

Diversity of Anaerobic Anoxygenic Phototrophic Purple Bacteria

Johannes F. Imhoff

Abstract The anaerobic phototrophic purple bacteria are a phylogenetically highly diverse group of bacteria with the common physiological property of performing anoxygenic photosynthesis under anaerobic conditions. They are representatives of the *Alpha*-, *Beta*-, and *Gammaproteobacteria*. More than 160 known species are classified into 57 genera, 12 families, and 7 orders of the *Proteobacteria*. A short historical review on the systematic treatment of the phototrophic purple bacteria and the actual state is presented. The phylogenetic relationship of the cultured phototrophic purple bacteria based upon 16S rRNA gene sequences of the type strains is shown in a comprehensive phylogenetic tree. Correlation and differences between taxonomic treatment and phylogenetic relatedness are discussed. As the 16S rRNA gene is only of limited value for biodiversity studies of functional groups of bacteria, the application of functional genes for these purposes gains importance and genes coding for bacteriochlorophyll synthesis (*bchY*), and reaction center proteins (*pufL* and *pufM*) have been applied for biodiversity studies of phototrophic purple bacteria. The correlation of phylogenetic relationships based on *pufLM* gene sequences with that of 16S rRNA gene sequences, the appropriate information content in the *pufLM* sequences (>1400 nt), and a database of *pufLM* sequences from many of the cultured purple bacteria make these genes a preferred target to study environmental communities of phototrophic purple bacteria.

Studies on the diversity of phototrophic purple bacteria in three representative habitats are discussed: an exceptionally well-developed microbial mat in a salt marsh from which a number of new phototrophic purple bacteria have been isolated (Sippewissett Salt Marsh, MA), the chemocline of a meromictic freshwater lake from which new species have been isolated and in which genetic diversity studies have been performed (Lake Cadagno, Switzerland), and a coastal lagoon (Baltic Sea lagoon at Stein, Germany) in which the diversity of phototrophic purple bacteria and the impact of changes in temperature and salinity on the community composition was studied using almost complete sequences of the *pufLM* genes.

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Introduction

Among the bacterial phyla with phototrophic bacteria, the *Proteobacteria* harbor the phototrophic purple bacteria with representatives of phototrophic purple sulfur bacteria in the *Gammaproteobacteria* and members of the purple nonsulfur bacteria in the *Alpha*- and *Betaproteobacteria* (Imhoff 2001d; Imhoff et al. 2005; Imhoff 2006a, b, c, d). The so-called aerobic phototrophic purple bacteria are close relatives of the anaerobic anoxygenic phototrophic purple bacteria. They have a primarily chemoheterotrophic metabolism and are aerobic respiring bacteria forming bacteriochlorophyll and a photosynthetic apparatus in the presence of oxygen.

Anaerobic anoxygenic phototrophic bacteria are major players in ecological niches, which primarily are strictly anoxic but extend to microoxic and even oxic conditions in the light (Pfennig 1977, 1989; Imhoff 1995; Imhoff et al. 2005; Madigan 1988; van Gernerden and Mas 1995). Their primary ecological niche is in stratified environments with countercurrent gradients of sulfide and oxygen, in freshwater, marine, and hypersaline habitats; in salt and soda lakes; in hot springs, cold waters, and sea ice; in coastal sediments; and in the chemocline of many lakes, fjords, and stratified water bodies. The habitats of purple sulfur bacteria generally are the lower part of the chemocline in sediments and waters, in which sulfide is present and light is available. More oxygen-sensitive representatives develop in the lower part where oxygen is absent, while more oxygen-tolerant species may occur in the upper part and even may make use out of the oxygen for respiratory purposes.

In this chapter, we will focus on the anaerobic phototrophic purple sulfur and purple nonsulfur bacteria and the advances in studies of their biodiversity over the past decades. We will use the term purple nonsulfur bacteria for all anaerobic anoxygenic purple *Alpha*- and *Betaproteobacteria* and the term purple sulfur bacteria for the *Gammaproteobacteria*.

A Short Historical Review on Systematic Studies of Phototrophic Purple Bacteria

Since the pioneering work of Winogradsky (1888) and the systematic treatments of phototrophic purple bacteria by Molisch (1907), who for the first time distinguished between the purple sulfur (*Thiorhodaceae*) and purple nonsulfur bacteria (*Athiorhodaceae*), more than a century ago, several important key steps in advancing our knowledge on the diversity of phototrophic purple bacteria have to be

mentioned. After the important contributions to the physiology of phototrophic bacteria by van Niel (van Niel 1931, 1944), the formulation of a suitable culture medium for phototrophic sulfur bacteria by Norbert Pfennig (Pfennig 1965; Pfennig and Lippert 1966; Pfennig and Trüper 1992; Imhoff 2006c) significantly stimulated the work on the physiology, ecology, and biodiversity of these bacteria (Pfennig 1967, 1977, 1989). The studies of Pfennig over the following decades resulted in the description of a number of new purple sulfur and purple nonsulfur bacteria (see Tables 1, 2, and 3) and also green sulfur bacteria. Together with Hans-Georg Trüper, a consequent systematic treatment of these bacteria based on phenotypic properties was implemented. Reevaluation of historical data on the taxonomy of phototrophic bacteria, formal description of species and definition of type and neotype strains of the phototrophic bacteria formed the fundament for all future taxonomic work on these bacteria (Pfennig and Trüper 1969, 1971, 1974). A key for the recognition of genera and species was established which basically used easily recognized phenotypical properties that could in part also be determined by microscopic examination of environmental samples or enrichment cultures. Oxidation of sulfide and deposition of elemental sulfur globules (inside or outside the cells) were major criteria to distinguish not only purple nonsulfur from purple sulfur bacteria but also the genus *Ectothiorhodospira* from other purple sulfur bacteria. Motility by flagella, formation of gas vesicles, shape and size of the cells, and structure of internal photosynthetic membrane systems were other criteria used for differentiation of the species and genera. A culture collection of type strains and reference cultures of anoxygenic phototrophic bacteria established by Pfennig and Trüper still is a reference for studies today (most of these strains are maintained in the author's lab and also available through DSMZ, Braunschweig, Germany). It is interesting to see that at that time only the genera *Rhodopseudomonas*, *Rhodospirillum*, and *Rhodomicrobium* were recognized in the *Rhodospirillaceae* family (purple nonsulfur bacteria) and ten genera (*Ectothiorhodospira*, *Thiospirillum*, *Chromatium*, *Thiocystis*, *Thiosarcina*, *Thiocapsa*, *Lamprocystis*, *Thiodictyon*, *Thiopedia*, and *Amoebobacter*) in the *Chromatiaceae* family (Pfennig and Trüper 1971, 1974). Altogether less than 40 species of phototrophic purple bacteria were known at that time (Pfennig and Trüper 1971). Today, more than 160 species of anoxygenic phototrophic purple bacteria are recognized in 28 genera (95 species) of purple nonsulfur bacteria and 29 genera (74 species) of purple sulfur bacteria. They are members of seven orders and more than 11 families of the *Proteobacteria* (Tables 1, 2, and 3).

The introduction of ribosomal RNA sequences (at the beginning oligonucleotide catalogues, later complete sequences) by Carl Woese into microbial phylogeny opened up completely new possibilities in diversity studies and systematics also of the phototrophic bacteria. Woese actually considered the *Proteobacteria* as "phototrophic purple bacteria and their relatives," presuming a crucial role of phototrophic purple bacteria in the evolution of *Proteobacteria* and the origin of *Proteobacteria* from phototrophic ancestors (Woese et al. 1984a, b, 1985; Woese 1987). The purple sulfur bacteria were *Gammaproteobacteria* and the purple nonsulfur bacteria representatives of *Alpha*- and *Betaproteobacteria* (Woese 1987).

The implementation of 16S rRNA gene sequences and phylogenetic considerations into the systematic treatment of phototrophic bacteria led to major changes in the

Table 1 *Alphaproteobacteria*: Purple nonsulfur bacteria

Order	Family	Genus abbr ^a	Species name	Reference	Previous names	Reference	Habitat
<i>Rhodospirillales</i>							
<i>Rhodospirillaceae</i>							
		<i>Rsp.</i>	<i>Rhodospirillum rubrum</i>	Molisch (1907)			Stagnant freshwater habitats
		<i>Phs.</i>	<i>Phaeospirillum fulvum</i>	Imhoff et al. (1998a)	<i>Rhodospirillum fulvum</i>	van Niel (1944)	Stagnant freshwater ponds
			<i>Phaeospirillum chandramohanii</i>	Kumar et al. (2009a)			Freshwater reservoir, India
			<i>Phaeospirillum molischianum</i>	Imhoff et al. (1998a)	<i>Rhodospirillum molischianum</i>	Giesberger (1947)	Stagnant freshwater ponds
			<i>Phaeospirillum oryzae</i>	Lakshmi et al. (2011c)			Paddy rhizosphere soil, India
			<i>Phaeospirillum tilakii</i>	Raj et al. (2012)			Freshwater habitat, bird sanctuary, India
		<i>Ros.</i>	<i>Roseospira mediosalina</i>	Imhoff et al. (1998a)	<i>Rhodospirillum mediosalinum</i>	Kompantseva and Gorlenko (1984)	Saline hot sulfur spring, Azerbaijan
			<i>Roseospira visakhapatnamensis</i>	Chakravarthy et al. (2007)			Marine saltern, India
			<i>Roseospira goensis</i>	Chakravarthy et al. (2007)			Marine saltern, India
			<i>Roseospira marina</i>	Guyoneaud et al. (2002)			Brackish-water lagoon of Certes, France
			<i>Roseospira navarrensis</i>	Guyoneaud et al. (2002)			Saline springs, Salinas de Oro, Spain
			<i>Roseospira thiosulfatophila</i>	Guyoneaud et al. (2002)			Coastal marine microbial mats
			<i>Pararhodospirillum photometricum</i>	Lakshmi et al. (2014)	<i>Rhodospirillum photometricum</i>	Molisch (1907)	Stagnant freshwater ponds
	<i>Pis.</i>		<i>Pararhodospirillum oryzae</i>	Lakshmi et al. (2014)	<i>Rhodospirillum oryzae</i>	Lakshmi et al. (2013)	Paddy rhizosphere soil, India
			<i>Pararhodospirillum sulfurexigens</i>	Lakshmi et al. (2014)	<i>Rhodospirillum sulfurexigens</i>	Kumar et al. (2008b)	Freshwater reservoir, India
	<i>Phi.</i>		<i>Phaeovibrio sulfidiphilus</i>	Lakshmi et al. (2011b)			Brackish-water, Nagapattinam, India
	<i>Rsa.</i>		<i>Rhodospira trueperi</i>	Pfennig et al. (1997)			Sippewissett Salt Marsh
	<i>Rcs.</i>		<i>Rhodocista centenaria</i>	Kawasaki et al. (1992)	<i>Rhodospirillum centenarium</i>	Favinger et al. (1989)	Thermopolis Hot Springs, Wyoming
			<i>Rhodocista pekingensis</i>	Zhang et al. (2003)			Wastewater treatment plant

