Photosynthetic electron transfer system is inoperative in anaerobic cells of Erythrobacter species strain OCh114* **Arch Microbiol**, vol. 142, pp. 12–17 PubMed

Oliver RL, Walsby AE.; 1984. *Direct evidence for the role of light-mediated gas vesicle collapse in the buoyancy regulation of Anabaena flos-aquae* **Limnol Oceanogr**, vol. 29, pp. 879–886 PubMed

Olson RJ, Chisholm SW, Zettler ER, Armbrust EV.; 1990a. *Pigment, size and distribution of Synechococcus in the North Atlantic and Pacific oceans* **Limnol Oceanogr**, vol. 35, pp. 45–58 PubMed

Olson RJ, Chisholm SW, Zettler ER, Altabet MA, Dusenberry JA.; 1990b. *Spatial and temporal distributions of prochlorophyte picoplankton in the North Atlantic Ocean* **Deep Sea Res**, vol. 37, pp. 1033–1051 PubMed

Olson JM.; 1998. *Chlorophyll organization and function in green photosynthetic bacteria* **Photochem Photobiol**, vol. 67, pp. 61–75 PubMed

Oparin AI.; 1938. *The origin of life* Macmillan New York,

Overmann J, Tilzer MM.; 1989a. *Control of primary productivity and the significance of photosynthetic bacteria in a meromictic kettle lake. Mittlerer Buchensee, West-Germany.* **Aquatic Sci**, vol. 51, pp. 261–278 PubMed

Overmann J, Pfennig N.; 1989b. *Pelodictyon phaeoclathratiforme sp. nov., a new brown-colored member of the Chlorobiaceae forming net-like colonies* **Arch Microbiol**, vol. 152, pp. 401–406 PubMed

Overmann J, Beatty JT, Hall KJ, Pfennig N, Northcote TG.; 1991a. *Characterization of a dense, purple sulfur bacterial layer in a meromictic salt lake* **Limnol Oceanogr**, vol. 36, pp. 846–859 PubMed

Overmann J, Lehmann S, Pfennig N.; 1991b. *Gas vesicle formation and buoyancy regulation in Pelodictyon phaeoclathratiforme (green sulfur bacteria)* **Arch Microbiol**, vol. 157, pp. 29–37 PubMed

Overmann J, Pfennig N.; 1992. *Buoyancy regulation and aggregate formation in Amoebobacter purpureus from Mahoney Lake* **FEMS Microbiol Ecol**, vol. 101, pp. 67–79 PubMed

Overmann J, Beatty JT, Hall KJ.; 1994. *Photosynthetic activity and population dynamics of Amoebobacter purpureus in a meromictic saline lake* **FEMS Microbiol Ecol**, vol. 15, pp. 309–320 PubMed

Overmann J, Beatty JT, Krouse HR, Hall KJ.; 1996. *The sulfur cycle in the chemocline of a meromictic salt lake* **Limnol Oceanogr**, vol. 41, pp. 147–156 PubMed

Overmann J.; 1997. *Mahoney Lake: A case study of the ecological significance of phototrophic sulfur bacteria In:* Jones JG (Eds.)*Advances in Microbial Ecology Vol. 15* Plenum Press New York, , pp. 251–288

Overmann J, Tuschak C, Fröstl JM, Sass H.; 1998. *The ecological niche of the consortium "Pelochromatium roseum"* **Arch Microbiol**, vol. 169, pp. 120–128 PubMed

Overmann J, Hall KJ, Northcote TG, Beatty JT.; 1999a. *Grazing of the copepod Diaptomus connexus on purple sulfur bacteria in a meromictic salt lake* **Environ Microbiol**, vol. 1, pp. 213–222 PubMed

