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The Core- and Pan-Genomes of Photosynthetic Prokaryotes

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1. Introduction

Genome sequencing projects are revealing new information about the distribution and evolution of photosynthesis and phototrophy, particularly in prokaryotes. Although coverage of the five phyla containing photosynthetic prokaryotes (Chlorobi, Chloroflexi, Cyanobacteria, Proteobacteria and Firmicutes) is limited and uneven, full genome sequences are now available for 82 strains from these phyla. In this chapter, we present data and comparisons that reflect recent advances in phototroph biology as a result of insights from genome sequencing. By performing a comprehensive analysis of the core-genome (the pool of genes shared by all phototrophic prokaryotes) and pan-genome (the global gene repertoire of all phototrophic prokaryotes: core genome + dispensable genome) along with available biological data for each organism, we address the following key questions: 1) what are the principal drivers behind the evolution and distribution of phototrophy and 2) how do environmental parameters correlate with genomic content to define niche partitioning and ecotype distributions in photic environments?

Over a decade has passed since the first phototrophic prokaryote, the cyanobacterium *Synechocystis* sp. PCC 6803, was completely sequenced (Kaneko et al., 1996). Since then, availability of an increasing diversity of newly sequenced species is accumulating in public databases at a sustained pace and there is little indication that this trend will level off in the near future (Raymond & Swingley, 2008). A deepening archive of complete genomes has enabled comparative genomic analyses, which has heavily influenced our views of genome evolution and uncovered the extent of gene sharing between organisms (Pallen & Wren, 2007). The analysis of pan-and core-genomes in particular allows us to link genome content to the relationship of organisms to one another and to their physical surroundings. For example, a low pan-genome diversity due to extensive overlap of metabolic function among groups of bacteria could reflect shared environmental habitats and resource utilization, while distinctive species that adapt to disparate environments would be expected to have a high pan-genome diversity. This approach was first developed by Tettelin et al. (2005) and Hogg et al. (2007) for tracking the number of unique genes among multiple strains of *Streptococcus agalactiae* and *Haemophilus influenzae*, respectively. Such analysis resulted in the determination of core-genes that encode functions related to the basic metabolism and phenotype of the species, and a pan-genome that consists of dispensable or unique genes that impart specific functionalities to individual strains.

Within prokaryotes, photosynthetic capability is present within five major groups, which include heliobacteria, green filamentous bacteria (*Chloroflexus* sp.), green sulfur bacteria (*Chlorobium* sp.), *Proteobacteria*, and *Cyanobacteria* (Blankenship, 1992; Gest & Favinger, 1983; Olson & Pierson, 1987; Vermaas, 1994). While only *Cyanobacteria*, which contain two distinct reaction centers linked to each other, are capable of oxygenic photosynthesis, other photosynthetic bacteria primarily carry out anoxygenic photosynthesis with a single reaction center. Traditionally, the phylogenetic relationship of these five distinct photosynthetic groups has been constructed by comparing sequences of the small subunit 16S rRNA gene (Ludwig & Klenk, 2001). But the use of the 16S rRNA gene is unable to resolve the relationships among these phototrophs with confidence, which is central to understanding their evolution. For example, phylogenetic trees based on a comparison of different combinations of 527 shared genes amongst all five photosynthetic prokaryote groups shows that no less than 15 different tree topologies can be constructed depending on the subset of genes used in the analysis, only one of which matches the traditional 16S rDNA tree (Raymond et al., 2002). In fact, comparing just those genes involved in photosynthesis supports no coherent relationship among the different photosynthetic bacteria either, indicating that such genes may have been subjects of lateral gene transfers (ibid).

Recent genome sequencing efforts have made whole genome data available for many more representatives of each of the five phyla of bacteria with photosynthetic members. To resolve the complicated relationship between bacterial phototrophy and evolutionary history, we describe an analysis of the 82 fully-sequenced photosynthetic prokaryotes to construct the pan- and core-genomes across all available strains. We present results showing various gene-based indicators of the relationship between genome and phenotype among these organisms. Not surprisingly, our findings describe new relationships between gene content and environmental habitat. These results add to a complete gene-based functional annotation of the phototrophic prokaryotes, and set the groundwork for continuing studies on genetic and evolutionary dynamics of this important photosynthetic community.

2. Whole-genome analysis of phototrophic prokaryotes

The list and summary details of 82 fully-sequenced photosynthetic species used in this study are shown in Table 1 (Lioliou et al., 2006). Every species exhibits common characteristics with other relatives in the same phylum. For example, the *Chlorobia* and heliobacteria (*Firmicutes*) are strictly anaerobic while the *Chloroflexia* and *Proteobacteria* are facultatively anaerobic. The *Chloroflexia* are alkali-trophic thermophiles whereas other phylum members are neutral pH mesophiles. Genome size is generally uniform among the *Chlorobia* and *Chloroflexia*, but varies widely among the *Cyanobacteria* and *Proteobacteria*. Furthermore, both *Chloroflexia* and *Proteobacteria* possess a pheophytin-quinone reaction center, while *Heliobacteria* and *Chlorobia* use an iron-sulfur reaction center. *Cyanobacteria* exclusively possesses two types of reaction centers. Both *Chlorobia* and *Cyanobacteria* are two phyla comprised entirely of photosynthetic representatives. Although most of the photosynthetic species are free-living organisms, *Nostoc* sp. PCC 7120, *Nostoc punctiforme* PCC 73102, and *Acaryochloris marina* MBIC11017 in the *Cyanobacteria* and *Bradyrhizobium* BTAi1, ORS278 and some *Methylobacterium* strains in the *Proteobacteria* form a mutual relationship with terrestrial plants and coral. The *Heliobacteria* (e.g., *Heliobacterium modesticaldum*) are the only photosynthetic members of the *Firmicutes*. The genome of *Heliobacillus mobilis*, the strain most studied biochemically, still remains proprietary and was not included in our analysis.