Acetobacteraceae					
<i>Rpi.</i>	<i>Rhodopila globiformis</i>	Imhoff et al. (1984)	<i>Rhodopseudomonas globiformis</i>	Pfennig (1974)	Yellowstone acidic sulfur spring, Thermopolis Hot Springs microbial mat
<i>Rva.</i>	<i>Rhodovastum atsumiense</i>	Okamura et al. (2009a)			Paddy soil, Japan
Rhizobiales					
Bradyrhizobiaceae					
<i>Rps.</i>	<i>Rhodopseudomonas palustris</i>	van Niel (1944)	<i>Rhodobacillus palustris</i>	Molisch (1907)	Freshwater and terrestrial habitats
	<i>Rhodopseudomonas rubila</i>	Akiba et al. (1983)			Rice field soil
	<i>Rhodopseudomonas faecalis</i>	Zhang et al. (2002)			Chicken feces
	<i>Rhodopseudomonas harwoodiae</i>	Ramana et al. (2012)			Sediment of soil pan, India
	<i>Rhodopseudomonas julia</i>	Kompantseva (1989)	<i>Rps. palustris</i>	Hiraishi et al. (1992)	Acidic sulfur spring
	<i>Rhodopseudomonas parapalustris</i>	Ramana et al. (2012)			Soil sample, India
	<i>Rhodopseudomonas pentothentextigens</i>	Kumar et al. (2013)			Paddy soil, India
	<i>Rhodopseudomonas pseudopalustris</i>	Ramana et al. (2012)			Freshwater habitats
	<i>Rhodopseudomonas rhodobacensis</i>	Hougardy et al. (2000)			Eutrophic freshwater pond
	<i>Rhodopseudomonas thermotolerans</i>	Kumar et al. (2013)			Paddy soil, India
<i>Rbl.</i>	<i>Rhodoblastus acidophilus</i>	Imhoff (2001b)	<i>Rhodopseudomonas acidiphila</i>	Pfennig (1969a)	Acidic freshwaters, peat bog pools
	<i>Rhodoblastus sphagnicola</i>	Kulichevskaya et al. (2006)			Acidic sphagnum peat bog, Russia
(continued)					

Table 1 (continued)

Order	Family	Genus abbr ^a	Species name	Reference	Previous names	Reference	Habitat
<i>Hyphomicrobiaceae</i>							
		<i>Rpl.</i>	<i>Rhodoplanes roseus</i>	Hiraishi and Ueda (1994b)	<i>Rhodopseudomonas rosea</i>	Janssen and Harfoot (1991)	Freshwater pond
			<i>Rhodoplanes elegans</i>	Hiraishi and Ueda (1994b)			Wastewater
			<i>Rhodoplanes oryzae</i>	Srinivas et al. (2014b)			Paddy soil
			<i>Rhodoplanes piscinae</i>	Chakravarthy et al. (2012)			Freshwater pond
			<i>Rhodoplanes pokkaliisoli</i>	Lakshmi et al. (2009)			Rice field soil, India
			<i>Rhodoplanes serenus</i>	Okamura et al. (2009b)			Freshwater pond
			<i>Rhodoplanes cryptolactis</i>	Okamura et al. (2007)			Thermopolis Hot Spring
		<i>Blc.</i>	<i>Blastochloris viridis</i>	Hiraishi (1997)	<i>Rhodopseudomonas viridis</i>	Stadtward-Demchick et al. (1990)	Stagnant freshwater bodies
			<i>Blastochloris sulfoviridis</i>	Hiraishi (1997)	<i>Rhodopseudomonas sulfoviridis</i>	Drews and Giesbrecht (1966)	Acidic sulfur spring
			<i>Blastochloris gulmargensis</i>	Ramana et al. (2011)			Cold sulfur spring at Gulmarg, India
	<i>Rhodobiaceae</i>	<i>Rmi.</i>	<i>Rhodomicrobium vannieli</i>	Duchow and Douglas (1949)			Freshwater, brackish and marine habitats
			<i>Rhodomicrobium udaipurense</i>	Ramana et al. (2013)			River water, India
		<i>Rbi.</i>	<i>Rhodobium orientis</i>	Hiraishi et al. (1995)			Seawater pools
			<i>Rhodobium gokarnense</i>	Srinivas et al. (2007d)			Saltern, India
		<i>Afi.</i>	<i>Affella marina</i>	Urdiaín et al. (2008)	<i>Rhodopseudomonas marina</i>	Imhoff (1983)	Marine coastal habitats
			<i>Affella pfennigii</i>	Urdiaín et al. (2008)	<i>Rhodobium marinum</i>	Hiraishi et al. (1995)	Brackish-water pond, Rangiroa Atoll, French Polynesia
					<i>Rhodobium pfennigii</i>	Caumette et al. (2007)	

<i>Rhodobacterales</i>						
<i>Rhodobacteraceae</i>						
<i>Ceb.</i>	<i>Cereibacter changlensis</i>	Suresh et al. (2015)	<i>Rhodobacter changlensis</i>	Kumar et al. (2007d)	Snow from Changla Pass, Himalaya, India	
<i>Rba.</i>	<i>Rhodobacter capsulatus</i>	Imhoff et al. (1984)	<i>Rhodopseudomonas capsulata</i>	Molisch (1907)	Stagnant freshwater	
	<i>Rhodobacter aestuarii</i>	Ramana et al. (2009)			Brackish-water microbial mat, mangrove forest, India	
	<i>Rhodobacter azotoformans</i>	Hiraishi et al. (1996)			Wastewater sewage plant	
	<i>Rhodobacter blasticus</i>	Kawasaki et al. (1993)	<i>Rhodopseudomonas blastica</i>	Eckersley and Dow (1980)	Eutrophic freshwater pond	
	<i>Rhodobacter johrrii</i>	Girija et al. (2010)			Jowar (sorghum) rhizosphere, India	
	<i>Rhodobacter maris</i>	Ramana et al. (2008)			Seashore sediment, India	
	<i>Rhodobacter megalophilus</i>	Arunasri et al. (2008)			Soil of Indian Himalaya	
	<i>Rhodobacter ovatus</i>	Srinivas et al. (2008)			“Pink Pond” polluted freshwater pond, India	
	<i>Rhodobacter sphaeroides</i>	Imhoff et al. (1984)	<i>Rhodopseudomonas sphaeroides</i>	van Niel (1944)	Stagnant freshwater bodies	
	<i>Rhodobacter veldkampii</i>	Hansen and Imhoff (1985)			Freshwater habitats	
	<i>Rhodobacter vinaykumarii</i>	Srinivas et al. (2007b)			Marine tidal waters, India	
	<i>Rhodobacter viridis</i>	Raj et al. (2013)			Stagnant freshwater, India	
<i>Rca.</i>	<i>Rhodobaca bogoriensis</i>	Milford et al. (2000)			Saline Soda Lake Bogoria, Kenya	
	<i>Rhodobaca barguzinensis</i>	Boldareva et al. (2008)			Saline Soda Lake Algin Russia	
<i>Rlb.</i>	<i>Rhodobaculum claviforme</i>	Bryantseva et al. (2015)			Saline Soda Lake Doroninskoe, Siberia	
<i>Rdv.</i>	<i>Rhodovulum sulfidophilum</i>	Hiraishi and Ueda (1994a)	<i>Rhodopseudomonas sulfidophila</i>	Hansen and Veldkamp (1973)	Marine coastal waters and sediments	
			<i>Rhodobacter sulfidophilus</i>	Imhoff et al. (1984)		
	<i>Rhodovulum adriaticum</i>	Hiraishi and Ueda (1994a)	<i>Rhodopseudomonas adriatica</i>	Neutzing et al. (1984)	Marine waters, Malo Jezero, Adria	
	<i>Rhodovulum aestuarii</i>	Divyasree et al. (2016)			Estuarine brackish-water, India	
	<i>Rhodovulum bhavnagarens</i>	Srinivas et al. (2012)			Colored pond, India	

(continued)

Table 1 (continued)