Overmann J, Coolen MJL, Tuschak C.; 1999b. *Specific detection of different phylogenetic groups of chemocline bacteria based on PCR and denaturing gradient gel electrophoresis of 16S rRNA gene*

fragments **Arch Microbiol**, vol. 172, pp. 83–94 PubMed

Overmann J, Hall KJ, Ebenhöh W, Chapman MA, Beatty JT.; 1999c. *Structure of the aerobic food chain in a meromictic lake dominated by purple sulfur bacteria* **Arch Hydrobiol**, vol. 144, pp. 127–156 PubMed

Oyaizu, H, Debrunner-Vossbrinck, B, Mandelco, L, Studier, JA, Woese, CR.; 1987. *The green non-sulfur bacteria: a deep branching in the eubacterial line of descent* **System Appl Microbiol**, vol. 9, pp. 47–53 PubMed

NR Pace.; 1997. *A molecular view of microbial diversity and the biosphere* **Science**, vol. 276, pp. 734–740 PubMed

Padan E.; 1979. *Impact of facultative anaerobic phototrophic metabolism and ecology of cyanobacteria* **Adv Microb Ecol**, vol. 3, pp. 1–48 PubMed

Padan E, Cohen Y.; 1982. *Anoxygenic photosynthesis* *In:* Botanical Monographs, vol. 19 (Eds.)*The biology of cyanobacteria* Blackwell Scientific Publications Oxford, , pp. 215–235

Palenik, B, Haselkorn, R.; 1992. *Multiple evolutionary origins of prochlorophytes, the chlorophyll b -containing prokaryotes* **Nature**, vol. 355, pp. 265–267 PubMed

Parkin TB, Brock TD.; 1980a. *The effects of light quality on the growth of phototrophic bacteria in lakes* **Arch Microbiol**, vol. 125, pp. 19–27 PubMed

Parkin TB, Brock TD.; 1980b. *Photosynthetic bacterial production in lakes: The effects of light intensity* **Limnol Oceanogr**, vol. 25, pp. 711–718 PubMed

TB Parkin, TD Brock.; 1981. *The role of phototrophic bacteria in the sulfur cycle of a meromictic lake* **Limnol Oceanogr**, vol. 26, pp. 880–890 PubMed

Pedrós-Alió C, Sala MM.; 1990. *Microdistribution and diel vertical migration of flagellated vs gas-vacuolate purple sulfur bacteria in a stratified water body* **Limnol Oceanogr**, vol. 35, pp. 1637–1644 PubMed

Peltier G, Schmidt GW.; 1991. *Chlororespiration: An adaptation to nitrogen deficiency in Chlamydomonas reinhardtii* **Proc Natl Acad Sci USA**, vol. 88, pp. 4791–4795 PubMed

A Pentecost.; 1984. *Effects of sedimentation and light intensity on mat-forming Oscillatoriaceae with particular reference to Microcoleus lyngyaceus Gomont* **J Gen Microbiol**, vol. 130, pp. 983–990 PubMed

Pfennig N, Trüper HG.; 1974. *The phototrophic bacteria* *In:* Buchanan RE, Gibbons NE (Eds.) *Bergey's manual of determinative bacteriology, 8th edition* Williams and Wilkins Baltimore, , pp. 24–64

Pfennig N.; 1978. *General physiology and ecology of photosynthetic bacteria* *In:* Clayton RK,

Sistrom WR (Eds.)*The Photosynthetic Bacteria* Plenum Press New York, , pp. 3–18

Pfennig N, Trüper HG.; 1989. *Anoxygenic phototrophic bacteria In:* Staley JT, Bryant MP, Pfennig N, Holt JG (Eds.)*Bergey's Manual of Systematic Bacteriology* Williams and Wilkins Baltimore, , pp. 1635–1709

Pfennig N, Lünsdorf H, Süling J, Imhoff JF.; 1997. *Rhodospira trueperi gen. nov., spec. nov., a new phototrophic Proteobacterium of the alpha group* **Arch Microbiol**, vol. 168, pp. 39–45 PubMed

Pierson BK, Castenholz RW.; 1974. *Studies of pigments and growth in Chloroflexus aurantiacus, a phototrophic filamentous bacterium* **Arch Microbiol**, vol. 100, pp. 283–305 PubMed