GENUS	ORGANISM NAME	SYMBOL	SIZE(Mb)	REACTION CENTER	OXYGEN REQUIREMENT	TEMPERATURE RANGE	PH	BIOTIC RELATIONSHIP'S	MOTILITY	GENOME DATA
<i>Helobacterium</i>	<i>Helobacterium modesticaldum</i> Ice1	heliom	3.1	Fe-S	Obligate anaerobe	Thermophile	6 – 7	Free living	Motile	NC_010337
<i>Chlorobaculum</i>	<i>Chlorobaculum parvum</i> NCIB 8327	cpnc1	2.3	Fe-S	Anaerobe	Mesophile	6.5 – 7.0	Free living	Nonmotile	NC_011027
<i>Chlorobaculum</i>	<i>Chlorobaculum tepidum</i> TL5	ctils	2.2	Fe-S	Obligate anaerobe	Thermophile	6.9 – 7.0	Free living	Nonmotile	NC_002932
<i>Chlorobium</i>	<i>Chlorobium chlorochromatii</i> Cd3	ccoad	2.6	Fe-S	Anaerobe	Mesophile	7.0 – 7.3	Free living	Motile	NC_007514
<i>Chlorobium</i>	<i>Chlorobium linicola</i> DSM 245	cl245	2.8	Fe-S	Anaerobe	Thermophile	6.8 – 7.1	Free living	Nonmotile	NC_010803
<i>Chlorobium</i>	<i>Chlorobium phaeovibrioides</i> DSM 265	cp265	2	Fe-S	Facultative	Mesophile	6.8 – 7.0	Free living	Nonmotile	NC_009337
<i>Chlorobium</i>	<i>Chlorobium phaeobacteroides</i> DSM 266	cp266	3.1	Fe-S	Facultative	Mesophile	6.7 – 7.0	Free living	Nonmotile	NC_008639
<i>Chlorobium</i>	<i>Chlorobium phaeobacteroides</i> BS1	cpbs1	2.7	Fe-S	Facultative	Mesophile	6.7 – 7.0	Free living	Nonmotile	NC_010831
<i>Chloroherpston</i>	<i>Chloroherpston thalassium</i> ATCC 35110	ct35110	3.3	Fe-S	Facultative	Mesophile	6.8	Free living	Nonmotile	NC_011026
<i>Pelodictyon</i>	<i>Pelodictyon luteolum</i> DSM 273	cl273	2.4	Fe-S	Anaerobe	Mesophile	6.5 – 7.0	Free living	Nonmotile	NC_007512
<i>Pelodictyon</i>	<i>Pelodictyon phaeoclathratiforme</i> BU-1	ppbu1	3	Fe-S	Anaerobe	Mesophile	6.5 – 7.0	Free living	Nonmotile	NC_011060
<i>Prosthecochloris</i>	<i>Prosthecochloris aestuarii</i> DSM 271	pa271	2.5	Fe-S	Anaerobe	Mesophile	6.5 – 7.0	Free living	Nonmotile	NC_011059 NC_011061
<i>Chloroflexus</i>	<i>Chloroflexus aggregans</i> DSM 9485	ca9485	4.7	Pheo-Q	Facultative	Thermophile	8 – 9	Free living	Motile	NC_011831
<i>Chloroflexus</i>	<i>Chloroflexus aurantiacus</i> J-10-f1	caj10	5.3	Pheo-Q	Facultative	Thermophile	8 – 9	Free living	Motile	NC_011075
<i>Chloroflexus</i>	<i>Chloroflexus</i> sp. Y-400-f1	cy400	5.3	Pheo-Q	Facultative	Thermophile	8 – 9	Free living	Motile	NC_012032
<i>Roseiflexus</i>	<i>Roseiflexus castenholzii</i> DSM 13941	rc13941	5.7	Pheo-Q	Facultative	Thermophile	7.8 – 8.2	Free living	Motile	NC_009767
<i>Roseiflexus</i>	<i>Roseiflexus</i> sp. RS-1	rrs1	5.8	Pheo-Q	Facultative	Thermophile	7.8 – 8.3	Free living	Motile	NC_009523
<i>Anabaena</i>	<i>Anabaena variabilis</i> ATCC 29413	av29413	6.4	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_007410 NC_007411 NC_007412 NC_007413 NC_014000
<i>Nostoc</i>	<i>Nostoc</i> sp. PCC 7120	n7120	6.4	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Symbiotic	Motile	NC_003240 NC_003241 NC_003267 NC_003270 NC_003270 NC_003272 NC_003273 NC_003276
<i>Nostoc</i>	<i>Nostoc punctiforme</i> PCC 73102	n73102	8.2	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Symbiotic	Motile	NC_010628 NC_010629 NC_010630 NC_010631 NC_010632 NC_010633
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> subsp <i>marinus</i> str. CCMP1375	pm1375	1.8	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_005042
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> subsp <i>pastoris</i> str. CCMP1986	pm1986	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_005072
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9211	pm9211	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_009976
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9215	pm9215	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_009840
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9301	pm9301	1.6	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_009091
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9303	pm9303	2.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_008820
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9312	pm9312	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_005077
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9313	pm9313	2.4	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_008817
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. MIT 9515	pm9515	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_008816
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> str. AS9601	pm9601	1.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_008819
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> subsp <i>pastoris</i> str. NATL1A	pmnatl1	1.9	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_008819
<i>Prochlorococcus</i>	<i>Prochlorococcus marinus</i> subsp <i>pastoris</i> str. NATL2A	pmnatl2	1.8	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_007335
<i>Synechococcus</i>	<i>Synechococcus</i> sp. PCC 7002	s7002	3.0	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_010475 NC_010476 NC_010477 NC_010478 NC_010479 NC_010480 NC_010474
<i>Synechococcus</i>	<i>Synechococcus</i> sp. CC9311	s9311	2.6	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_008319
<i>Synechococcus</i>	<i>Synechococcus</i> sp. CC9605	s9605	2.5	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_007516
<i>Synechococcus</i>	<i>Synechococcus</i> sp. CC9902	s9902	2.2	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_007513
<i>Synechococcus</i>	<i>Synechococcus</i> sp. JA-2-3Ba	sja23b	3.0	Fe-S, Pheo-Q	Facultative	Thermophile	6 – 8	Free living	Motile	NC_007775
<i>Synechococcus</i>	<i>Synechococcus</i> sp. JA-3-3Ab	sja33a	2.9	Fe-S, Pheo-Q	Facultative	Thermophile	6 – 8	Free living	Motile	NC_007776
<i>Synechococcus</i>	<i>Synechococcus</i> sp. RCC307	srcc307	2.2	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_009482
<i>Synechococcus</i>	<i>Synechococcus</i> sp. WH 7803	swh7803	2.4	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_009481
<i>Synechococcus</i>	<i>Synechococcus</i> sp. WH 8102	swh8102	2.4	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_005070
<i>Synechococcus</i>	<i>Synechococcus elongatus</i> PCC 6301	se6301	2.7	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_005676