Order	Family	Genus abbr ^a	Species name	Reference	Previous names	Reference	Habitat
			<i>Rhodovulum euryhalinum</i>	Hiraishi and Ueda (1994a)	<i>Rhodobacter euryhalinus</i>	Kompantseva (1985)	Marine coastal waters
			<i>Rhodovulum imhoffii</i>	Srinivas et al. (2007a)			Aquaculture pond, India
			<i>Rhodovulum iodotum</i>	Straub et al. (1999)			Marine coastal habitat
			<i>Rhodovulum kholense</i>	Kumar et al. (2008a)			Mangrove forest in Khola, India
			<i>Rhodovulum lacipuniceii</i>	Chakravarthy et al. (2009)			Saline pond near Sappada, India
			<i>Rhodovulum mangrovi</i>	Nupur et al. (2014)			Mangrove forest
			<i>Rhodovulum marinum</i>	Srinivas et al. (2006)			Tidal waters, India
			<i>Rhodovulum phaeoclacus</i>	Lakshmi et al. (2011a)			Saltern at Kanyakumari, India
			<i>Rhodovulum robignosum</i>	Straub et al. (1999)			Marine coastal sediment
			<i>Rhodovulum salis</i>	Srinivas et al. (2014a)			Salt pan, India
			<i>Rhodovulum steppense</i>	Kompantseva et al. (2010)			Soda Lakes, Siberia, Russia
			<i>Rhodovulum strictum</i>	Hiraishi and Ueda (1995)			Tidal seawater pools
			<i>Rhodovulum tesquicola</i>	Kompantseva et al. (2012)			Brackish-water Soda Lake, Siberia, Russia
			<i>Rhodovulum viride</i>	Srinivas et al. (2014a)			Colored pond at Chirala, India
			<i>Rhodovulum visakhapatnamense</i>	Srinivas et al. (2007c)			Tidal waters, India
<i>Rub.</i>			<i>Rubribacterium polymorphum</i>	Boldareva et al. (2009)			Soda Lake, Siberia
<i>Rhodothalassiales</i>							
<i>Rhodothalassaceae</i>							
<i>Rts.</i>			<i>Rhodothalassium salexitgens</i>	Imhoff et al. (1998a)	<i>Rhodospirillum salexitgens</i>	Drews (1981)	Evaporated seawater pools, Oregon
Genera of uncertain affiliation							
<i>Rhv.</i>			<i>Rhodovibrio salinarum</i>	Imhoff et al. (1998a)	<i>Rhodospirillum salinarum</i>	Nissen and Dundas (1984)	Salty pond of solar saltern, Portugal
			<i>Rhodovibrio sodomensis</i>	Imhoff et al. (1998a)	<i>Rhodospirillum sodomense</i>	Mack et al. (1993)	Sediment from the Dead Sea, Israel
<i>Rss.</i>			<i>Roseospirillum parvum</i>	Glaeser and Overmann (1999)			Sippewissett Salt Marsh

Note: All type species are shown in bold

^aGenus abbreviations are used in conformance with recommendations of the subcommittee on the taxonomy of phototrophic bacteria of the International Committee on Systematics of Prokaryotes (Imhoff and Madigan 2004; Madigan and Imhoff 2007)

Table 2 *Betaproteobacteria*: Purple nonsulfur bacteria

Order	Family	Genus abbr ^a	Species name	Reference	Previous names	Reference	Habitat
<i>Rhodocyclus</i>							
<i>Rhodocyclusaceae</i>							
		<i>Rcy.</i>	<i>Rhodocyclus purpureus</i>	Pfennig (1978)			Wastewater lagoon
			<i>Rhodocyclus tenuis</i>	Imhoff et al. (1984)	<i>Rhodospirillum tenue</i>	Pfennig (1969b)	Freshwater ponds
<i>Burkholderiales</i>							
<i>Comamonadaceae</i>							
		<i>Rfx.</i>	<i>Rhodoferax fermentans</i>	Hiraishi et al. (1991)			Ditchwater, activated sludge
			<i>Rhodoferax antarcticus</i>	Madigan et al. (2000)			Antarctic freshwater Lake Fryxell
		<i>Rvi.</i>	<i>Rubrivivax gelatinosus</i>	Willems et al. (1991)	<i>Rhodocystis gelatinosa</i>	Molisch (1907)	Stagnant freshwater
					<i>Rhodopseudomonas gelatinosa</i>	van Niel (1944)	
					<i>Rhodocyclus gelatinosus</i>	Imhoff et al. (1984)	
			<i>Rubrivivax benzoatilyticus</i>	Ramana et al. (2006)			Paddy soil, India

Note: All type species are shown in bold

^aGenus abbreviations are used in conformance with recommendations of the subcommittee on the taxonomy of phototrophic bacteria of the International Committee on Systematics of Prokaryotes (Imhoff and Madigan 2004; Madigan and Imhoff 2007)

Table 3 *Gammaproteobacteria*: Purple sulfur bacteria - *Chromatiaceae* and *Ectothiorhodospiraceae*

Genus abbr ^a	Species name	Reference	Previous name	Reference	Habitat ^b
<i>Chromatiales</i>					
<i>Chromatiaceae</i>					
<i>Tca.</i>	<i>Thiocapsa roseopersicina</i>	Winogradsky (1888)			Common in estuarine habitats, sewage lagoons
	<i>Thiocapsa imhoffii</i>	Asao et al. (2007)			Soda Lake, Soap Lake, USA
	<i>Thiocapsa litoralis</i>	Puchkova et al. (2000)			White Sea coastal sediment
	<i>Thiocapsa marina</i>	Caumette et al. (2004)			Marine coastal sediments
	<i>Thiocapsa pendens</i>	Guyoneaud et al. (1998)	<i>Amoebobacter pendens</i>	Pfennig and Trüper (1971)	Mud and stagnant water, sulfur springs
	<i>Thiocapsa rosea</i>	Guyoneaud et al. (1998)	<i>Amoebobacter roseus</i>	Winogradsky (1888)	Mud and stagnant water, sulfur springs
<i>Tlp.</i>	<i>Thiolamprovum pedioforme</i>	Guyoneaud et al. (1998)	<i>Amoebobacter pedioformis</i>	Eichler and Pfennig (1986)	Wastewater pond, Taiwan
<i>Tba.</i>	<i>Thiobaca trueperi</i>	Rees et al. (2002)			Eutrophic freshwater lake, Australia
<i>Lpc.</i>	<i>Lamprocystis roseopersicina</i>	Schroeter (1886)			Mud and stagnant water
	<i>Lamprocystis purpurea</i>	Imhoff (2001a)	<i>Amoebobacter purpureus</i>	Eichler and Pfennig (1988)	Chemocline of freshwater lakes
<i>Tdc.</i>	<i>Thiodictyon elegans</i>	Winogradsky (1888)			Mud and stagnant freshwater, sulfur springs
	<i>Thiodictyon bacillosum</i>	Pfennig and Trüper (1971)	<i>Amoebobacter bacillosum</i>	Winogradsky (1888)	Mud and stagnant freshwater, sulfur springs
<i>Isc.</i>	<i>Isochromatium buderii</i>	Imhoff et al. (1998b)	<i>Chromatium buderii</i>	Trüper and Jannasch (1968)	Estuarine sediments, salt flats
<i>Pha.</i>	<i>Phaebacterium nitratireducens</i>	Napur et al. (2015)			Coringa mangrove forest sediment, India

<i>Chr.</i>	<i>Chromatium okenii</i>	Perty (1852)	<i>Monas okenii</i>	Ehrenberg (1838)	Stagnant freshwater
	<i>Chromatium weissei</i>	Perty (1852)			Stagnant freshwater
<i>Tcs.</i>	<i>Thiocystis violacea</i>	Winogradsky (1888)			Stagnant freshwater and marine habitats
	<i>Thiocystis cadagnonensis</i>	Peduzzi et al. (2011)			Chemocline Lake Cadagno
	<i>Thiocystis chemoclinalis</i>	Peduzzi et al. (2011)			Chemocline Lake Cadagno
	<i>Thiocystis gelatinosa</i>	Pfennig and Trüper (1971)	<i>Thiothece gelatinosa</i>	Winogradsky (1888)	Stagnant freshwater and marine habitats
	<i>Thiocystis minor</i>	Imhoff et al. (1998b)	<i>Chromatium minus</i>	Winogradsky (1888)	Stagnant freshwaters
	<i>Thiocystis violascens</i>	Imhoff et al. (1998b)	<i>Chromatium violascens</i>	Perty (1852)	Stagnant freshwaters
<i>Trc.</i>	<i>Thiorhodococcus minor</i>	Guyoneaud et al. (1997)			Sediment of coastal lagoon, Arcachon Bay
	<i>Thiorhodococcus bheemicus</i>	Kumar et al. (2007b)			Marine aquaculture pond, India
	<i>Thiorhodococcus drewsii</i>	Zaar et al. (2003)			Microbial mat, Sippewissett Salt Marsh
	<i>Thiorhodococcus fuscus</i>	Lakshmi et al. (2015)			Sediment of Chilika Lagoon, India
	<i>Thiorhodococcus kakinadensis</i>	Kumar et al. (2007b)			Marine tidal waters, India
	<i>Thiorhodococcus manitoliphagus</i>	Rabold et al. (2006)			White Sea estuary
	<i>Thiorhodococcus modestakaliphilus</i>	Sucharita et al. (2010a)			Sediment of Chilika Lagoon, India
<i>Tpc.</i>	<i>Thiophaeococcus mangrovi</i>	Kumar et al. (2008d)			Brackish-water sediment, mangrove forest, India
	<i>Thiophaeococcus fuscus</i>	Divyasree et al. (2014)			Sediment from Chilika Lagoon, India
<i>Alc.</i>	<i>Allochromatium vinosum</i>	Imhoff et al. (1998b)	<i>Chromatium vinosum</i>	Winogradsky (1888)	Stagnant freshwater and marine habitat
	<i>Allochromatium minutissimum</i>	Imhoff et al. (1998b)	<i>Chromatium minutissimum</i>	Winogradsky (1888)	Stagnant waters and sediments
	<i>Allochromatium phaeobacterium</i>	Srinivas et al. (2009)			Brackish-water near Bheemili, India

(continued)

Table 3 (continued)