B K Pierson, A Oesterle, G L Murphy.; 1987. *Pigments, light penetration and photosynthetic activity in the multi-layered microbial mats of Great Sippewisset Salt Marsh, Massachussets* **FEMS Microbiol Ecol**, vol. 45, pp. 365–376 PubMed

Pierson, BK, Olson, JM.; 1989. *Evolution of photosynthesis in anoxygenic photosynthetic procaryotes In:* Cogen, Y, Rosenberg, E (Eds.)*Microbial Mats: Physiological Ecology of Benthic Microbial Communities* Am Soc Microbiol Washington, DC, , pp. 402–427

B K Pierson, V M Sands, J L Frederick.; 1990. *Spectral irradinace and distribution of pigments in a highly layered microbial mat* **Appl Environ Microbiol**, vol. 56, pp. 2327–2340 PubMed

B K Pierson, D Valdez, M Larsen, E Morgan, E E Mack.; 1994. *Chloroflexus-like organims from marine and hypersaline environments: distribution and diversity* **Photosynthesis Res**, vol. 41, pp. 35–52 PubMed

Pierson BK, Castenholz RW.; 1995. *Taxonomy and physiology of filamentous anoxygenic phototrophs In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 31–47

Post AF, de Wit R, Mur LR.; 1985. *Interactions between temperature and light intensity on growth and photosynthesis of the cyanobacterium Oscillatoria agardhii* **J Plankton Res**, vol. 7, pp. 487–495 PubMed

M Potts.; 1994. *Desiccation tolerance in prokaryotes* **Microbiol Rev**, vol. 58, pp. 755–805 PubMed

LM Proctor, JA Fuhrman.; 1990. *Viral mortality of marine bacteria and cyanobacteria* **Nature**, vol. 343, pp. 60–62 PubMed

L Prufert-Bebout, F Garcia-Pichel.; 1994. *Field and cultivated Microcoleus chthonoplastes: the search for clues to its prevalence in marine microbial mats In:* L J Stal, P Caumette (Eds.)*Microbial Mats. Structure, development and environmental significance* Springer-Verlag New York, , pp.

Ragatz L, Jiang Z-Y, Bauer C, Gest H.; 1994. *Phototactic purple bacteria* **Nature**, vol. 370, pp. 104 PubMed

Ragatz L, Jiang Z-Y, Bauer CE, Gest H.; 1995. *Macroscopic phototactic behaviour of the purple*

photosynthetic bacterium Rhodospirillum centenum **Arch Microbiol**, vol. 163, pp. 1–6 PubMed

Rau GH.; 1980. *Carbon-13/Carbon-12 variation in subalpine lake aquatic insects: Food source implications* **Can J Fish Aquat Sci**, vol. 37, pp. 742–746 PubMed

Rebeiz CA, Lascelles J.; 1982. *Biosynthesis of pigments in plants and bacteria In:* Godvindjee (Eds.)*Energy Conversion by Plants and Bacteria, Vol I* Academic Press New York, , pp. 699–780

R H Reeves.; 1996. *16S ribosomal RNA and the molecular phylogeny of the Cyanobacteria* **Nova Hedwiga**, vol. 112, pp. 55–67 PubMed

Repeta DJ, Simpson DJ, Jørgensen BB, Jannasch HW.; 1989. *Evidence for the existence of anoxygenic photosynthesis from the distribution of bacteriochlorophylls in the Black Sea* **Nature**, vol. 342, pp. 69–72 PubMed

Richaud P, Marrs BL, Vermiglio A.; 1986. *Two modes of interaction between photosynthetic and respiratory electron chains in whole cells of Rhodopseudomonas capsulata* **Biochim Biophys Acta**, vol. 850, pp. 265–263 PubMed