<i>Synechococcus</i>	<i>Synechococcus elongatus</i> PCC 7942	se7942	2.7	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007604 NC_007695
<i>Synechocystis</i>	<i>Synechocystis</i> sp. PCC 6803	s6803	3.6	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_009911 NC_005231 NC_005232 NC_005229 NC_005230
<i>Acaryochloris</i>	<i>Acaryochloris marina</i> MBIC11017	ammibc	6.5	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Symbiotic	Nonmotile	NC_009925 NC_009926 NC_009927 NC_009928 NC_009929 NC_009930 NC_009931 NC_009932 NC_009933 NC_009934
<i>Cyanothece</i>	<i>Cyanothece</i> sp. ATCC 51142	c51142	5.5	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Nonmotile	NC_010546 NC_010542 NC_010543 NC_010539 NC_010547 NC_010541
<i>Cyanothece</i>	<i>Cyanothece</i> sp. PCC 7424	c7424	5.9	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Nonmotile	NC_011729 NC_011737 NC_011730 NC_011732 NC_011733 NC_011734 NC_011738
<i>Cyanothece</i>	<i>Cyanothece</i> sp. PCC 7425	c7425	5.4	Fe-S, Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Nonmotile	NC_011884 NC_011883 NC_011882
<i>Cyanothece</i>	<i>Cyanothece</i> sp. PCC 8801	c8801	4.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_011726 NC_011723 NC_011727 NC_011721
<i>Cyanothece</i>	<i>Cyanothece</i> sp. PCC 8802	c8802	4.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_013161 NC_013160 NC_013167 NC_013168 NC_013163
<i>Gloeobacter</i>	<i>Gloeobacter violaceus</i> PCC 7421	gv7421	4.7	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_005125
<i>Microcystis</i>	<i>Microcystis aeruginosa</i> NIES-843	ma843	5.8	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_011026
<i>Thermosynechococcus</i>	<i>Thermosynechococcus elongatus</i> BP-1	tebp1	2.6	Fe-S, Pheo-Q	Aerobe	Thermophile	6 – 8	Free living	Nonmotile	NC_004113
<i>Trichodesmium</i>	<i>Trichodesmium erythraeum</i> IMS101	teims	7.8	Fe-S, Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_008312
<i>Methylobaculum</i>	<i>Methylobaculum silvestris</i> BL2	msb2	4.3	Pheo-Q	Aerobe	Psychrotolerant	5 – 6.5	Free living	Nonmotile	NC_011666
<i>Bradyrhizobium</i>	<i>Bradyrhizobium</i> sp. BTAi1	bbtai	8.3	Pheo-Q	Facultative	Mesophile	6 – 8	Symbiotic	Motile	NC_009485 NC_009475
<i>Bradyrhizobium</i>	<i>Bradyrhizobium</i> sp. ORS278	bor278	7.5	Pheo-Q	Facultative	Mesophile	6 – 8	Symbiotic	Motile	NC_009445
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> BisA53	rpa53	5.5	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_008435
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> BisB18	rpb18	5.5	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007925
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> BisB5	rpb5	4.9	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007558
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> CGA009	rpcga	5.5	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_005286 NC_005297
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> HaA2	rpha	5.3	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007778
<i>Rhodopseudomonas</i>	<i>Rhodopseudomonas palustris</i> TIE-1	rptie	5.7	Pheo-Q	Obligate aerobe	Mesophile	6 – 8	Free living	Motile	NC_011004
<i>Methylobacterium</i>	<i>Methylobacterium</i> sp. 4-46	m446	7.7	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_010511 NC_010574 NC_010373
<i>Methylobacterium</i>	<i>Methylobacterium chloromethanicum</i> CM4	mccm4	5.8	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_011757 NC_011760 NC_011758
<i>Methylobacterium</i>	<i>Methylobacterium extorquens</i> AM1	meam1	6.9	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_012808 NC_012807 NC_012809 NC_012810 NC_012811
<i>Methylobacterium</i>	<i>Methylobacterium extorquens</i> DM4	medm4	6.1	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_012888 NC_012889 NC_012987
<i>Methylobacterium</i>	<i>Methylobacterium extorquens</i> PA1	mepa1	5.5	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_011072
<i>Methylobacterium</i>	<i>Methylobacterium populi</i> BJ001	mpbj	5.8	Pheo-Q	Acrobe	Mesophilic	6 – 8	Free living	Motile	NC_010725 NC_010721 NC_010727
<i>Methylobacterium</i>	<i>Methylobacterium radiotolerans</i> JCM 2831	mrjcm	6.1	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_010505 NC_010509 NC_010510 NC_010514 NC_010502 NC_010504 NC_010517 NC_010518 NC_010507
<i>Dinoroseobacter</i>	<i>Dinoroseobacter shibae</i> DFL 12	dsdfl	3.8	Pheo-Q	Facultative	Mesophile	6.5 – 9	Free living	Motile	NC_009952
<i>Jannaschia</i>	<i>Jannaschia</i> sp. CCS1	jcs1	4.3	Pheo-Q	Obligate aerobe	Mesophile	6 – 8	Free living	Nonmotile	NC_007802 NC_007801
<i>Rhodobacter</i>	<i>Rhodobacter capsulatus</i> SB1003	rc1003	3.7	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_014034 NC_014035
<i>Roseobacter</i>	<i>Roseobacter denitrificans</i> OCh 114	rd114	4.1	Pheo-Q	Aerobe	Mesophile	6 – 8	Free living	Motile	NC_008209 NC_008386 NC_008387 NC_008388 NC_008389
<i>Rhodobacter</i>	<i>Rhodobacter sphaeroides</i> KD131	rs131	4.5	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_011963 NC_011958 NC_011962 NC_011960
<i>Rhodobacter</i>	<i>Rhodobacter sphaeroides</i> ATCC 17025	rs17025	3.2	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_009428 NC_009430 NC_009431 NC_009432 NC_009433 NC_009429
<i>Rhodobacter</i>	<i>Rhodobacter sphaeroides</i> ATCC 17029	rs17029	4.4	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_009049 NC_009050 NC_009040
<i>Rhodobacter</i>	<i>Rhodobacter sphaeroides</i> 2.4.1	rs241	4.1	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007493 NC_007494 NC_009007 NC_007488 NC_007489 NC_007490 NC_009008
<i>Rhodospirillum</i>	<i>Rhodospirillum centenum</i> SW	rcsw	4.4	Pheo-Q	Facultative	Mesophile/Thermo tolerar	6 – 8	Free living	Motile	NC_011420
<i>Rhodospirillum</i>	<i>Rhodospirillum rubrum</i> ATCC 11170	rr11170	4.4	Pheo-Q	Facultative	Mesophile	6 – 8	Free living	Motile	NC_007643 NC_007641
<i>Allochromatium</i>	<i>Allochromatium vinosum</i> DSM 180	av180	3.6	Pheo-Q	Anaerobe	Mesophile	6 – 8	Free living	Motile	NC_013851 NC_013852 NC_013862
<i>Halorhodospira</i>	<i>Halorhodospira halophila</i> SL1	hlsl1	2.7	Pheo-Q	Anaerobe	Mesophile	6 – 8	Free living	Motile	NC_008789

