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CHAPTER ONE

# A Time to Scatter Genes and a Time to Gather Them: Evolution of Photosynthesis Genes in Bacteria

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## Contents



## Abstract

Genome sequencing opened entirely new avenues for studying the evolution of photosynthesis. By systematically comparing sequences of photosynthesis-related genes and their products in phototrophic members of diverse bacterial lineages, it has become possible to delineate their common and distinct traits, analyse their evolutionary relationships, and reconstruct the likely scenarios for the overall evolution of the photosynthetic machinery. We consider here the comparative genomics data on the distribution of photosynthesis genes among certain representatives of six bacterial phyla, Acidobacteria, Chlorobi, Chloroflexi, Cyanobacteria, Firmicutes, and Proteobacteria, but not in their respective close relatives, and put these data in a broader geochemical context. We address the tentative nature of the first photosynthetic organisms, the driving forces behind their origin, and review the evidence for the early origin of abiogenic photosynthesis.

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## 1. INTRODUCTION

p0010 Photosynthesis is a key biological process that may have emerged even before the origin of life on the Earth and played a key role in shaping the

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planet and its atmosphere. Indeed, abiogenic photosynthesis – synthesis of the first organic molecules on the Hadean Earth from $CO_2$ and $H_2O$ driven by the energy of solar UV radiation – most likely contributed the necessary precursors for the formation of the first cells (Guzman & Martin, 2009, 2010; Moore & Webster, 1913; Mulkidjanian, 2009; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press; Mulkidjanian & Galperin, 2009; Schoonen, Smirnov, & Cohn, 2004; Zhang, Martin, Friend, Schoonen, & Holland, 2004; Zhang et al., 2007). At the next step, anoxygenic photosynthesis provided a ready way for harnessing the energy of the Sun into the accumulation of bacterial biomass (Sleep, 2010; Sleep & Bird, 2007, 2008), which ultimately allowed the gradual emergence of complex multicellular organisms.

p0015 The subsequent emergence of oxygenic photosynthesis dramatically changed the conditions on the planet by providing the readily available acceptor of electrons for the electron-transport chains of the increasingly complex organisms, and by creating the ozone shield that protected these organisms from the damaging short-wave UV radiation (Garcia-Pichel, 1998). Finally, through acquisition of cyanobacterial symbionts, the ability to conduct photosynthesis was conferred to several lineages of eukaryotic cells, which led to the emergence of apicomplexans, diatoms, red and brown algae, and green plants (Green, 2011; Keeling, 2009, 2010).

p0020 Accordingly, the problem of origin and evolution of photosynthesis is a core element in any concept of the origin and evolution of life on Earth. The complexity of this problem is exacerbated by a certain degree of confusion regarding the fossil data. The early naive reports of full-fledged fossils of trichomic cyanobacteria-like microorganisms in the Early Archaean (Schopf, 1993; Schopf & Packer, 1987) have been disputed (Brasier et al., 2002) and are largely being neglected. However, later findings of carbon (graphite) deposits associated with likely microbial mats (Tice & Lowe, 2004, 2006) have again pushed the time of emergence of photosynthetic microbes back to the ~3.5 billion years ago mark. Furthermore, geochemical analyses explained the origin of 3.8 Gy old carbon-rich deposits (black shales) as originating from anoxygenic photosynthesis (Sleep & Bird, 2007, 2008). That said, biochemical characterization of those fossils still remains out of reach, forcing researchers to seek alternative ways to study the origins of photosynthesis.

p0025 Genome sequencing opened an entirely new avenue for studying the evolution of photosynthesis. By systematically comparing sequences of photosynthesis-related genes – and their products – in phototrophic members

of diverse bacterial lineages, it has become possible to delineate their common and distinct traits, analyse their evolutionary relationships, and reconstruct the likely scenarios for the overall evolution of the photosynthetic machinery.

p0030 Some time ago, we used comparative genomics to analyse the distribution of photosynthesis-related genes in different lineages and, specifically, delineated cyanobacterial clusters of orthologous groups of proteins (Cyanobacterial clusters of Orthologous Groups of proteins (CyOGs)) (Mulkidjanian et al., 2006). As part of that work, we have noticed that 84 CyOGs were exclusively shared by cyanobacteria and plants and/or other plastid-carrying eukaryotes, such as diatoms or apicomplexans. That set included 49 CyOGs with known functions, which were all involved in photosynthesis, and 35 families of uncharacterized proteins that could also be involved in photosynthesis. In the same article we compared the distribution of photosynthesis-related genes in cyanobacteria with that in other phototrophic prokaryotes. Based on this analysis, we suggested that photosynthesis originated among the direct ancestors of cyanobacteria – anoxygenic procyanobacteria – and that members of other phyla obtained their photosynthesis genes via lateral gene transfer.

p0035 Given several recently published comprehensive reviews on the evolution of photosynthesis (Bryant & Frigaard, 2006; Bryant et al., 2012; Gupta, 2012; Hohmann-Marriott & Blankenship, 2011), in this chapter we provide an update of our earlier genome analysis and also attempt to consider the problem of the evolution of photosynthesis in a broader geochemical context. We check to what extent our predictions on the photosynthetic function of 35 uncharacterized enzymes were correct, briefly address the tentative nature of the first photosynthetic organisms, and review the evidence for an early origin of abiogenic photosynthesis.