Rippka R, Deruelles J, Waterbury JB, Herdman M, Stanier RY.; 1979. *Generic assignments, strain histories and properties of pure cultures of cyanobacteria* **J Gen Microbiol**, vol. 111, pp. 1–61 PubMed

Rödig J, Jock S, Klug G.; 1999. *Coregulation of the synthesis of bacteriochlorophyll and pigment-binding proteins in Rhodobacter capsulatus* **Arch Microbiol**, vol. 171, pp. 198–204 PubMed

K Rudi, D M Skulberg, K S Jakobsen.; 1998. *Evolution of cyanobacteria by exchange of genetic material among phylogenetically related strains* **J Bacteriol**, vol. 180, pp. 3453–3461 PubMed

Ruff-Roberts AL, Kuenen JG, Ward DM.; 1994. *Distribution of cultuvated and uncultivated cyanobacteria and Chloroflexus-like bacteria in hot spring microbial mats* **Appl Environ Microbiol**, vol. 60, pp. 697–704 PubMed

M J Sackett, J P Armitage, E E Sherwood, T P Pitta.; 1997. *Photoresponses of the purple nonsulfur bacteria Rhodospirillum centenum and Rhodobacter sphaeroides* **J Bacteriol**, vol. 179, pp. 6764–6768 PubMed

Sánchez O, van Gemerden H, Mas J.; 1998. *Acclimation of the photosynthetic response of Chromatium vinosum to light-limiting conditions* **Arch Microbiol**, vol. 170, pp. 405–410 PubMed

Schenk HEA.; 1992. *Cyanobacterial symbioses In:* Balows A, Trüper HG, Dworkin M, Harder W, Schleifer K-H*The Prokaryotes* Springer New York, , pp. 3819–3854

H Schiller, H Senger, H Miyashita, S Miyashi, H Dau.; 1997. *Light-harvesting in Acaryochloris marina—Spectroscopic characterization of a Chlorophyll d-dominated photosynthetic antenna system* **FEBS Letters**, vol. 410, pp. 433–436 PubMed

Shiba T, Simidu U, Taga N.; 1979. *Distribution of aerobic bacteria which contain bacteriochlorophyll a* **Appl Environ Microbiol**, vol. 38, pp. 43–45 PubMed

Shiba T, Harashima K.; 1986. *Aerobic photosynthetic bacteria* **Microbiological Sciences**, vol. 3, pp. 377–378 PubMed

Shiba T.; 1989. *Overview of the aerobic photosynthetic bacteria* *In:* Harashima K, Shiba T, Murata N (Eds.)*Aerobic Photosynthetic Bacteria* Springer-Verlag Berlin, , pp. 1–8

Shimada K.; 1995. *Aerobic anoxygenic phototrophs* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic photosynthetic bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 105–122

Sidler WA.; 1994. *Phycobilisome and phycobiliprotein structures* *In:* Bryant DA (Eds.)*The Molecular Biology of Cyanobacteria* Kluwer Academic Publishers Dordrecht, Boston, London, , pp. 139–216

Sinninghe Damsté JS, Wakeham SG, Kohnen MEL, Hayes JM, de Leeuw JW.; 1993. *A 6, 000-year sedimentary molecular record of chemocline excursions in the Black Sea* **Nature**, vol. 362, pp. 827–829 PubMed

Sirevåg R.; 1995. *Carbon metabolism in green bacteria* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 871–883

W R Sistrom, M Griffiths, R Y Stanier.; 1956. *The biology of a photosynthetic bacterium which lacks colored carotenoids* **J Cell Comp Physiol**, vol. 48, pp. 473–515 PubMed

Skyring GW, Bauld J.; 1990. *Microbial mats in coastal environments* **Adv Microb Ecol**, vol. 11, pp. 461–498 PubMed

R C Smith, K S Baker.; 1981. *Optical properties of the clearest seawaters* **Appl. Optics**, vol. 20, pp. 177–184 PubMed