Table 1. Summary of 82 photosynthetic prokaryotes with whole-genome sequences

2.1 Clustering of ortholog groups of photosynthetic prokaryotes

All of the 312,254 protein sequences from 82 photosynthetic prokaryote genomes were collected and clustered with the Markov clustering algorithm Ortho-MCL (Chen et al., 2006). Ortho-MCL is a graph-clustering algorithm designed to identify homologous proteins based on sequence similarity and distinguish true orthologs from paralogous relationships without computationally intensive phylogenetic analysis. Upon clustering, 41,824 proteins (13.3%) were removed due to the absence of detectable sequence similarities (BLASTP; $E=10^{-5}$) and 272,686 (86.7%) were assigned to clusters. To assess clustering performance we modified a method described by Frech and Chen (2010) whereby both false-positive (the number of proteins that are found in two or more separate clusters) and false-negative (number of proteins that are found in wrong clusters) results were calculated using both the KEGG (Kanehisa & Goto, 2000) and COG (Natale et al., 2000) databases as a reference. An inflation index is then calculated that controls cluster granularity and gene family size while limiting error (Huerta-Cepas et al., 2008). The inflation parameter impacts the calculation of the number of shared orthologs in each phylum.

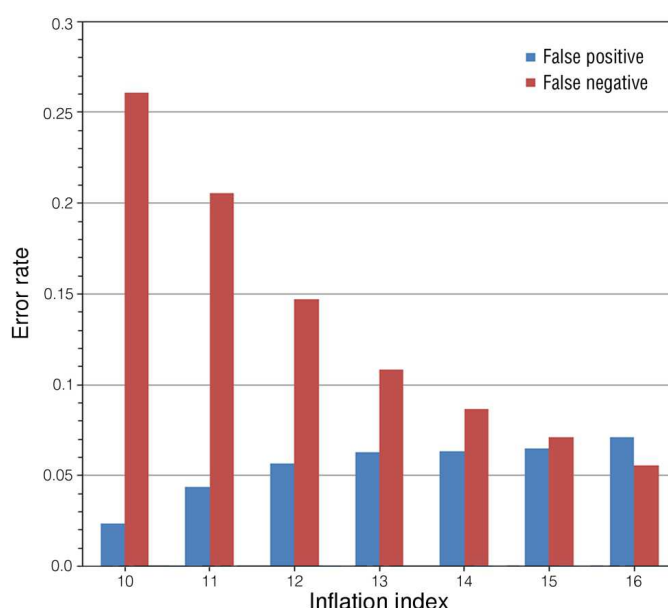


Fig. 1. Estimate of false positive and false negative error rate during ortholog clustering

As Figure 1 shows, an increasing false-positive rate is anti-parallel to decreasing false-negative rate in the inflation parameter. In order to obtain an adequate clustering result, we adjusted the Ortho-MCL program parameters such that reference ortholog clusters compared to both KEGG and COG are classified correctly to minimize erroneous clustering of orthologous groups (inflation index of 15). In our analysis, each predicted orthologous group was evaluated and corrected based on information from both KEGG and COG databases.

2.2 The assembly of core- and pan-genomes

The pan-genome of all 82 species contains 312,254 genes that form 23,362 ortholog clusters. Based on the clustering results, we observed that every photosynthetic prokaryote shares large portions of its genes with others. 204,074 genes that represent 74.8% of the entire data were found to co-exist in at least two organisms from any phyla (“multi-shares”; Figure 2).

The number of gene clusters specific to a particular phylum is much smaller. Both *Cyanobacteria* and *Proteobacteria* possess 32,316 (11.8%) and 30,717 (11.3%) phylum-specific gene clusters, respectively, whereas both *Chlorobi* and *Chloroflexi* have 2,290 (0.8%) and 3,123 (1.1%) gene clusters, respectively. Additionally, 16,665 genes of all species (6.1%) are in common (that is, are contained in the phototrophic prokaryote core-genome). On the surface, this result suggests a remarkable degree of overlap in the gene composition across all five major phyla of photosynthetic prokaryotes.

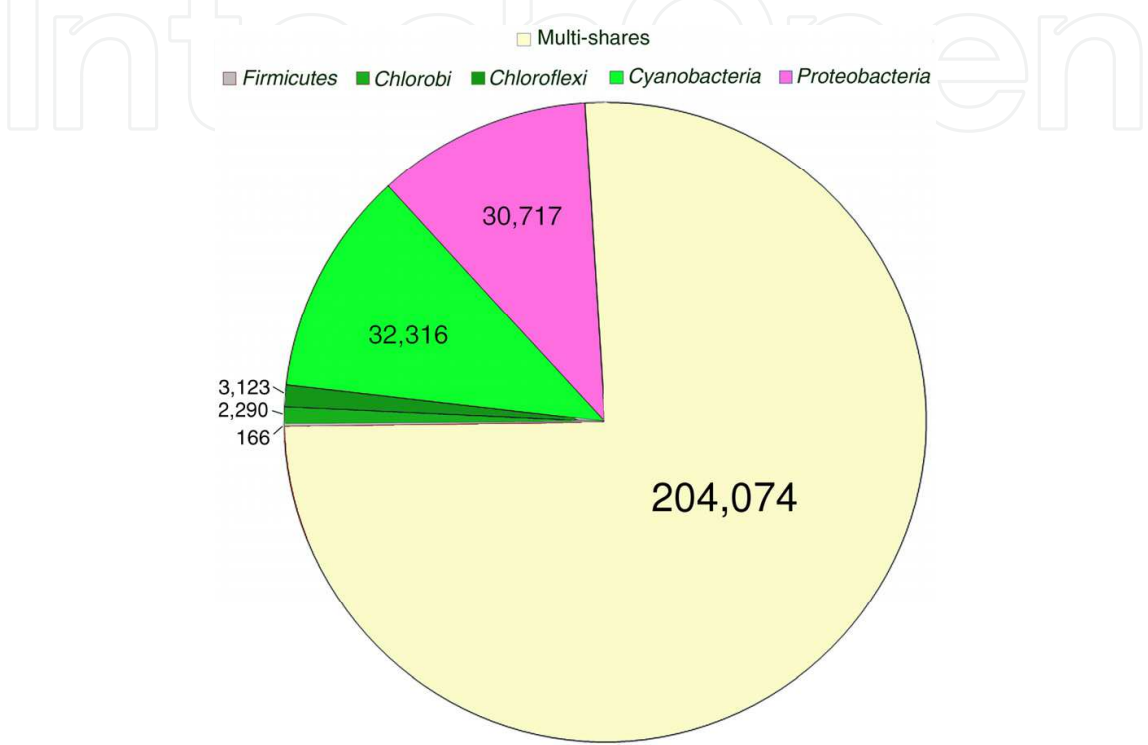


Fig. 2. Distribution of clustered genes within the pan-genome of the five photosynthetic bacterial phyla. Numbers indicate the number of genes specific to each group.