## s0015 2. PHOTOSYNTHESIS GENES OF CYANOBACTERIA AND PLANTS

p0040 A comparative study of cyanobacterial genomes several years ago described a set of 1054 protein families, referred to as core CyOGs, that had been encoded in at least 14 of the 15 complete cyanobacterial genomes available at that time (Mulkidjanian et al., 2006). Of those 1054 core CyOGs, 84 protein families were found exclusively in cyanobacteria and plants (*Arabidopsis thaliana*, rice, the red algae *Cyanidioschyzon merolae* and *Porphyra purpurea*, and/or the diatom *Thalassiosira pseudonana*).

Some of those 84 proteins had been previously shown to participate in photosynthesis as components of photosystems I and II, light-harvesting antennas, and so on. However, members of 35 protein families with the same phylogenetic distribution had no known function (Mulkidjanian et al., 2006). We have reasoned that the proteins encoded in (nearly) all cyanobacterial genomes and at least some chloroplast-containing eukaryotes, but not in any other bacterial or eukaryotic genomes were likely to either directly participate in photosynthesis or have photosynthesis-related functions.

p0045 This proposal had been partly verified by the analysis of the proteins with similar phylogenetic profiles that, although not yet properly annotated in the public databases, had been experimentally characterized by that time. One of these was GENOMES UNCOUPLED4 (GUN4) protein, a cofactor of Mg-chelatase, which had been proposed to regulate chlorophyll biosynthesis and intracellular signalling (Larkin, Alonso, Ecker, & Chory, 2003). This protein is encoded in *Synechocystis* sp. PCC 6803 by three paralogous genes, *sll0558*, *sll1380*, and *slr1958*, and crystal structures of Sll0558 and its orthologue from *Thermosynechococcus elongatus* have been solved (PDB entries 1Y6I and 1Z3X, respectively (Davison et al., 2005; Verdecia et al., 2005)). While this protein is currently the subject of intensive research (Adhikari et al., 2011), the corresponding entries in public databases (e.g. P72583 in UniProt (The UniProt Consortium, 2012)) are still annotated as 'Ycf53-like' proteins, although protein domain databases, such as Pfam (Punta et al., 2012) already identify them as members of the GUN4 family.

p0050 In another interesting case, a *Chlamydomonas reinhardtii* protein Tab2, an orthologue of the *Synechocystis* sp. PCC 6803 protein Sll2002, has been characterized as an RNA-binding protein that specifically interacts with an upstream region of the mRNA of the *psaB* gene and is required for translation of the *psaB* product, photosystem I reaction centre (RC) protein, and the assembly of the photosystem I complex (Dauvillee, Stampacchia, Girard-Bascou, & Rochaix, 2003). Shortly after that, an *A. thaliana* orthologue of Tab2 (At3g08010, designated ATAB2) was shown to bind to the 5′-untranslated regions in the mRNA of *psaB* and several other chloroplast genes, including *psbA*, *psbB*, and *psbD/C* (Barneche, Winter, Crevecoeur, & Rochaix, 2006). Curiously, while some plant Tab2 proteins are marked as such, cyanobacterial members of the Tab2 family are still listed as uncharacterized proteins, and the corresponding protein family (PF06485 in Pfam) is referred to as domain of unknown function, DUF1092 (Punta et al., 2012).

p0055 In the past several years, some of these 35 proteins predicted to have photosynthesis-related functions have been experimentally characterized,

either in cyanobacteria, or in plants, and in some cases in both groups. Table 1.1 shows 12 such proteins, listing their locus tags in *Synechocystis* sp. PCC 6803, assigned gene names, their current annotations, orthologs in *A. thaliana* (where available) or in red algae, and the respective entries in the public databases, UniProt and Pfam (Punta et al., 2012; The UniProt Consortium, 2012). These data clearly demonstrate the predictive power of the phylogenetic patterns: all experimentally characterized proteins indeed turned out to be involved in photosynthesis, either as auxiliary or regulatory subunits of the photosynthetic reaction complexes, or, in case of AtpI, as an assembly factor of the $H^+$-ATP synthase complex (Table 1.1). Ten of the 12 proteins have been found in all cyanobacterial and plant genomes. One of the remaining two proteins, Ycf34, was encoded in all cyanobacteria and in chloroplasts of diatoms and red and brown algae but apparently lost among green plants. Finally, Ycf86 has been found so far only in cyanobacteria and red algae.