Sorokin YI.; 1970. *Interrelations between sulphur and carbon turnover in meromictic lakes* **Arch Hydrobiol**, vol. 66, pp. 391–446 PubMed

Stackebrandt E, Embley M, Weckesser J.; 1988. *Phylogenetic, evolutionary, and taxonomic aspects of phototrophic bacteria* *In:* Olson JM, Stackebrandt E, Trüper HG (Eds.)*Green Photosynthetic Bacteria* Plenum Publishing Cooperation New York, , pp. 201–215

Stackebrandt E, Rainey FA, Ward-Rainey N.; 1996. *Anoxygenic phototrophy across the phylogenetic spectrum: current understanding and future perspectives* **Arch Microbiol**, vol. 166, pp. 211–223 PubMed

Stam WT, Boele-Bos SA, Stulp BK.; 1985. *Genotypic relationships between Prochloron samples from different localities and hosts as determined by DNA-DNA reassociations* **Arch Microbiol**, vol. 142, pp. 340–341 PubMed

R Y Stanier.; 1977. *The position of cyanobacteria in the world of phototrophs* **Carlsberg Res. Comm.**, vol. 42, pp. 77–98 PubMed

Steenbergen CLM, Korthals HJ.; 1982. *Distribution of phototrophic microorganisms in the anaerobic and microaerophilic strata of Lake Vechten (The Netherlands)* **Limnol Oceanogr**, vol. 27, pp. 883–895 PubMed

Steudel R.; 1989. *On the nature of the 'elmental sulfur' (S_0) produced by sulfur-oxidizing bacteria- a model for S_0 globules* *In:* Schlegel HG, Bowien B (Eds.)*Autotrophic Bacteria* Springer Verlag New York, , pp. 289–303

Steudel R, Holdt G, Visscher PT, van Gemerden H.; 1990. *Search for polythionates in cultures of Chromatium vinosum after sulfide incubation* **Arch Microbiol**, vol. 153, pp. 432–437 PubMed

Strauß G, Fuchs G.; 1993. *Enzymes of a novel autotrophic CO_2 fixation pathway in the phototrophic bacterium Chloroflexus aurantiacus, the hydroxypropionate cycle* **Eur J Biochem**, vol. 215, pp. 633–643 PubMed

Suttle CA, Chan AM, Cottrell MT.; 1990. *Infection of phytoplankton by viruses and reduction of primary productivity* **Nature**, vol. 347, pp. 467–469 PubMed

Suttle CA, Chan AM, Feng C, Garza DR.; 1993. *Cyanophages and sunlight: A paradox* *In:* Guerrero R, Pedrós-Alió C (Eds.)*Trends in Microbial Ecology* Spanish Society for Microbiology Barcelona, , pp. 303–307

Suwanto A, Kaplan S.; 1989. *Physical and genetic mapping of the Rhodobacter sphaeroides 2.4.1 genome: genome size, fragment identification, and gene localization* **J Bacteriol**, vol. 171, pp. 5840–5849 PubMed

Suzuki JY, Bauer CE.; 1995. *A prokaryotic origin for light-dependent chlorophyll biosynthesis of plants* **Proc Natl Acad Sci USA**, vol. 92, pp. 3749–3753 PubMed

Swoager WC, Lindstrom ES.; 1971. *Isolation and counting of Athiorhodaceae with membrane filters* **Appl Microbiol**, vol. 22, pp. 683–687 PubMed

Takahashi K, Wada E, Sakamoto M.; 1990. *Carbon isotope discrimination by phytoplankton and photosynthetic bacteria in monomictic Lake Fukami-ike* **Arch Hydrobiol**, vol. 120, pp. 197–210 PubMed

T Tanada, K Kitadokoro, Y Higuchi, K INaka, A Yasui, PE Deruiter, APM Eker, K Miki.; 1997. *Crystal structure of DNA photolyase from Anacystis nidulans* **Nature Struct. Biol**, vol. 4, pp. 887–891 PubMed