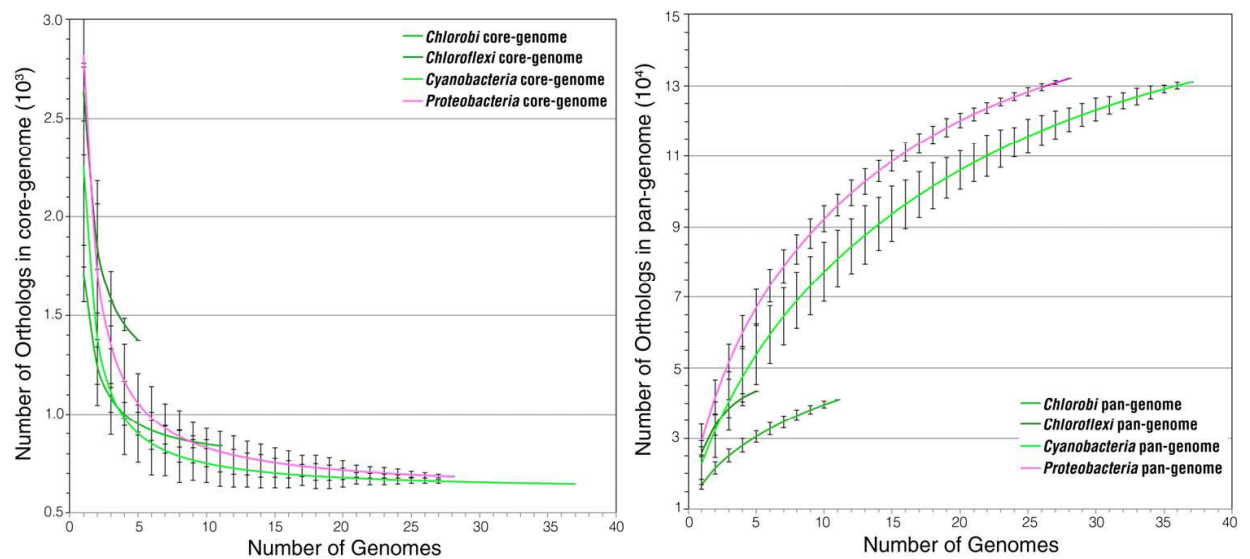


Fig. 3. Plot of the contraction of the core-genome (left) or expansion of the pan-genome (right) as the number of photosynthetic prokaryote genomes analyzed is increased.

To estimate the change of the core-genome size within a particular phyla upon sequential addition of each new genome sequence, a plot was extrapolated by fitting a power law function to the data (Figure 3). As more genomes are compared, there is an asymptotic decline in the number of core orthologs in every phyla, similar to observations for *Streptococcus* (Lefebure & Stanhope, 2007) and *Prochlorococcus* genomes (Kettler et al., 2007). The pan-genome, in contrast, was determined by the plot of the numbers of new orthologs, which fit a decaying exponential curve (Figure 3). The gene accumulation curve for each phyla is clearly far from saturated.

2.3 The core- and pan-genomes of phototrophic prokaryotes

The results of the clustering analysis to determine the core- and pan-genome sizes for each phylum and all phyla together is shown in Figure 4. The size of the phylum core-genomes are: 819 genes in the *Chlorobi*, 1,392 in the *Chloroflexi*, 619 in the *Cyanobacteria*, and 644 in the *Proteobacteria*. The core-genome of all 82 phototrophs considered together consists of 268 genes shared by all organisms. This overall core-genome encompasses a large number of housekeeping genes involved in genetic processes and metabolism and a small number of genes involved in cellular and environmental processes. The housekeeping genes involved in genetic processes include DNA polymerase, ligase, and helicase for DNA replication; RNA polymerase, ribosomal proteins, and tRNA synthetases for translation; and chaperones and signal peptidase for post-translational processes. The housekeeping genes involved in metabolism are mainly involved in the biosynthesis of amino acids, nucleotides, and coenzymes, and a few key enzymes such as transketolase, phosphoglycerate mutase, phosphoglycerate kinase of the glycolysis, acetyl-CoA carboxylase of the tricarboxylic acid (TCA) cycle, H⁺-transporting ATPase, acyl carrier protein, and UDP-N-acetylmuramate-L-alanine ligase for the biosynthesis of bacterial cell wall are preserved. Moreover, we identified the chlorophyll-synthesizing enzymes that include porphobilinogen synthase, oxygen-independent coproporphyrinogen III oxidase, magnesium chelatase, chlorophyll synthase, magnesium-protoporphyrin O-methyltransferase, and light-independent protochlorophyllide reductase. For both cellular and environmental processes, glycosyltransferase for cell membrane biogenesis, phosphate transport system proteins, signal recognition SRP54, and sec-independent protein TatC for membrane transport were identified, suggesting that transferring phosphate and translocating membrane proteins are universal in photosynthetic organisms. The large proportion of housekeeping genes responsible for nearly all major genetic functions and the biosynthesis for both amino acids and nucleotides is understandable since these genes are essential for basic life functions. We observed a paucity of genes involved in both cellular and environmental processes in the overall core-genome. This observation supports the view in which essential life functions are unchanging while nonessential or environment-specific functions are found in a flexible genome (Kettler et al., 2007).

Core-genomes were also calculated in a pairwise fashion between photosynthetic phyla to gauge the number of shared orthologs in a given pair of phyla pan-genomes (Figure 5). Each circle in the figure is proportional to the size (number in the circle) of the shared orthologs. Although these results are heavily influenced by the size of the dataset for an individual phyla, it provides a provisional measure of shared genes between phyla.