Genus abbr ^a	Species name	Reference	Previous name	Reference	Habitat ^b
	<i>Allochrochromatium renukae</i>	Kumar et al. (2008c)			Brackish-water pool, India
	<i>Allochrochromatium warmingii</i>	Imhoff et al. (1998b)	<i>Chromatium warmingii</i>	Migula (1900)	Stagnant freshwater with sulfide
	<i>Allochrochromatium humboldtianum</i>	Serrano et al. (2015)			Coastal sediment, Callao Bay Peru
<i>Tch.</i>	<i>Thermochromatium tepidum</i>	Imhoff et al. (1998b)	<i>Chromatium tepidum</i>	Madigan (1986)	Hot springs
<i>Pch.</i>	<i>Phaeochromatium fluminis</i>	Shivali et al. (2012)	<i>Marichromatium fluminis</i>	Sucharita et al. (2010b)	Baitarani River sediment, India
<i>Mch.</i>	<i>Marichromatium gracile</i>	Imhoff et al. (1998b)	<i>Chromatium gracile</i>	Strzeszewski (1913)	Stagnant marine and estuarine habitats
	<i>Marichromatium bheemlicum</i>	Kumar et al. (2007a)			Marine aquaculture pond, India
	<i>Marichromatium chrysaorae</i>	Shivali et al. (2011)			Jellyfish from seashore, India
	<i>Marichromatium indicum</i>	Arunasri et al. (2005)			Mangrove forest soil, India
	<i>Marichromatium litoris</i>	Shivali et al. (2011)			Sandy beach, India
	<i>Marichromatium purpuratum</i>	Imhoff et al. (1998b)	<i>Chromatium purpuratum</i>	Imhoff and Trüper (1980)	Marine habitats
<i>Trv.</i>	<i>Thiorhodovibrio winogradskyi</i>	Overmann et al. (1992)			Saline Lake Mahoney, Canada
<i>Rbc.</i>	<i>Rhabdochromatium marinum</i>	Dilling et al. (1995)			Sippewissett Salt Marsh
<i>Thc.</i>	<i>Thiohalocapsa halophila</i>	Imhoff et al. (1998b)	<i>Thiocapsa halophila</i>	Caumette et al. (1991)	Solar saltern microbial mat, Salin-de-Giraud, France
	<i>Thiohalocapsa marina</i>	Kumar et al. (2009b)			Marine aquaculture pond near Bheemili, India
<i>Lpb.</i>	<i>Lamprobacter modestohalophilus</i>	Gorlenko et al. (1979)			Saline lakes, Turkmenia, Ukraine
<i>Hch.</i>	<i>Halochromatium salexigens</i>	Imhoff et al. (1998b)	<i>Chromatium salexigens</i>	Caumette et al. (1988)	Solar saltern microbial mat Salin-de-Giraud, France
	<i>Halochromatium glycolicum</i>	Imhoff et al. (1998b)	<i>Chromatium glycolicum</i>	Caumette et al. (1997)	Microbial mats of Solar Lake, Sinai

	<i>Halochromatium roseum</i>	Kumar et al. (2007c)			Marine solar saltern at Kakimada, India
<i>Tco.</i>	<i>Thiococcus pfennigii</i>	Imhoff et al. (1998b)	<i>Thiocapsa pfennigii</i>	Eimhjellen (1970)	Mud and water with sulfide
<i>Tac.</i>	<i>Thioalkalococcus limnaeus</i>	Bryantseva et al. (2000)			Sediments of saline Soda Lakes, Siberia, Russia
<i>Tfc.</i>	<i>Thioflavococcus mobilis</i>	Imhoff and Pfennig (2001)			Sippewissett Salt Marsh
<i>Tpd.</i>	<i>Thiopedia rosea</i>	Winogradsky (1888)			Freshwater, brackish and marine habitats
<i>Tsp.</i>	<i>Thiospirillum jenense</i>	Migula (1900)	<i>Ophidomonas jenensis</i>	Ehrenberg (1838)	Mud and freshwater containing sulfide
<i>Ectothiorhodospiraceae</i>					
<i>Ect.</i>	<i>Ectothiorhodospira mobilis</i>	Trüper (1968)			Salt Lakes, estuaries, salt flats containing sulfide
	<i>Ectothiorhodospira halobalkaliphila</i>	Imhoff and Söling (1996)			Saline salt and Soda Lakes
	<i>Ectothiorhodospira marina</i>	Imhoff and Söling (1996)			Marine coastal sediments
	<i>Ectothiorhodospira marismortui</i>	Oren et al. (1989)			Dead Sea
	<i>Ectothiorhodospira shaposhnikovii</i>	Cherni et al. (1969)			Ponds and lakes containing sulfide
	<i>Ectothiorhodospira vacuolata</i>	Imhoff et al. (1981)			Saline salt and Soda Lakes
	<i>Ectothiorhodospira salini</i>	Ramana et al. (2010)			Solar saltern sediment, India
	<i>Ectothiorhodospira variabilis</i>	Gorlenko et al. (2009)			Saline Soda Lake Um-Risha, Wadi Natrun, Egypt
	<i>Ectothiorhodospira magna</i>	Bryantseva et al. (2010)			Saline Soda Lake Doroninskoe, Russia
<i>Eis.</i>	<i>Ectothiorhodosinus mongolicus</i>	Gorlenko et al. (2004)			Saline Soda Lake Dzun Uldzim, Mongolia
<i>Trs.</i>	<i>Thiorhodospira sibirica</i>	Bryantseva et al. (1999)			Saline Soda Lakes, Siberia, Russia

(continued)

Table 3 (continued)

Genus abbr ^a	Species name	Reference	Previous name	Reference	Habitat ^b
<i>Hlr</i> :	<i>Halorhodospira halophila</i>	Imhoff and Siling (1996)	<i>Ectoithiorhodospira halophila</i>	Raymond and Sistro (1969)	Highly saline Soda Lakes, Wadi Natrun
	<i>Halorhodospira abdelmalekii</i>	Imhoff and Siling (1996)	<i>Ectoithiorhodospira abdelmalekii</i>	Imhoff and Truper (1981)	Highly saline Soda Lakes, Wadi Natrun
	<i>Halorhodospira halochloris</i>	Imhoff and Siling (1996)	<i>Ectoithiorhodospira halochloris</i>	Imhoff and Truper (1977)	Highly saline Soda Lakes, Wadi Natrun
	<i>Halorhodospira neutriphila</i>	Hirschler-Rea et al. (2003)			Microbial mat, saltern Salin-de-Giraud, France

Note: All type species are shown in bold

^aGenus abbreviations are used in conformance with recommendations of the subcommittee on the taxonomy of phototrophic bacteria of the International Committee on Systematics of Prokaryotes (Imhoff and Madigan 2004; Madigan and Imhoff 2007)

^bCommon property of all habitats of purple sulfur bacteria is the presence of sulfide and light

taxonomy of these bacteria. First of all, in a reclassification of the purple nonsulfur bacteria, the *Betaproteobacteria* were separated from the *Alphaproteobacteria*. Several new genera were formed, with the recognition of some bacteria previously classified as *Rhodopseudomonas* and *Rhodospirillum* species included into the new genera *Rhodocyclus*, *Rhodopila*, and *Rhodobacter* (Imhoff et al. 1984). Also the genus *Ectothiorhodospira* was recognized as a separate family, the *Ectothiorhodospiraceae* besides the *Chromatiaceae* (Imhoff 1984), and later the two genera *Ectothiorhodospira* and *Halorhodospira* were distinguished in this family (Imhoff and Söling 1996). After these first fundamental changes in systematics of phototrophic purple bacteria and based on more extensive analyses of the phylogeny of 16S rRNA genes in these bacteria, a number of additional modifications have been proposed in the years that followed. The *Chromatiaceae* were rearranged according to their phylogenetic relations, and several new genera were proposed to distinguish the known species according to both phenotypic and genetic similarities (Imhoff et al. 1998b; Guyoneaud et al. 1998). Also a number of purple nonsulfur bacteria were reclassified in order to achieve better congruence between systematic treatment and phylogeny. The great heterogeneity of species treated in the genus *Rhodopseudomonas* was recognized, and two species with bacteriochlorophyll b were transferred to a new genus as *Blastochloris viridis* and *Blastochloris sulfoviridis* (Hiraishi 1997). *Rhodopseudomonas acidophila* was transferred to *Rhodoblastus acidophilus* (Imhoff 2001b), and *Rhodopseudomonas blastica* was transferred to *Rhodobacter blasticus* (Kawasaki et al. 1993). Also the marine species of *Rhodobacter* were removed to the genus *Rhodovulum* (Hiraishi and Ueda 1994a); *Rhodopseudomonas rosea* was recognized as a member of the new genus *Rhodoplanes* (Hiraishi and Ueda 1994b), and *Rhodospirillum centenum* was transferred to *Rhodocista centenaria* (Kawasaki et al. 1992). The heterogeneity of species recognized as members of the genus *Rhodospirillum* was further resolved by removing a number of these species into new genera (Imhoff et al. 1998a). More recently, *Rhodospirillum photometricum* and related species were transferred to the new genus *Pararhodospirillum* as *Pararhodospirillum photometricum* (Lakshmi et al. 2014). These reclassifications and the general conformity of the new systematic treatment with phylogenetic relations paved the way for biodiversity studies and species recognition in the environment based on genetic sequence information. The current systematic treatment of the species of phototrophic purple bacteria is shown in Tables 1, 2, and 3.

The Diversity of Phototrophic Purple Bacteria

Much of the motivation to study bacterial systematics comes from the desire to understand the phylogeny and evolution of the bacteria; their species-specific diversity in the environment, including aspects of adaptation of species to changing environmental conditions; their competition in the environment; and the biogeographic distribution on a species-specific level.

Several approaches are used to obtain information on the biodiversity of microbial communities. The classical approach involves the separation and isolation of microbial strains, the characterization of pure cultures, and the identification and

description of species. This approach is appropriate to identify and characterize components of the community and to determine their physiological properties but is less suited to depict the species diversity within a sample.

The molecular, metagenetic approach uses genetic tools to separate DNA molecules or amplified PCR products and uses the sequence information to determine the genetic diversity within a sample. With this approach, the diversity of a community can be approached and known species can be recognized on the basis of their sequence, but identification and characterization of unknown species are not possible.