RK Thauer, K Jungermann, K Decker.; 1977. *Energy conservation in chemotrophic anaerobic bacteria* **Bacteriolog Rev**, vol. 41, pp. 100–180 PubMed

Theroux SJ, Redlinger TE, Fuller RC, Robinson SJ.; 1990. *Gene encoding the 5.7-kilodalton chlorosome protein of Chloroflexus aurantiacus: regulated message levels and a predicted carboxy-terminal protein extension* **J Bacteriol**, vol. 172, pp. 4497–4504 PubMed

Thomas RH, Walsby AE.; 1985. *Buoyancy regulation in a strain of Microcystis* **J Gen Microbiol**, vol. 131, pp. 799–809 PubMed

Thorne SW, Newcomb EH, Osmond CB.; 1977. *Identification of chlorophyll b in extracts of prokaryotic algae by fluorescence spectroscopy* **Proc Natl Acad Sci**, vol. 74, pp. 575–578 PubMed

Trüper HG, Pfennig N.; 1978. *Taxonomy of the Rhodospirillales In:* Clayton RK, Sistrom WR (Eds.) *The photosynthetic bacteria* Plenum Publishing Corp. New York, , pp. 19–27

Trüper HG, Pfennig N.; 1981. *Characterization and identification of the anoxygenic phototrophic bacteria In:* Starr MP, Stolp H, Trüper HG, Balows A, Schlegel HG (Eds.)*The prokaryotes: A handbook on habitats, isolation and identification of bacteria* Springer-Verlag New York, , pp. 299–312

S Turner.; 1887. *Molecular systematics of oxygenic photosynthetic bacteria* **Plant Syst Evol**, vol. 11, pp. 13–52 PubMed

Urakami T, Komagata K.; 1984. *Protomonas, a new genus of facultatively methylotrophic bacteria* **Int J Syst Bacteriol**, vol. 34, pp. 188–201 PubMed

Urbach, E, Robertson, DL, Chrisholm, SW.; 1992. *Multiple evolutionary origins of prochlorophytes within the cyanobacterial radiation* **Nature**, vol. 355, pp. 267–270 PubMed

Utkilen HC, Skulberg OM, Walsby AE.; 1985. *Buoyancy regulation and chromatic adaptation in planktonic Oscillatoria species: alternative strategies for optimizing light absorption in stratified lakes* **Arch Hydrobiol**, vol. 104, pp. 407–417 PubMed

van den Ende FP, Laverman AM, van Gemerden H.; 1996. *Coexistence of aerobic chemotrophic and anaerobic phototrophic sulfur bacteria under oxygen limitation* **FEMS Microbiol Ecol**, vol. 19, pp. 141–151 PubMed

van den Ende, H, van de Peer, Y, Perry, J, de Wachter, R.; 1990. *5S rRNA sequences of representatives of the genera Chlorobium, Prosthecochloris, Thermomicrobium, Cytophaga, Flavobacterium, Flexibacter and Saprospira and a discussion of the evolution of eubacteria in general* **J Gen Microbiol**, vol. 136, pp. 11–18 PubMed

van Gemerden H.; 1967. *In the bacterial sulfur cycle of inland waters* University of Leiden

vanGemerden H.; 1974. *Coexistence of organisms competing for the same substrate: An example among the purple sulfur bacteria* **Microb Ecol**, vol. 1, pp. 104–119 PubMed

van Gemerden H, Tughan CS, de Wit R, Herbert RA.; 1989. *Laminated microbial ecosystems on sheltered beaches in Scapa Flow, Orkney Islands* **FEMS Microbial Ecol**, vol. 62, pp. 87–102

van Gemerden H, Mas J.; 1995. *Ecology of phototrophic sulfur bacteria* *In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic photosynthetic bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 49–85

J J van Thor, C W Mullineaux, H P C Matthijs, K J Hellingwert.; 1998. *Light harvesting and state transitions in cyanobacteria* **Bot Acta**, vol. 111, pp. 430–443

van Valen, LM, Maiorana, VC.; 1980. *The archaebacteria and eukaryotic origins* **Nature**, vol. 287, pp. 248–250