p0060 These recent data provide additional support to the original prediction that proteins with the same phylogenetic pattern (encoded in the genomes of photosynthetic organisms but not in the genomes of non-photosynthetic organisms) should have photosynthesis-related functions. In Table 1.2, we list 23 such proteins that have not yet been experimentally characterized. They all represent widespread protein families that have been annotated as domain of unknown function, DUFs, in Pfam (Punta et al., 2012). Again, several of these proteins are encoded in chloroplasts of diatoms and red and brown algae, but seem to have been lost from green plants. Others are found in (nearly) all photosynthetic organisms and represent attractive targets for future experimental research.

s0020 ## 3. EVOLUTION OF THE PHOTOSYNTHESIS GENE SET

s0025 ### 3.1. The Common Photosynthesis Gene Set

p0065 Phototrophic organisms depend on chlorophyll-containing photosynthetic RCs of type I and/or of type II (RC1 and RC2, respectively). Photosynthetic RCs are found in organisms that belong to several distinct prokaryotic and eukaryotic lineages. However, all eukaryotic phototrophs appear to have inherited their photosynthetic organelles, plastids, from cyanobacteria. In contrast, among prokaryotes, phototrophy has been found in representatives of several different phyla. Photosynthesis is found, in addition to the Cyanobacteria, in the Bacteroidetes/Chlorobi group (e.g. *Chlorobium tepidum*), Firmicutes (e.g. *Heliobacillus mobilis*), Acidobacteria (*Candidatus Chloracidobacterium thermophilum*), Chloroflexi (e.g. *Chloroflexus aurantiacus*),

t0010 **Table 1.1** Recently characterized conserved cyanobacterial and plant proteins

| Locus | Length, aa | Gene name | Updated annotation | Plant homologue | UniProt entry | Pfam domain | References |
|---|---|---|---|---|---|---|---|
| sll1321 | 160 | AtpI | ATP synthase assembly protein I (Atp1) | At2g31040 | P27196 | ATP_synt_I | (Suzuki, Ozaki, Sone, Feniouk, & Yoshida, 2007) |
| ssl3364 | 73 | CP12 | Thioredoxin-regulated chloroplast protein CP12 | At2g47400 | P73654 | CP12 | (Erales, Lignon, & Gontero, 2009; Gontero & Maberly, 2012; Howard et al., 2011) |
| sll1414 | 215 | psb29 (THF1) | Photosystem II biogenesis protein psb29 (THF1) | At2g20890 | P73956 | Thylakoid Format | (Keren, Ohkawa, Welsh, Liberton, & Pakrasi, 2005) |
| sll1509 | 112 | Ycf20 | Chloroplast protein Ycf20 involved in dissipation of absorbed light energy | At5g43050 | P72983 | DUF565 | (Jung & Niyogi, 2010) |
| ssl1417 | 69 | Ycf33 | Photosystem I protein Ycf33 involved in cyclic electron transport | At4g16410 | P74788 | DUF751 | (Ohtsuka, Oyabu, Kashino, Satoh, & Koike, 2004) |

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|---|---|---|---|---|---|---|---|---|
| sll0933 | 126 | PAM68 | Photosystem II biogenesis protein Sll0933 | At5g52780 | P72865 | DUF3464 | | (Armbruster et al., 2010; Rengstl, Oster, Stengel, & Nickelsen, 2011) |
| slr0815 | 111 | CCR2 | Thylakoid membrane protein involved in photosystem II response to cold stress | At3g17930 | P74048 | DUF3007 | | (Li, Gao, Yin, & Xu, 2012) |
| ssl0352 | 62 | NdhS | NADPH: plastoquinone oxidoreductase subunit NdhS (CRR31) | At4g23890 | P74795 | DUF3252 | | (Battchikova et al., 2011; Yamamoto, Peng, Fukao, & Shikanai, 2011) |
| ssl3451 | 77 | SipA | Regulator of cyanobacterial sensor kinase NblS (Hik33) | At5g20935 | P73286 | DUF3148 | | (Espinosa, Fuentes, Burillo, Rodriguez-Mateos, & Contreras, 2006; Sakayori, Shiraiwa, & Suzuki, 2009) |