Ideally diversity studies of phototrophic bacteria combine aspects of both approaches, and culture-dependent studies that include the characterization of the isolates are accompanied by genetic analyses determining the phylogenetic relationship of the bacteria within the sample. If untreated environmental samples are diluted in agar deeps or on agar plates with a proper medium for phototrophic bacteria, the cultured biodiversity can be estimated by selection of representative colonies and their characterization by microscopic examination and sequence analysis of the 16S rRNA gene or other suitable genes. If the number of colonies are counted and associated to phylotypes according to sequence information and phenotypic properties, a rough estimation of the diversity of phototrophic bacteria is possible with this method (Imhoff 2006c). Although not commonly used, this combined approach is a valuable alternative to pure metagenetic approaches with the advantage of better resolution and higher specificity and the possibility to approach ecological questions.

The Cultured Diversity of Phototrophic Purple Bacteria

Over the decades, the presence, abundance, and activities of phototrophic purple bacteria were studied in freshwater and marine habitats on the basis of microscopic observations and culture studies. For these analyses, a systematic treatment based on morphological and easily recognizable phenotypic characteristics (motility by flagella, formation of gas vesicles, shape and size of the cells, and structure of internal photosynthetic membrane systems, gas vesicles, absorption spectra and photosynthetic pigments, substrate utilization in particular oxidation of sulfide and thiosulfate) was a solid basis (Pfennig and Trüper 1974; Imhoff 2001d). These criteria maintain to be of major relevance for the taxonomic characterization of species and are included in the guidelines for the description of new species of phototrophic bacteria (Imhoff and Caumette 2004). Most of the species descriptions since the 1970s used these criteria, later with additional support by molecular analysis of cellular components and sequence information of the 16S ribosomal RNA molecule.

Much of the work on the systematics of phototrophic purple bacteria over the past decades has been made, and the overwhelming majority of species have been described by a few experts in this field, with a clear habitat focus related to the location of their research laboratory. In the lab of Pierre Caumette (Arcachon and Pau, France), the focus was on the work on coastal lagoons and marine salterns in southern France and on the isolation of new moderately halophilic purple sulfur bacteria including, among others, *Halochromatium salexigens*, *Thiohalocapsa halophila*,

and *Halorhodospira neutriphila* from marine salterns and *Thiorhodococcus minor* and *Roseospira* species from coastal lagoons (Tables 1 and 3). The work of Mike Madigan (Carbondale, IL) had a clear focus on phototrophic bacteria from hot springs in the USA but included other extreme habitats such as permanently cold Antarctic lakes, soda lakes, and the Dead Sea with new species descriptions of *Thermochromatium tepidum*, *Thiocapsa imhoffii*, *Rhodoferax fermentans*, *Rhodobaca bogoriensis*, and *Rhodovibrio sodomensis* (Tables 1, 2, and 3). Japanese freshwater and marine sources were studied by Akira Hiraishi (Toyohashi, Japan), and several new genera and species were described such as *Rhodoferax fermentans*, *Rhodovastum atsumiense*, *Rhodobium orientis*, *Rhodoplanes elegans*, and *Rpl. serenus* (Tables 1 and 2). Many of the saline and hypersaline waters, alkaline soda lakes, and other extreme environments of Russia (Siberia) and also of Mongolia and Kasachstan were studied by the group of Vladimir Gorlenko (Moscow, Russia) (to a great part together with Elena Kompantseva and Irina Bryantseva). Most of his isolates of new genera and species were derived from alkaline soda lakes and from salt lakes, e.g., *Thiorhodospira sibirica*, *Ectothiorhodosinus mongolicus*, *Thioalkalicoccus limnaeus*, and *Rubribacterium polymorphum* (Tables 1, 2, and 3). The focus of the author's group (Bonn and Kiel, Germany) was on marine habitats and African soda lakes, and a number of species were described, many in cooperation with P. Caumette, V. Gorlenko, and Ch. Sasikala (Tables 1, 2, and 3). In more recent years since 2005, more than 40 new species have been isolated from Indian sources by the groups of Ch. Sasikala and Ch.V. Ramana (Hyderabad, India) (in part together with A.P. Kumar and T.N.R. Srinivas) (Tables 1, 2, and 3).

Based on 16S rRNA gene sequences of the type strains, the phylogenetic relationship of the species is depicted in Fig. 1. Data on the species including references, previous names, and habitats are compiled in Tables 1, 2, and 3 for the *Alpha*-, *Beta*-, and *Gammaproteobacteria*. Also the higher taxonomic ranks, families, and orders in which the genera are grouped are included. The type species of the genera are shown in bold face and recommended genus abbreviations are depicted. This three-letter code is in conformance with the recommendations of the subcommittee on the taxonomy of phototrophic bacteria of the International Committee on Systematics of Prokaryotes (Imhoff and Madigan 2004; Madigan and Imhoff 2007). The following abbreviations were added as suggestions to the three-letter code for the recently described genera: *Ceb.* *Cereibacter*, *Rhb.* *Rhodobaculum*, *Rub.* *Rubribacterium*, *Afi.* *Afifella*, *Pas.* *Pararhodospirillum*, *Phv.* *Phaeovibrio*, *Rva.* *Rhodovastum*, *Pha.* *Phaeobacterium*, *Tpc.* *Thiophaeococcus*, and *Pch.* *Phaeochromatium*.

The high diversity of phototrophic *Alphaproteobacteria* is demonstrated by their presence in three orders and a number of families. Their phylogenetic relations are well represented by the distribution in the *Rhodobacterales* (*Rhodobacteriaceae*), *Rhizobiales* (*Bradyrhizobiaceae*, *Hyphomicrobiaceae*, and *Rhodobiaceae*), and *Rhodospirillales* (*Rhodospirillaceae* and *Acetobacteraceae*) as shown in the phylogenetic tree in Fig. 1 and in Table 1. While most of the species and genera are well aligned phylogenetically, an apparent lack of clear association to any of the established families within the *Alphaproteobacteria* is given for *Rts. salexigens*, *Rss.*

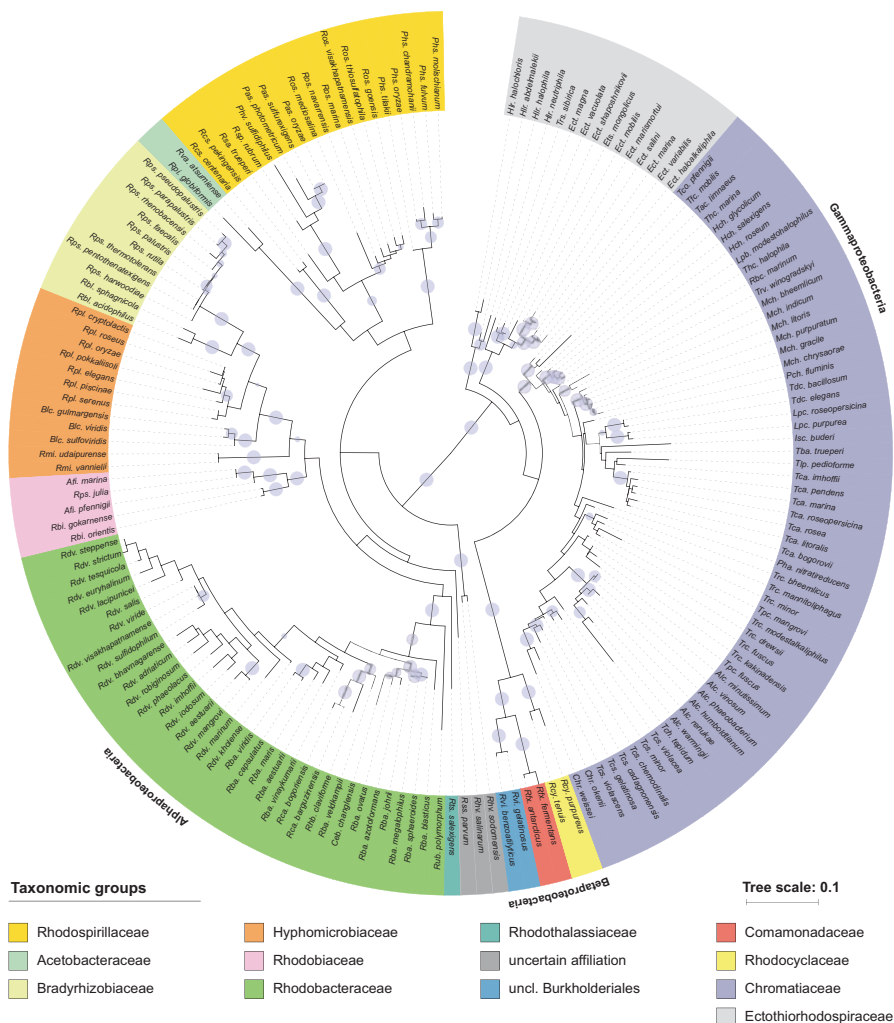


Fig. 1 Phylogenetic relationship of the species of anaerobic anoxygenic phototrophic purple bacteria based on 16S rRNA gene sequences of their type or neotype strains. Sequences used were 1459 nt in length and were aligned using SILVA and the alignment was corrected manually. A maximum likelihood (ML) phylogenetic tree was calculated from the edited alignment with the program IQ-TREE6 v1.4.2. The optimal substitution model given the data under consideration was determined by IQ-TREE to be TN+G+R5. “Ultrafast bootstrap approximation” 8 (UFBoot) was used to provide branch support values with 1000 bootstrap replicates. Branch support values were assigned onto the original ML tree. The calculated phylogenetic tree was midpoint-rooted using the R package phangorn 9 v2.0.3 and bootstrap values >95 % are indicated in the tree by light blue circles

parvum, and the two *Rhodovibrio* species, all of which are well adapted to marine/saline or even highly saline habitats. Their exact affiliation in the phylogenetic tree remains unclear. The genera of the *Betaproteobacteria* are assigned to the families *Rhodocyclaceae* (*Rhodocyclus*) and the *Comamonadaceae* (*Rhodoferrax*), while

Rubrivivax is not clearly affiliated to a family so far (Imhoff 2005). Also the separation of the families *Chromatiaceae* and *Ectothiorhodospiraceae* in the *Chromatiales* is well depicted in the phylogenetic relationship of the 16S rRNA gene (Fig. 1).