G W M Vanderstaay, N Yurkova, B R Green.; 1998. *The 38KDa Chlorophyll a/b protein of the prokaryote Prochlorothrix hollandica is encoded by a divergent Pcb gene* **Plant Mol Biol**, vol. 36, pp. 706–716

Veldhuis MJW, van Gemerden H.; 1986. *Competition between purple and brown phototrophic bacteria in stratified lakes: sulfide, acetate, and light as limiting factors* **FEMS Microbiol Ecol**, vol. 38, pp. 31–38

Vermaas WFJ.; 1994. *Evolution of heliobacteria: Implications for photosynthetic reaction cneter complexes* **Photosynth Res**, vol. 41, pp. 285–294

Wagner-Huber R, Brunisholz R, Frank G, Zuber H.; 1988. *The BChl c/e- binding polypeptides from chlorosomes of green photosynthetic bacteria* **FEBS Lett**, vol. 239, pp. 8–12

Wakao N, Yokoi N, Isoyama N, Hiraishi A, Shimada K, Kobayachi M, Kise H, Iwaki M, Itoh S, Takaishi S, Sakurai Y.; 1996. *Discovery of natural photosynthesis using Zn-containing bacteriochlorophyll in an aerobic bacterium Acidiphilium rubrum* **Plant Cell Physiol**, vol. 37, pp. 889–896

Wakim B, Oelze J.; 1980. *The unique mode of adjusting the composition of the photosynthetic apparatus to different environmental conditions by Rhodospirillum tenue* **FEMS Microbiol Lett**, vol. 7, pp. 221–223

Walsby AE.; 1978. *The properties and buoyancy-providing role of gas vacuoles in Trichodesmium Ehrenberg* **Br Phycol J**, vol. 13, pp. 103–116

AE Walsby.; 1994. *Gas vesicles* **Microbiol Rev**, vol. 58, pp. 94–144

Ward, DM, Weller, R, Shiea, J, Castenholz, RW, Cohen, Y.; 1989. *Hot springs microbial mats: Anoxygenic and oxygenic mats of possible evolutionary significance* *In:* Cohen, Y, Rosenberg, E (Eds.)*Microbial Mats: Physiological Ecology of Benthic Microbial Communities* Am Soc Microbiol Washington, DC, , pp. 3–15

Waterbury JB, Wiley JM, Franks DG, Valois FW, Watson SW.; 1985. *A cyanobacterium capable of swimming motility* **Science**, vol. 230, pp. 74–76

Waterbury JB, Watson SW, Valois FW, Franks DG.; 1986. *Biological and ecological characterization of the marine unicellular cyanobacterium Synechococcus In:* Platt T, Li WKW (Eds.)*Photosynthetic Picoplankton* Can Bull Fish Aquat Sci 214 , pp. 71–120

Waterbury JB, Valois FW.; 1993. *Resistance to co-occurring phages enables marine Synechococcus communities to coexist with cyanophages abundant in seawater* **Appl Environ Microbiol**, vol. 59, pp. 3393–3399 PubMed

Watson SW, Novitsky TJ, Quinby HL, Valois FW.; 1977. *Determination of bacterial number and biomass in the marine environment* **Appl Environ Microbiol**, vol. 33, pp. 940–946 PubMed

Weller R, Bateson MM, Heimbuch BK, Kopczynski ED, Ward DM.; 1992. *Uncultivated cyanobacteria, Chloroflexus-like inhabitants, and spirochete-like inhabitants of a hot spring microbial mat* **Appl Environ Microbiol**, vol. 58, pp. 3964–3969 PubMed

Wellington, CL, Bauer, CE, Beatty, JT.; 1992. *Photosynthesis gene superoperons in purple non-sulfur bacteria: The tip of the iceberg?* **Can J Microbiol**, vol. 38, pp. 20–27 PubMed