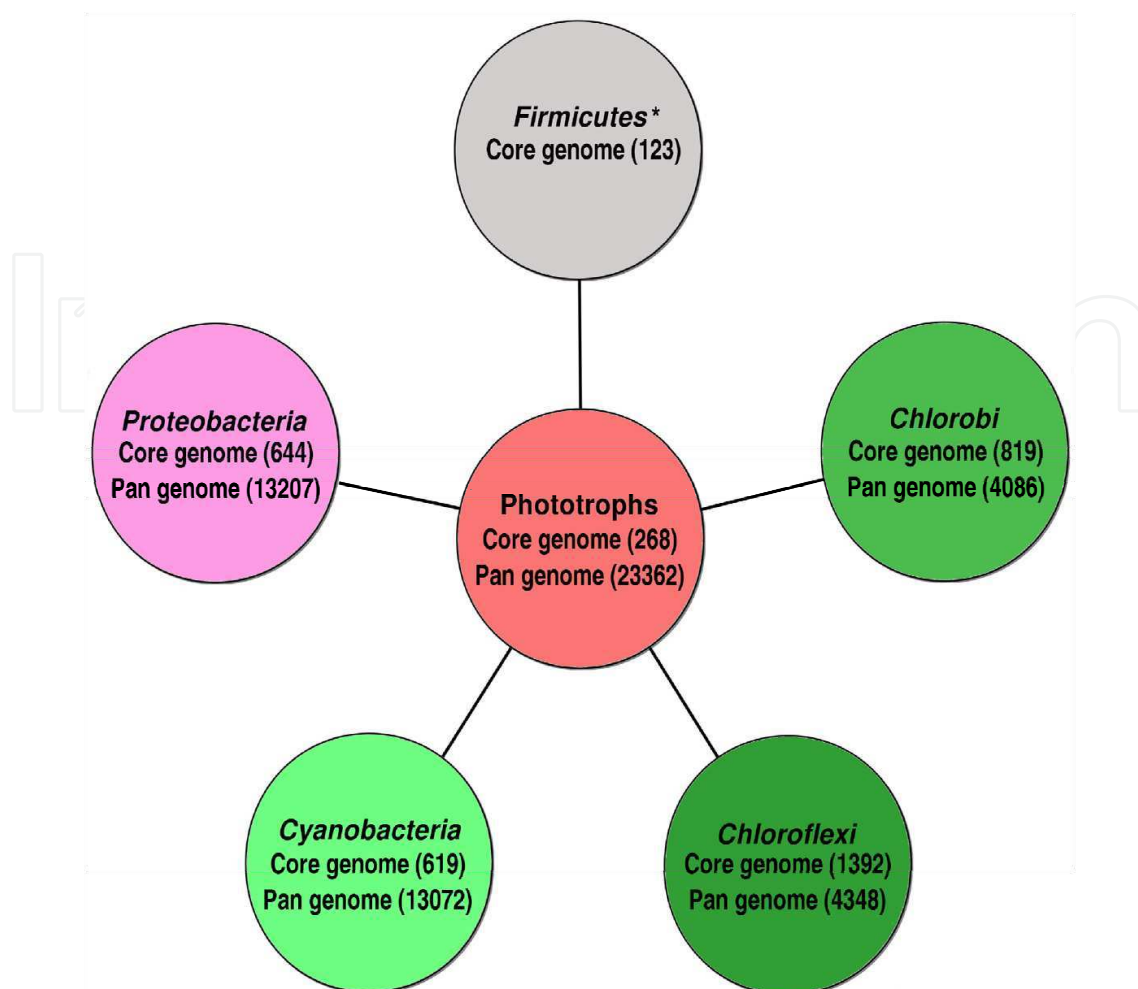


Fig. 4. Both core- and pan-genomes present in all five photosynthetic phyla. Each colored circle represents a phylum: *Firmicutes* (grey), *Chlorobi* (green), *Chloroflexi* (dark-green), *Proteobacteria* (purple), *Cyanobacteria* (light-green), and all phyla together (red). Numbers represent the ortholog clusters contained within the core genome or pan genome of each phylum. * The *Firmicutes*, with only a single sequenced genome, lack a pan genome.

2.3.1 *Heliobacteria* (*Firmicutes*)

Given that there was only a single fully-sequenced genome from the phototrophic *Heliobacteria* (*Firmicutes*) available for study, the core genome of *Heliobacteria* was provisionally constructed by excluding those genes that are homologous to any known genes from the other sequence-available *Firmicutes*. It is worth noting that although there are four *heliobacteria* genera containing a total of ten species that have been formally described: *Heliobacterium*, *Heliobacillus*, *Heliophilum*, and *Heliorestis*, the phototrophic *Heliobacterium modesticaldum* is the only sequenced bacteria representing them (Sattley et al., 2008). When *H. modesticaldum* was compared with the available bacterial genomes of the *Firmicutes*, we identified 123 ortholog clusters tentatively assigned to the core-genome of this organism. Genes encoding proteins involved in major genetic, cellular, and environmental processes and metabolism are very limited. This may be partly due to their mutualistic relationship with plants. Other major ortholog groups in this core-genome are involved in sporulation. The previous examination of several other *Heliobacteria* species for sporulating genes has

indicated that sporulation gene presence may be universal within the heliobacteria (Kimble-Long & Madigan, 2001). It should be noted that a set of genes involved in bacteriochlorophyll (Bchl) g biosynthesis, not found in other phototrophs, were frequently reported in other heliobacteria species (reviewed in Asao & Madigan, 2010). These enzymes were not clustered into the core-genome due to their absence in the non-phototrophic *Firmicutes*. Additional genome sequences from the heliobacteria group will aid in our understanding of their specific core-genome.

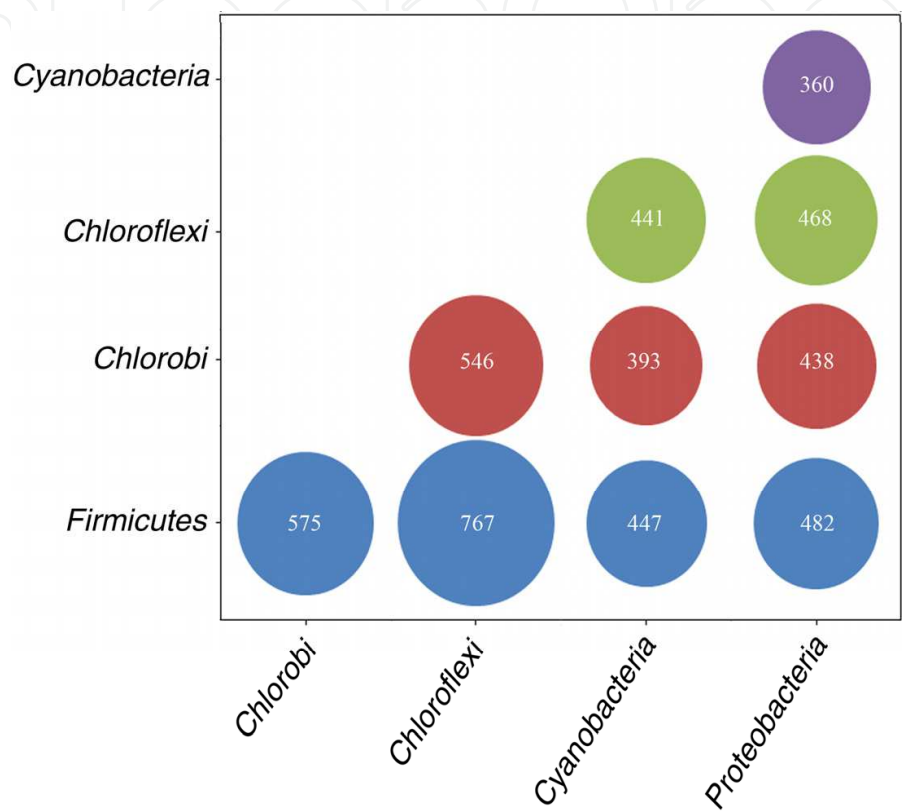


Fig. 5. Pairwise comparison of shared ortholog groups between phyla

2.3.2 *Chlorobi*

The *Chlorobia* core-genome contains 819 genes representing 30-40% of the total genes in a given *Chlorobia* genome. As a phyla, they are very similar with respect to gene content compared to the other phototrophic prokaryotes. In addition to the components of the core-genome for all species, the *Chlorobia* core orthologs are composed of major metabolism genes such as the electron transport chain that supports photosynthesis and sulfur oxidation, the reductive TCA cycle supporting carbon fixation and transport, and others for the biosynthesis of amino acids, lipids, and coenzymes. The core-genome also contains the type I reaction center unique to the *Chlorobi*. Our findings are similar to other recent reports (Davenport et al., 2010). In addition to those identified orthologs for central metabolism, we also identified genes involved in the biosynthesis of Bchl, carotenoids, and the photosynthetic “chlorosome” apparatus. Most pigment-synthesizing enzymes operate downstream of the metabolic pathways for final products like Bchl *c*, *d*, chlorobactene, and γ-carotene, which are located on the chlorosome to harvest light. A few metal and inorganic compound transporters for iron, nickel, and molybdate as well as the major facilitator

superfamily (MFS) transporter, were identified. Since the *Chlorobi* species are capable of fixing nitrogen, preserving these transport systems is necessary to support this process. A total of 1,774 ortholog clusters are assigned to the pan-genome of *Chlorobia*. Most of these are associated with phylogenetically close species and have functions such as secretion, extracellular constituents, and cell wall biogenesis. These are conspicuous features of the genera *Chlorobium* and *Prosthecochloris*. Although the *Chlorobia* have been well-characterized biochemically and microbiologically (Frigaard & Bryant, 2004), our finding that the *Chlorobia* possess a relatively uniform core-genome complemented by a relatively limited set of accessory genes enhancing cellular activities provides further insight into their anoxygenic phototrophic lifestyle. The core-and pan-genome pattern suggests a largely vertical inheritance that has preserved the core-genome needed for major cellular activities--a result of living in environmentally stable niches.