However, the taxonomic treatment is not always well represented in the phylogenetic relations: On the basis of the depicted phylogenetic relationship, *Ectothiorhodosinus mongolicus* clusters between species of *Ectothiorhodospira*, *Lamprobacter modestohalophilus* is highly similar to *Halochromatium* species, the genus *Thiorhodococcus* forms two or three clusters, and the two species of *Thiophageococcus* are clustering within two of these groups. Also, species of *Rhodobaca*, *Rhodobaculum*, and *Cereibacter* cluster within the *Rhodobacter* clade (Fig. 1). These examples need careful further studies for clarification of their systematic treatment.

There are also some ambiguities on the level of the species identification. Several pairs of species have almost identical sequences. *Rps. rutila* has a sequence identical to that of *Rps. palustris* (0.03 % difference) and is regarded as a later subjective synonym of *Rps. palustris* (Hiraishi et al. 1992). Quite similar the sequence of *Rps. julia* is identical to that of *Afi. marina*, and this species should as well be regarded as a subjective synonym of *Afi. marina*. Also 16S rRNA gene sequences of *Alc. vinosum* and *Alc. minutissimum* are identical (0.00 % difference) as has been noted earlier (Serrano et al. 2011). Further couples of species with highly similar 16S rRNA gene sequences (less than 0.05 % dissimilarity) are *Rdv. viride*/*Rdv. visakhapatnamense*, *Rba. sphaeroides*/*Rba. megalophilus*, *Rba. megalophilus*/*Rba. johrii*, *Rps. thermotolerans*/*Rps. pentothenatexigens*, *Rmi. vannielii*/*Rmi. udaipurensis*, and *Pas. oryzae*/*Pas. sulfurexigens*. As far as the used sequence information is concerned, the species within the indicated couples may be regarded as identical at the species level, i.e., represent subjective synonyms. A careful reevaluation of these species is required in order to confirm the existence of two separate species in the given examples.

In parts, the phylogenetic relationship correlates with some phenotypic properties that are common to close neighbors. For example, three species of bacteriochlorophyll b-containing *Chromatiaceae* are close relatives, and the internal photosynthetic membrane structure is a distinctive property of these three bacteria (tubules) to other *Chromatiaceae* (vesicles) and to the *Ectothiorhodospiraceae* (lamellae). Though cell morphology is not a core property for identification of species, even morphological properties maybe common features at least of some phylogenetically related groups, e.g., the budding mode of cell division (*Rhodopseudomonas* and *Rhodoblastus* species) and the spiral shape in some purple nonsulfur bacteria (*Rhodospirillum*, *Phaeospirillum*, *Roseospira*, *Pararhodospirillum*, *Rhodospira*, and *Rhodocista* species).

In addition, habitat preferences are depicted in the phylogenetic relatedness. For many of the genera, a specific preference for a special type of habitat is visible (Tables 1, 2, and 3). A few examples of the *Alphaproteobacteria* can demonstrate this observation: *Phaeospirillum*, *Rhodoplanes*, and *Rhodobacter* species prefer freshwater habitats; *Roseospira*, *Rhodovibrio*, *Rhodovulum*, and *Rhodobium* species preference marine and saline habitats; *Rhodoblastus* species live in acidic peat bogs; and *Rhodobaca* species live in alkaline soda lakes. The preference of all *Ectothiorhodospiraceae* for saline and alkaline conditions and of *Halorhodospira* species for highly saline and alkaline habitats is well known. Many *Chromatiaceae*,

e.g., *Marichromatium* and *Thiorhodococcus* species, have a clear preference for marine habitats, while species of other genera such as *Thiocystis*, *Chromatium*, and *Lamprocystis* were found in freshwater habitats and a group around *Halochromatium* and *Thiohalocapsa* species includes species with elevated salt tolerance (see Table 3). Obviously, the preference for a specific set of physicochemical conditions in the environment preselects species of phototrophic purple bacteria with a potential to thrive in a particular habitat. Most obvious in this context is the clear difference between purple bacteria found in the chemocline of freshwater lakes and in marine coastal sediments or lagoons.

The Biodiversity of Environmental Communities of Purple Bacteria

Sequence information is predestined to link bacterial systematics and environmental biodiversity studies of phototrophic bacteria because sequence information is now well established as a property in systematics of phototrophic bacteria. A first important step for the possible identification of species of phototrophic purple bacteria in environmental DNA sequences was the establishment of a phylogenetic-based taxonomy supported by 16S rRNA gene sequences (Imhoff 1984; Imhoff et al. 1984; Imhoff and Söling 1996; Imhoff et al. 1998a, b; Guyoneaud et al. 1998; Kawasaki et al. 1992, 1993; Hiraishi 1997; Hiraishi and Ueda 1994a). Because sequence information becomes easily available from environmental communities, from individual clones, as well as from complete metagenomes, it can supply information about the diversity of a particular genetically targeted function in a species-specific resolution.

In order to establish a measure for the species diversity in environmental samples based on genetic sequence information, phylotypes can be defined on the basis of environmental 16S rRNA gene sequences. If a distinction of phylotypes is made at a sequence level that compares to the level of distinction between species with pure cultures (Stackebrandt and Ebers 2006), phylotypes can be used to approach the species diversity of environmental communities. If environmental clone sequences are sufficiently similar to known species, represented by their type strains, it is quite likely that they are belonging to this species or are close relatives thereof. If considerations concerning sequence similarities as a rough guide for species differentiation of pure cultures are transferred to sequences from the environment, species recognition and an estimate of the species diversity in environmental samples can be achieved with phylotypes as an equivalent to the taxonomic defined species.

However, pitfalls of applying 16S rRNA-based approaches to the analysis of communities of anoxygenic phototrophic bacteria, in particular the phototrophic *Proteobacteria*, were realized and are due to the close phylogenetic relationship between phototrophic and non-phototrophic *Proteobacteria*. Even close phylogenetic neighbors may perform different physiological functions. Specific sequence stretches of the 16S rRNA gene that would clearly allow identification of phototrophic representatives in complex mixtures of environmental samples

and distinguish these from non-phototrophic relatives could not be identified. Therefore, many metagenetic studies that focus on sequences of the 16S rRNA gene do not supply clear information on the presence and diversity of phototrophic bacteria in the studied samples. In consequence, increasing research activities are concerned with the application of functional genes to characterize the diversity of functional microbial groups, including anoxygenic phototrophic bacteria (Imhoff 2016).

Functional Gene Studies

In order to specifically study the biodiversity of phototrophic bacteria and their responses to environmental factors, genetic tools were established targeting *pufL* and *pufM* genes of the reaction center proteins (Nagashima et al. 1997; Achenbach et al. 2001; Karr et al. 2003; Tank et al. 2009) and the *bchY* gene of the biosynthesis of bacteriochlorophyll (Yutin et al. 2009).

The *bchY* gene, encoding the Y subunit of chlorophyllide reductase, is at a branch point in the biosynthesis of chlorophyll and bacteriochlorophyll (Chew and Bryant 2007). This gene is present in all known anoxygenic phototrophic bacteria, but absent in oxygenic phototrophs, and therefore, it is suited for targeting the bacteriochlorophyll-containing anoxygenic phototrophic bacteria (Yutin et al. 2009). The comparable low information in the amplified sequences (approx. 500 nt) is certainly a limitation of the used primers. The phylogenetic diversity of phototrophic bacterial communities based on these *bchY* gene sequences was studied in Lake Kinneret and in the Mediterranean Sea (Yutin et al. 2009), but extended studies on environmental samples and in particular a comprehensive database with reference sequences from type strains of cultured anoxygenic phototrophic bacteria are so far lacking.

The *pufLM* genes encode for the light (L) and medium (M) subunit of the photosynthetic reaction center type II structural proteins of all phototrophic *Proteobacteria* (purple sulfur bacteria, purple nonsulfur bacteria, as well as aerobic phototrophic purple bacteria producing bacteriochlorophyll and forming a photosynthetic apparatus) and in addition of the phototrophic members of the Chloroflexi (Nagashima et al. 1997; Tank et al. 2009). A primer system which amplifies the combined sequence information of *pufL* and *pufM* genes (products of >1450 nt length) was used to build a comprehensive database of *pufLM* gene sequences of most of the recognized type strains of the purple sulfur bacteria (Tank et al. 2009) and to study the biodiversity of phototrophic purple bacteria in the environment (Tank et al. 2011; Thiel et al. 2010). The phylogenetic relationship demonstrated by *pufLM* gene sequences of the purple sulfur bacteria (*Gammaproteobacteria*) was in good correlation to that of 16S rRNA gene sequences (Tank et al. 2009). In context with the phylogenetically based taxonomy of the purple sulfur bacteria (Imhoff et al. 1998a, b; Guyoneaud et al. 1998) and based on the established *pufLM* sequence data, this correlation very much supports the recognition of species in environmental samples using *pufLM* gene sequences.

Molecular genetic studies to characterize the communities of phototrophic purple bacteria based on sequences of the *pufM* gene revealed a remarkable high diversity

in different habitats (Achenbach et al. 2001; Karr et al. 2003; Asao et al. 2011; Hirose et al. 2012), although the sequence information obtained was quite low (less than 400 nt). Two case studies of salt lakes in the Chilean highland (Thiel et al. 2010, see Chap. 13) and of a coastal lagoon of the Baltic Sea (Tank et al. 2011) highlight the possibilities of this approach to study the diversity of communities of phototrophic purple bacteria. In order to compare the sequence data from environmental samples with those from type and reference strains on a systematic level, phylotypes were defined for the *pufLM* sequences. Considering different evolutionary rates of the *pufLM* genes compared to the 16S rRNA gene, borderlines of 86 and 95 % sequence similarity of the *pufLM* genes were proposed for the distinction of genera and species of the purple sulfur bacteria (Tank et al. 2009, 2011).