D C J Wessels, B Büdel.; 1995. *Epilithic and cryptoendolithic cyanobacteria of Clarens Sandstone Cliffs in the Golden Gate Highlands National Park, South Africa* **Bot Acta**, vol. 108, pp. 220–226 PubMed

Whatley JM.; 1977. *The fine structure of Prochloron* **New Phytol**, vol. 79, pp. 309–313 PubMed

Whittaker RH, Likens GE.; 1975. *The biosphere and man In:* Lieth H, Whittaker RH (Eds.)*Primary productivity of the biosphere* Springer-Verlag New York, , pp. 305–328

Widdel F, Schnell S, Heising S, Ehrenreich A, Assmus B, Schink B.; 1993. *Ferrous iron oxidation by anoxygenic phototrophic bacteria* **Nature**, vol. 362, pp. 834–836 PubMed

Woese CR, Gibson J, Fox GE.; 1980. *Do genealogical patterns in photosynthetic bacteria reflect interspecific gene transfer?* **Nature**, vol. 283, pp. 212–214 PubMed

Woese CE.; 1987. *Bacterial evolution* **Microbiol Rev**, vol. 51, pp. 221–271 PubMed

Wraight CA, Clayton RK.; 1973. *The absolute quantum efficiency of bacteriochlorophyll photooxidation in reaction centres of Rhodopseudomonas spheroides* **Biochim Biophys Acta**, vol. 333, pp. 246 PubMed

Wu H, Green M, Scranton MI.; 1997. *Acetate cycling in the water column and surface sediment of Long Island Sound following a bloom* **Limnol Oceanogr**, vol. 42, pp. 705–713 PubMed

Yildiz, FH, Gest, H, Bauer, CE.; 1992. *Conservation of the photosynthesis gene cluster in Rhodospirillum centenum* **Mol Microbiol**, vol. 6, pp. 2683–2691 PubMed

Yurkov V, van Gemerden H.; 1993. *Impact of light/dark regime on growth rate, biomass formation and bacteriochlorophyll synthesis in Erythromicrobium hydrolyticum* **Arch Microbiol**, vol. 159, pp.

84–89 PubMed

Yurkov V, Gad'on N, Angerhofer A, Drews G.; 1994. *Light-harvesting complexes of aerobic bacteriochlorophyll-containing bacteria Roseococcus thiosulfatophilus, RB3 and Erythromicrobium ramosum, E5 and the transfer of excitation energy from carotenoids to bacteriochlorophyll* **Z Naturforsch**, vol. 49(c), pp. 579–586 PubMed

Yurkov W, Beatty JT.; 1998. *Isolation of aerobic anoxygenic photosynthetic bacteria from black smoker plume waters of the Juan de Fuca Ridge in the Pacific Ocean* **Appl Environ Microbiol**, vol. 64, pp. 337–341 PubMed

Zehnder AJB, Stumm W.; 1988. *Geochemistry and biogeochemistry of anaerobic habitats In:* Zehnder AJB (Eds.)*Biology of Anaerobic Microorganisms* Wiley-Liss New York, , pp. 1–38

Zevenboom W, Mur LR.; 1984. *Growth and photosynthetic response of the cyanobacterium Microcystis aeruginosa in relation tophotoperiodicity and irradiance* **Arch Microbiol**, vol. 139, pp. 232–239 PubMed

Zuber H., Cogdell R.J.; 1995. *Structure and organization of purple bacterial antenna complexes In:* Blankenship RE, Madigan MT, Bauer CE (Eds.)*Anoxygenic Photosynthetic Bacteria* Kluwer Academic Publishers Dordrecht, The Netherlands, pp. 315–348

Zucconi AP, Beatty JT.; 1988. *Posttranscriptional regulation by light of the steady state levels of mature B800-850light-harvesting complex in Rhodobacter capsulatus* **J Bacteriol**, vol. 170, pp. 877–882 PubMed