2.3.3 *Chloroflexi*

The *Chloroflexi* core-genome contains 1,392 ortholog clusters, the largest size among the five phototrophic groups. It reflects roughly 35% of the genes of a *Chloroflexus* species' genome. The functional composition of this core-genome is somewhat similar to that of the *Chlorobi* core-genome, since many core genes involved in both genetic and cellular processes were cross-identified. However, the core set also contains type II reaction centers, NADH dehydrogenase, and cytochrome *c* oxidase, similar to the *Proteobacteria* but different from the *Chlorobi*. Moreover, many transporters for metal ions, inorganic and organic compounds, as well as two-component histidine kinases for signal transduction were identified in the *Chloroflexi* but not seen in the *Chlorobi*. The conservation of functionally diverse transporters with signal-transduction histidine kinases may be related to a more dynamic life-style. Generally, *Chloroflexus* is a photoheterotroph and usually found in the lower layers of microbial mats with cyanobacteria growing above it that provide organic byproducts. The *Chloroflexi* core-genome possesses numerous heat shock proteins, chaperones, and signal peptidases involved in protein folding and translocating processes that likely serve to reinforce protein structures in the thermophilic *Chloroflexus* species. For genes involved in major metabolic pathways, the core-genes appear to be largely conserved across all photosynthetic phyla. Although the *Chloroflexi* are found to be distinctive from the *Chlorobi*, they do have some common characteristics such as the absence of intra-cytoplasmic membrane structures and chlorosomes on their plasma membranes. They also use the same Bchl *a* and *c* biosynthesis pathways.

The *Chloroflexi* pan-genome contains 4,348 genes, and in contrast to the *Chlorobi* pan-genome it is comprised of more putative genes for extracellular constituents, inter-cellular communication, and other physiological and biochemical activities. For example, genes involved in the 3-hydroxypropionate pathway for carbon fixation were found. But generally, the *Chloroflexi* core-genome equips most of the major functional genes for a wide range of metabolisms such as synthesis of organic compounds, energy production, transport, genetic processing, etc. Such coverage throughout most cellular activities makes the core-genome of the *Chloroflexi* similar in character to that of *Chlorobia*.

2.3.4 *Cyanobacteria*

Representing the largest sampled phylogenetic clade of the phototrophic prokaryotes, the *Cyanobacteria* have 37 completely sequenced genomes available for analysis, resulting in the

smallest core- (619 genes) and largest pan-genome (13,072 genes) of all five phyla. The proportion of genes designated “core” with respect to any cyanobacterial genome varies from less than 10% (in the the non-*Prochlorococcus*/*Synechococcus* genomes) to nearly 38% for *Prochlorococcus* and *Synechococcus* strains. The core orthologs are responsible for several major reactions such as the Calvin cycle, glycolysis, the incomplete TCA cycle, and pathways to synthesize amino acids and cofactors. Two types of photosystems (PS I and PS II) and the participating electron transport chain for oxygenic photosynthesis are also included.

The large pan-genome of cyanobacteria appears to support diverse abilities and processes. There are many genes found in the pan-genome that carry out metabolic activities unrelated to photosynthesis. For example, *M. aeruginosa* NIES-843 produces a diverse range of toxins with the non-ribosomal peptide synthetases (Kaneko et al., 2007). These enzymes produce neurotoxins and hepatotoxins that cause a variety of human illnesses, and are responsible for deaths in native and domestic animals. *T. erythraeum* IMS101 can perform nitrogen fixation in the presence of oxygen (Sandh et al., 2011). *Nostocaceae* species generally have an unbranched filamentous cell type, develop heterocysts, and possess multiple plasmids. In contrast, *Prochlorococcus* and *Synechococcus* species have a small round shape with no plasmids. Finally, a large number of genes identified in members of the *Nostocaceae* and *A. marina* MBIC11017 have unknown functions. Judging by the life style of these cyanobacterial species, which have a mutualistic relationship with terrestrial plants (Baker et al., 2003) and coral (Marquardt et al., 1997), it is possible that these genes are involved in supporting inter-communication and mutualism with their host.

2.3.5 Proteobacteria

The *Proteobacteria* contain 644 core gene clusters and 13,207 non-redundant genes in the pan genome. The percentage of core genes in any of the *Proteobacteria* genomes varies from 10% to 25%, similar to the results obtained for the *Cyanobacteria*. This is because the *Proteobacteria* is the second major photosynthetic group with 28 completely sequenced genomes from phylogenetically distinct clades. The *Proteobacteria* core-genome preserves most of the key enzymes essential to major cellular activities, similar to other core-genomes. The type II reaction center and light-harvesting proteins are in the core genome, the former of which was also identified in the *Chloroflexi*. Nevertheless, the additional orthologs coding for the bacterial flagella, chemotaxis, and respiratory electron transfer chain proteins unique to the *Proteobacteria* were also identified. Both flagella and chemotaxis help cells move either toward nutrients or away from unfavourable living conditions and both anaerobic and aerobic respiration supports chemo-heterotrophic growth when phototrophic growth is not possible. Thus, integrating both cell mobility and respiration to the *Proteobacteria* core genome suggests an ecological advantage of adaptation to a broader range of living environments than other phototrophic phyla.

In contrast to the core-genome, the characteristics of the pan-genome are widely diverse--from variant types of nitrogen assimilation, carbon assimilation, and hydrogen metabolism to inter-cellular communications and nodulation. Such vast variety in the functional repertoire associated with the pan-genome can give the *proteobacteria*, such as *Rhodobacter*, *Rhodopseudomonas*, and *Rhodospirillum* genera, a broad range of growth conditions for anaerobic phototrophy and aerobic chemoheterotrophy in the absence of light (Larimer et al., 2004; Lu et al., 2010; Mackenzie et al., 2007). Over 50 genes associated with nodulation

were identified in the diazotrophic *Bradyrhizobiaceae* and *Rhizobiaceae*. Most photosynthetic bacteria in these two orders are capable of forming mutualistic symbiosis with terrestrial plants by fixing nitrogen inside special structures called legumes. Genes for hydrogen production or metabolizing C₁-compounds such as methane were identified in *Rhodopseudomonas*, some *Rhodobacteraceae*, and *Methylobacterium*. These traits have garnered much-warranted attention for their potential ability to reduce CH₄ (greenhouse gas) emission (Eller & Frenzel, 2001; Lidstrom & Chistoserdova, 2002). Based on the construction of both core- and pan-genomes, photosynthetic members in the *Proteobacteria* exhibit the greatest gene diversity amongst all phyla studied. This diversity reflects their ability to grow chemoheterotrophically as well as phototrophically, which makes them better at living in a broader range of environments than the *Cyanobacteria*.