Selected Habitats of Phototrophic Purple Bacteria

Much of the work on the ecology and the communities of anoxygenic phototrophic bacteria has been made in freshwater lakes; in stratified water bodies of fjords and even the Black Sea; also in coastal habitats including coastal lagoons, microbial mats, and sediments; and of course in extreme habitats such as hot springs, salt and soda lakes, and cold habitats such as Antarctic waters and sea ice. From these habitats but also from peat bogs and from waste water treatment plants, paddy soils, and others, purple bacteria have been isolated (Tables 1, 2, and 3). The work on the general ecology of phototrophic bacteria, their ecological relevance, their occurrence in various types of habitats, and their physiology have been discussed in a number of reviews before (Madigan 1988; Imhoff 1988, 1992, 2001c; Pfennig 1989; van Gemerden and Mas 1995). In the following, representative examples are presented

1. of microbial mats from coastal marine habitats, which are well characterized, and from which a diverse number of new species have been isolated (Sippewissett Salt Marsh, MA),
2. of a freshwater chemocline in which cultivation-dependent approaches and molecular diversity studies have been successfully combined (Lake Cadagno, Switzerland), and
3. of a coastal lagoon, in which a most comprehensive analysis of the diversity of phototrophic purple sulfur bacteria has been made using *pufLM* gene sequences specifically targeting the phototrophic purple bacteria (Baltic Sea lagoon at Stein, Germany).

Sippewissett Salt Marsh, MA, USA

Phototrophic purple bacteria are common to marine coastal habitats, and in tidal sediments of estuaries and the Wadden Sea, diverse communities of these bacteria develop worldwide. One of the most prominent examples of such a marine habitat where

phototrophic bacteria occur in visible masses and from which several new species have been isolated is represented by the sandy sediments of the Great Sippewissett Salt Marsh and its intertidal flats (MA, USA) (Trüper 1970; Nicholson et al. 1987; Pfennig et al. 1997; Glaeser and Overmann 1999; Imhoff and Pfennig 2001). A detailed analysis of the different layers of these well-developed microbial mats based on microscopic studies and pigment analysis revealed three distinct layers of phototrophic bacteria between a top layer of algae and cyanobacteria and the black bottom sediment with actively sulfate-reducing bacteria (Nicholson et al. 1987).

The uppermost of these three layers was pink and dominated by spherical purple sulfur bacteria most likely representatives of *Thiocapsa* (*Thiocapsa roseopersicina* and *Thiocapsa rosea*, including former *Amoebobacter* species) and also forms resembling *Marichromatium* and *Thiocystis* species (Nicholson et al. 1987). The layer below was distinctive peach-colored and largely contained bacteria with bacteriochlorophyll b, which were supposed to represent *Thiococcus pfennigii* (the only purple sulfur bacterium with bacteriochlorophyll b known at this time). The bacteria of the lowermost green and thinnest layer, which was not always present, were identified as green sulfur bacteria of the genus *Prosthecochloris* (Nicholson et al. 1987). This described pattern of layers very well reflects the properties of the different phototrophic bacteria, in particular concerning their pigmentation and physiological properties.

Thiocapsa roseopersicina and other purple bacteria of the top layer contain bacteriochlorophyll a, while the peach-colored layer contains predominantly bacteria with bacteriochlorophyll b (which have a special advantage in sandy sediments where long wavelength radiation penetrates especially deep) and the green sulfur bacteria in the lower layer contain bacteriochlorophyll c. All of these pigments have different absorption windows (700–750 nm for bchl c, 805–930 nm for bchl a, >1000 nm for bchl b), and the bacteria can therefore easily develop below the chlorophyll a-containing top layer (absorption maximum at 680 nm) and independent from each other. As not only the quality but also the quantity of light matters, it is interesting to see that the bacteriochlorophyll b-containing bacteria with their long-range absorption maxima beyond 1000 nm have a special niche in the sandy sediments below those purple bacteria having bchl a. In addition, the lowermost position of the green sulfur bacteria matches with known experiences in sediments and waters and relates to the special antenna organelles, the chlorosomes, which enable these bacteria to grow at the lowermost amounts of light available for photosynthesis. Also, the relations to sulfide and oxygen perfectly match with the distribution of the phototrophic bacteria in different layers. While the green sulfur bacteria are the most sulfide-tolerant and most sensitive to oxygen, many purple sulfur bacteria not only tolerate oxygen but also can perform oxic respiration (Kämpf and Pfennig 1980, 1986). In particular *Thiocapsa roseopersicina* is metabolically highly flexible and known to be well adapted to diurnal changes of oxic and anoxic conditions, performing photosynthesis in the presence of sulfide during (the onset of) daytime and performing aerobic respiration after depletion of sulfide, also growing as a chemolithotroph or chemoorganotroph in the dark (Kämpf and Pfennig 1980, 1986; De Wit and Van Gemerden 1987, 1990; Schaub and Van Gemerden 1993). These properties predestine this bacterium as a major player in the topmost layer of the phototrophic bacterial mats. The possibility to consume diffusing oxygen, including

the oxygen produced in the top layer of the microbial mat, by the upper layer of purple sulfur bacteria protects the layers below with more oxygen-sensitive bacteriochlorophyll b-containing purple sulfur bacteria from the oxygen (Pfennig 1989).

In a preliminary characterization of the diversity of the green sulfur bacteria in samples from Sippewissett Salt Marsh using *fmoA* and 16S rRNA gene sequences, clone sequences related to *Prosthecochloris aestuarii* and to *Chlorobaculum* species were identified (Alexander and Imhoff 2006), supporting and extending the previous findings. A corresponding analysis of the phototrophic purple bacteria in these mats has not been made so far. However, a number of new phototrophic purple bacteria were isolated from these mats suggesting a high, so far unrecognized diversity of phototrophic purple bacteria in the mats. The isolated purple sulfur bacteria from this habitat include strains of *Thiocystis violascens* (formerly *Chromatium violascens*) and *Thiocystis violacea* (Trüper 1970) and a number of new species. Bacteriochlorophyll b-containing bacteria first isolated from these microbial mats include the purple sulfur bacterium *Thioflavicoccus mobilis* (Imhoff and Pfennig 2001), which is a close relative of *Thiococcus pfennigii*, and the purple nonsulfur bacterium *Rhodospira trueperi* (Pfennig et al. 1997). Also *Rhabdochromatium marinum*, which is an obligate phototrophic and strictly anaerobic bacterium, was isolated from a microbial mat of Great Sippewissett Salt Marsh (Dilling et al. 1995). In addition, *Thiorhodococcus drewsii* was isolated from Sippewissett Salt Marsh (Zaar et al. 2003), and finally the purple nonsulfur bacterium *Roseospirillum parvum* with antenna bacteriochlorophyll complexes absorbing at approx. 930 nm originated from this salt marsh (Glaeser and Overmann 1999). It is amazing to see the high degree of novelty in the isolated phototrophic bacteria from this habitat, and a comprehensive study on the metagenomic diversity of the communities of phototrophic bacteria in this salt marsh would be a highly demanding task.

Lake Cadagno, Switzerland

Meromictic lakes represent the most important freshwater habitat of phototrophic sulfur bacteria. In these lakes a more or less stable chemocline is formed, and if light penetrates down to this zone, massive developments of phototrophic sulfur bacteria (generally in company with purple nonsulfur bacteria) develop. In a number of recent studies, phototrophic purple sulfur bacteria from Lake Cadagno were isolated, and in addition the community was characterized by sequence analysis of the 16S rRNA gene.

Lake Cadagno is a small meromictic lake located at 1923 m elevation in the Swiss Alps. It is 21 m deep, and during spring and summer time a permanent chemocline exists at approx. 10 m depth in which phototrophic purple bacteria develop (Fischer et al. 1996; Schanz et al. 1998). Based on microscopic studies and photopigment analysis, the predominance of the okenone-containing *Chromatium okenii* and *Lamprocystis purpurea* forming a 2 m deep zone at the sulfide/oxygen interface was found (Schanz et al. 1998). In agreement with these studies, the molecular analysis of the bacterial community composition at the chemocline revealed clone

sequences closely related to *Chromatium okenii*, *Lamprocystis purpurea*, and *Lamprocystis roseopersicina* (Bosshard et al. 2000a; Tonolla et al. 1999) and a seasonal dominance of *Chromatium okenii* during the summer months and of *Lamprocystis purpurea* during autumn (Bosshard et al. 2000b). Later, also clone sequences related to *Thiocystis* species were found (Tonolla et al. 2005), and two new species were described from isolates of this lake, *Thiocystis chemoclinalis* and *Thiocystis cadagnonensis* (Peduzzi et al. 2011). Despite seasonal and long-term changes, the diversity of the phototrophic bacterial community of Lake Cadagno appears typical of low-light chemocline habitats with the dominance of okenone-containing purple bacteria and green sulfur bacteria. More detailed molecular studies targeting specifically the phototrophic purple and green bacteria are expected to demonstrate a more diverse community in this lake as is known till now.