Taken together, we have identified core-genes responsible for phylum-specific reactions. We have also observed a wide variety of accessory functions supporting smaller groups of bacteria. The core-genome assembled from a group of closely related bacteria represents a backbone of essential components regulating the adaptability to specific niches. Our results indicate that the gene content of each phylum-specific core is distinctive and can exemplify the very different evolutionary histories of the major photosynthetic groups, where the accessory components comprising the pan-genomes provide fitness advantages in distinct habitats.

2.4 Phylogeny of photosynthetic prokaryotes using the pan-genome

Construction of both core- and pan-genomes of all photosynthetic bacteria provides a novel opportunity to determine the phylogenetic relationship among these prokaryotes. Several methods have been used to evaluate the phylogenies of different bacterial groups such as single-gene phylogenies (e.g., 16S rDNA), concatenated sequences of photosynthesis-related proteins (Rokas et al., 2003), and signature sequences of house-keeping proteins (Gupta, 2003). The sequences compared in these methods are necessarily present in all analyzed species. Here, we present a phylogeny that is formulated using the clustered pan-genome that does not rely on a universally shared collection of genes. Hierarchical clustering with resampling 100 times was performed based on a relative Manhattan distance calculated on the presence/absence of an ortholog between a given pair of genomes (Snipen & Ussery, 2010). It in essence generates a tree based on shared gene content. Figure 6 shows the resulting tree.

There is broad agreement with this tree and traditional single-gene phylogenies. But surprisingly, the topology of the tree shows that both *A. vinosum* DSM 180 and *H. halophila* SL1, both belonging to the γ -*Proteobacteria* class, are situated outside of the *Proteobacteria* clade and positioned between the *Chlorobi* and *Firmicutes*. We investigated in detail the gene content of these two organisms and found that *A. vinosum* DSM 180 has lost most of the *Proteobacteria*-specific orthologs, while *H. halophila* SL1 contains more shared orthologs with *A. vinosum* DSM 180 than between the other purple bacteria species. Another unusual topology is found in the *Proteobacteria* clade where both *Rhodobacter* and *Rhodospirillum* families are closer to the *Rhodopseudomonas* genus, which belongs phylogenetically to the *Rhizobia* within the *Bryodrhizobia* and *Methylobacterium* families.

We further utilized the pan-genome to reveal a three-dimensional relationship between individual species and the major photosynthetic lineages. By performing a multidimensional scaling analysis of the ortholog distribution across all 82 species, we found that related species were clustered in groups reflecting their phyla (Figure 7). While the *Heliobacteria*, *Chlorobi*, and *Chloroflexi* species occupied a central space, the *Proteobacteria* and *Cyanobacteria* were greatly

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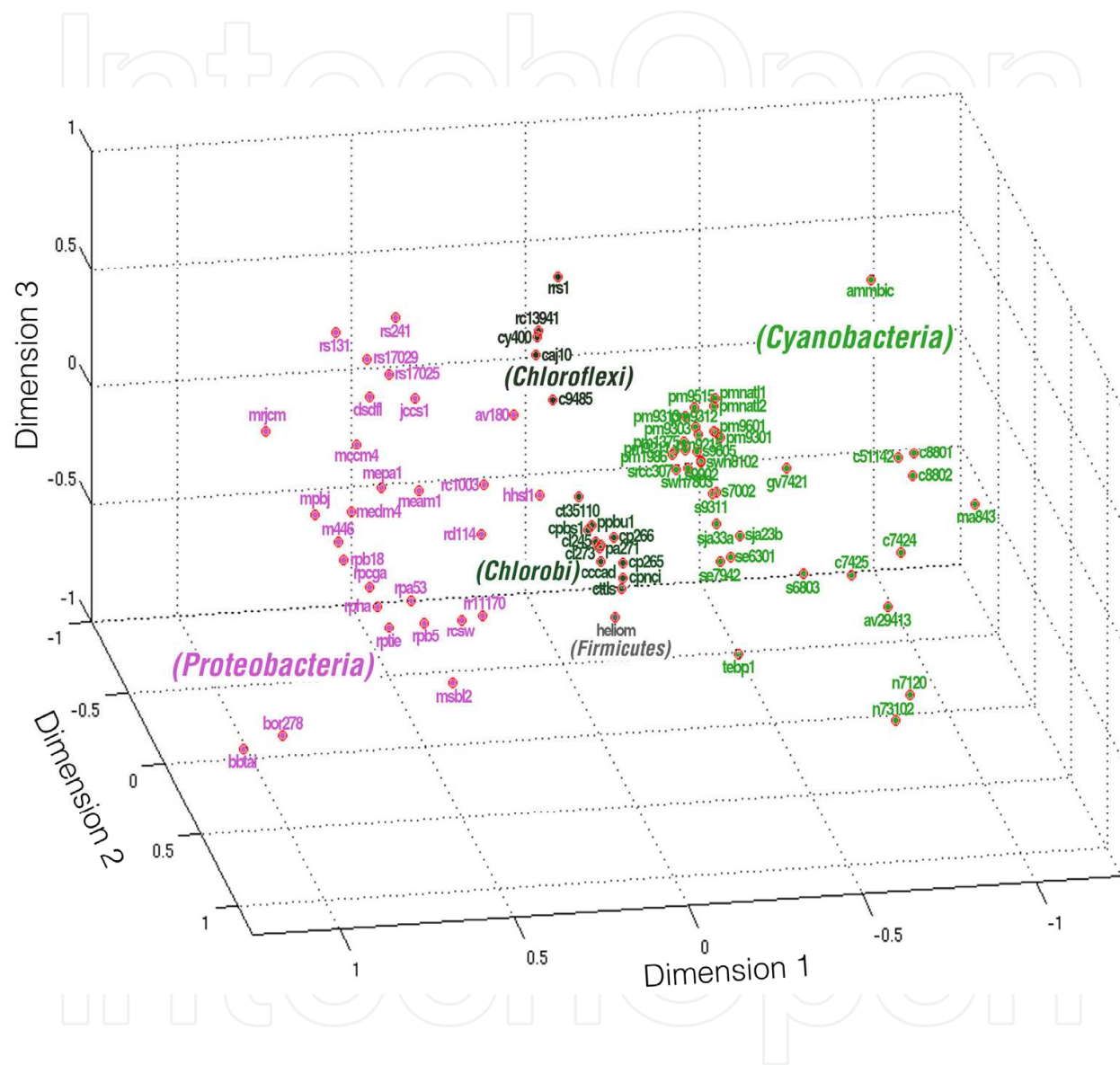


Fig. 7. Multidimensional scaling analysis showing the organization of 82 photosynthetic prokaryotes in a pan-genomic distribution.

3. Acknowledgements

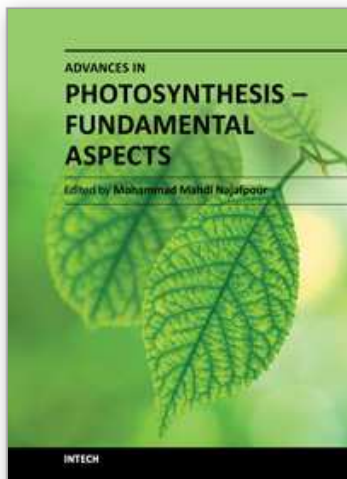
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