Baltic Sea Coastal Lagoon, Germany

Coastal lagoons are habitats related to typical coastal sediment habitats not permanently covered by water (coastal sediments in estuaries and the Wadden Sea) and also to marine salterns. Whenever sea water and organic matter is locked into coastal lagoons, the onset of active sulfate reduction rapidly creates conditions suitable for the development of anoxygenic phototrophic sulfur bacteria not only in the sediment but also in the water body. The reservoirs of phototrophic bacteria within the coastal sediments provide the initial “feeding” of the populations that develop in the lagoons. Often phototrophic sulfur bacteria are forming massive colored blooms in coastal sediments and lagoons accompanied by purple nonsulfur bacteria (Imhoff 1988, 2001c). Depending on the strength of the sun light and the water regime (evaporation versus dilution with fresh seawater or rain), the concentration of salts in the lagoons may increase and species with increased salt tolerance or salt requirement may be favored. Such changes can create conditions comparable to the situation in the intermediate concentration range of marine salterns. Therefore, it is expected that the three different types of habitats share a number of common species of phototrophic bacteria. Indeed, a number of moderately halophilic *Chromatiaceae* have been isolated from and are considered common inhabitants of both marine coastal lagoons and salterns (Table 3).

In a coastal lagoon of the Baltic Sea in the Kiel Bight, the biodiversity of phototrophic purple bacteria was studied on the basis of *pufLM* gene sequences (Tank et al. 2009, 2011). In order to establish the species diversity, the sequences were arranged in phylotypes. The great majority of *pufLM* phylotypes of the community from this lagoon belonged to the purple sulfur bacteria. A few single clones from aerobic phototrophic *Proteobacteria* were also present in the habitat. The purple sulfur bacteria were affiliated to genera and species typically found in such or similar habitats, including the genera *Marichromatium*, *Thiorhodovibrio*, *Thiorhodococcus*, *Allochromatium*, *Thiocapsa*, and *Thiocystis* (Fig. 2). Some sequences were also related to moderately halophilic *Halochromatium* and *Thiohalocapsa* species first isolated from solar salterns (Caumette et al. 1988, 1991, 1997). From a total of 20

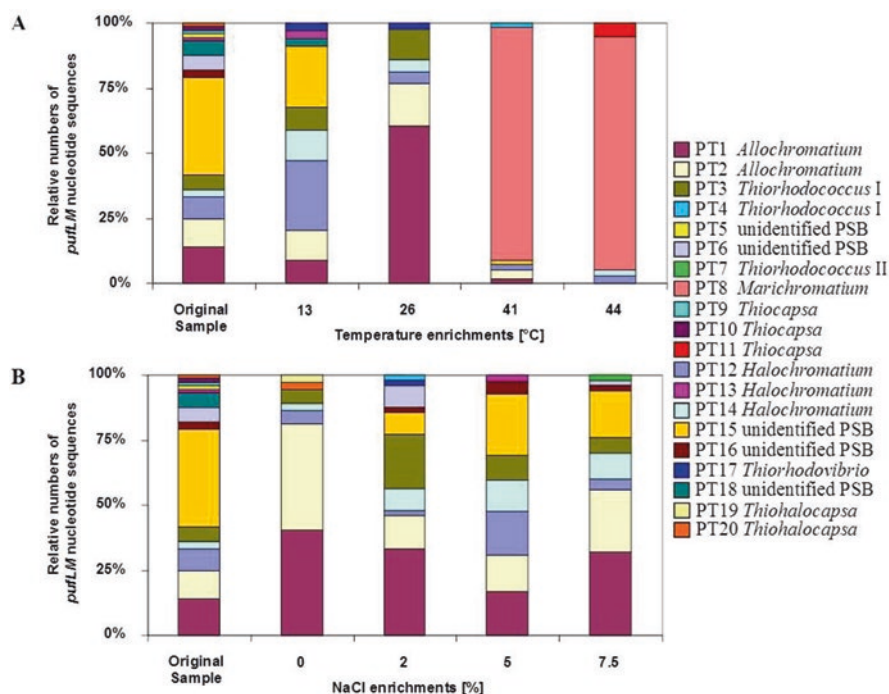


Fig. 2 The contribution of different phylotypes to the community of purple sulfur bacteria in a Baltic Sea lagoon on the basis of *pufLM* gene sequences is shown. The figure depicts the relative composition in the sample and under experimental conditions with variation of temperature and salt concentration as indicated (From Tank et al. 2011)

identified phylotypes of purple sulfur bacteria, five could be clearly assigned to type strains of known species, ten additional phylotypes to a genus, and only five phylotypes had sequence similarities (83.4–85.6%) slightly below the proposed limit of 86% *pufLM* sequence similarity to the closest known type strain, which was proposed as a borderline value for the inclusion into genera (Tank et al. 2011). Thus, most of the purple sulfur bacteria of this lagoon more or less were known at the genus level, but novelty of these bacteria was high at the species level. In contrast, *pufLM* sequences of aerobic phototrophic purple bacteria of *Alpha*- and *Gammaproteobacteria* were generally below 84% similar to the next known relative type strain, in most cases even far below 80% similarity (Tank et al. 2011).

As this type of habitat is subjected to considerable changes in temperature and salt content during daily and seasonal cycles, the impact of these parameters on the community composition was measured under controlled conditions in the laboratory (Tank et al. 2011). In these experiments, a considerable impact on the community structure was found within studied ranges of temperature (13–44 °C, at 2% salts) and salinity (0–7.5% NaCl, at 23.5 °C). The highest diversity of identified phylotypes was observed in the natural sample (at 23.5 °C and 2% salinity), the lowest diversity at temperatures of 26 °C and higher and in the absence of salt (Fig. 2). With the exception of three phylotypes found as single clones in the environmental sample, all others

were retrieved at least from one of the experimental conditions. In addition, six phylotypes that were not detected in the environmental sample showed up alongside the applied salt and temperature gradients (Tank et al. 2011). Among these were phylotypes most similar to the type strains of *Trc. mannitoliphagus* (99.8% similar), *Trc. kakinadensis* (98.2% similar), and *Mch. gracile* (100% similar). This result is quite remarkable and indicates an even higher diversity in the environmental sample than resolved by its direct molecular analysis. It also points out the general limitation of molecular, metagenetic/metagenomic biodiversity studies in environmental samples.

Significant changes in the relative composition of the phylotypes were seen along the range of salt concentrations but more drastic changes in response to the temperature (Fig. 2). Five phylotypes related to *Allochromatium vinosum* (PT1, PT2), *Halochromatium roseum* (PT12, PT14), and *Trc. mannitoliphagus* (PT3) represented approx. 45% of the clone sequences in the habitat and the majority of sequences under all conditions, except at temperatures above 40 °C (Fig. 2). They were the exclusive representatives found at 26 °C, with the exception of a single clone related to *Thiorhodovibrio winogradskyi* (PT17). The major phylotype in the environmental sample (40% abundance of PT15) was distantly related to *Thiorhodovibrio winogradskyi* and apparently was dependent on the presence of salt (not found at 0% NaCl) and low temperatures (only present at 13 °C).

Most dramatic changes of the community were seen with the increase of temperature. A single phylotype of *Mch. gracile* (100% similar), which was not detected at lower temperatures and not in the habitat sample, absolutely dominated the communities at temperatures above 40 °C (Fig. 2, Tank et al. 2011). *Mch. gracile* has been repeatedly isolated from marine coastal habitats before, but the preference for elevated temperatures was not noted as a general property of this species (Imhoff 1988, 2001a). However, the dominance at 40 °C supports findings of Serrano et al. (2009) who characterized a slightly thermophilic strain of this species as a biotype. The clear preference of *Mch. gracile* for elevated temperatures points to an obvious competitive advantage in shallow-water habitats which are heated during daytime.

A remarkable aspect of this work is the finding that media and cultivation conditions used were appropriate for all purple sulfur bacteria which were found in the environmental sample by the genetic approach. It also demonstrates the great advantage of functional genes in biodiversity studies but also the high flexibility and diversity of purple sulfur bacteria communities in the coastal habitats and their potential to adapt to changing environmental conditions.

Conclusions

A common property of all phototrophic purple bacteria is the presence of a photosynthetic apparatus and the performance of phototrophic growth under anaerobic conditions, though phylogenetically they are members of *Alpha*-, *Beta*-, and *Gammaproteobacteria* and found in several orders and families of these classes (Fig. 1, Tables 1, 2, and 3).

They are important ecological players at the light-receiving chemocline in all types of habitats. Different phototrophic purple bacteria are living in freshwater and in marine and hypersaline habitats; special species are adapted to alkaline or acidic conditions, to cold or hot temperatures. In addition, different light conditions, concentrations of sulfide and oxygen, and different physicochemical conditions define their ecological niches. In reflection of all of these factors that determine distribution and occurrence of the species and in consideration of the results of first detailed metagenetic studies specifically targeting the phototrophic purple bacteria, a much higher diversity of species very likely exists than known to date.

The possibility to approach the diversity of phototrophic purple bacteria with genetic methods specifically targeting the photosynthetic reaction center proteins opens up possibilities to specifically study the environmental diversity of this group of bacteria with high resolution. Probably one of the most detailed diversity studies of a community of phototrophic purple sulfur bacteria and also one with the highest resolution toward detection of members of this group of bacteria (longest used sequence stretch and highest specificity for the group) has been performed with *pufLM* genes as a target (Tank et al. 2011). The results on the analysis of the community from a coastal lagoon are remarkable for different reasons.

1. Despite the highly selective specificity of the *pufLM* target, almost a third of the total phylotypes recognized was detected only after experimental modification of the environmental conditions but not in the environmental sample itself. This incomplete coverage of the environmental community even by highly specific functional gene probes quite likely demonstrates a general limitation of metagenetic and metagenomic biodiversity studies.
2. Changes in physicochemical conditions, especially of the temperature, can cause dramatic shifts in the community composition. This indicates a quite specific adaptation of individual species to selected environmental conditions. It also reflects a high flexibility of the environmental community to adapt to changing conditions and thereby may explain the incomplete coverage of the metagenetic approach, which comes to its limits if certain bacteria are present at very low abundance.

A few relevant case studies using *pufLM* sequences demonstrate that the broad application of this approach is suited to deliver diversity profiles of many different habitats and to study the dynamic changes therein. In a long-term perspective, the comparison of communities using *pufLM* genes allows to address questions of biogeographic distribution, habitat specificity, and ecological niche identification of species on a global scale. We are currently at the beginning of this era.

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