*Continued*

**Table 1.1** Recently characterized conserved cyanobacterial and plant proteins—cont'd

| Locus | Length, aa | Gene name | Updated annotation | Plant homologue | UniProt entry | Pfam domain | References |
|---|---|---|---|---|---|---|---|
| slr0575 | 184 | APE1 | Acclimation of photosynthesis to environment (APE1) protein, affects chlorophyll fluorescence | At5g38660 | Q55403 | DUF2854 | (Walters, Shephard, Rogers, Rolfe, & Horton, 2003) |
| ssr1425 | 84 | Ycf34 | Fe–S cluster chloroplast protein Ycf34, regulator of the photosynthetic electron transport | CypaCp008 | P74777 | Ycf34 | (Wallner et al., 2012) |
| ssr2998 | 78 | petP (Ycf86) | Cytochrome $b_6f$ complex subunit petP (CP19, Ycf86) | PopuCp097* | P72798 | DUF2862 | (Volkmer et al., 2007) |

*Found only in cyanobacteria and in red algae.

t0015 **Table 1.2** Uncharacterized conserved cyanobacterial and plant proteins

| Locus | Length, aa | Gene name | Plant homolog | UniProt entry | Pfam domain |
|---|---|---|---|---|---|
| slr1638 | 117 | PM23 | At1g63610 | P74354 | DUF760 |
| sll0661 | 131 | Ycf35 | CypaCp141 | Q55981 | DUF1257 |
| sll0584 | 169 | Ycf36 | At5g67370 | Q55866 | DUF1230 |
| sll1702 | 198 | Ycf51 | CypaCp078 | P73690 | DUF2518 |
| sll1879 | 543 | Ycf55 | PopuCp018 | P74126 | DUF3685 |
| sll1737 | 153 | Ycf60 | At2g47840 | P73387 | – |
| slr0503 | 353 | Ycf66 | MapoCp005* | F7UTS9 | Ycf66_N |
| slr1699 | 244 | – | At5g47860 | P73194 | DUF1350 |
| sll1656 | 189 | – | At2g15290 | P72815 | DUF3611 |
| slr0438 | 119 | – | At3g15110 | Q55125 | DUF3082 |
| slr0589 | 185 | – | At3g26710 | P74727 | DUF3529 |
| slr1470 | 134 | – | At1g14345 | P74154 | DUF304 |
| slr1052 | 367 | – | At3g26580 | P73017 | TPR_16 |
| sll1071 | 264 | – | At5g52970 | P73281 | Repair_ PSII |
| slr0948 | 190 | – | At1g59840 | P74315 | DUF2930 |
| sll0272 | 156 | – | At2g04039 | P74394 | DUF2996 |
| sll2013 | 179 | – | At5g39520 | P73665 | DUF1997 |
| slr1195 | 154 | – | At5g08400 | P73343 | DUF3531 |
| slr1660 | 214 | – | CR066† | P74661 | DUF3172 |
| slr1702 | 214 | – | At5g27560 | P73200 | DUF1995 |
| ssr3188 | 89 | – | At5g52960 | P73653 | DUF3143 |
| slr0598 | 118 | – | At3g19900 | P74744 | DUF3067 |
| ssl3829 | 88 | – | At5g39210 | P73675 | DUF3571 |

*_Marchantia polymorpha_ and some other green plants.
†_Chlamydomonas reinhardtii_ and other green algae.

and in three different classes of Proteobacteria: α-Proteobacteria (e.g. *Rhodopseudomonas palustris*), β-Proteobacteria (e.g. *Rubrivivax gelatinosus*), and γ-Proteobacteria (e.g. *Chromatium vinosum*). The first three phyla have photosynthetic RCs that are similar to the cyanobacterial PSI and use low-potential FeS clusters as electron acceptors (RC1 type). The RCs of members of Proteobacteria and Chloroflexi (RC2 type) use bound quinones as ultimate electron acceptors and are similar to the cyanobacterial PSII (although lacking the oxygen-evolving complex) (Bryant et al., 2012; Hohmann-Marriott & Blankenship, 2011).

p0070 While in 2006 it was not clear whether non-phototrophic Chlorobi exist, they have now been found and characterized (Iino et al., 2010; Liu et al., 2012). Hence, now only Cyanobacteria are left without non-phototrophic members (Table 1.3).

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t0020 **Table 1.3** Phototrophic bacteria with completely sequenced genomes and their heterotrophic relatives

| Taxonomy* | Representative organism (GenBank genome entry) | Proteins | Photosystem | $CO_2$ assimilation | Photoautotrophic growth | References |
|---|---|---|---|---|---|---|
| **Phylum: *Acidobacteria*** | | | | | | |
| | *Candidatus* Chloracidobacteriumthermophilum (CP002514, CP002515) | 3054 | RCI | N/A | No | (Bryant et al., 2007; Garcia Costas et al., 2012) |
| | *Terriglobus saanensis* (CP002467) | 4180 | – | N/A | No | (Mannisto, Rawat, Starovoytov, & Haggblom, 2011; Rawat, Mannisto, Bromberg, & Haggblom, 2012) |
| **Phylum: *Chlorobi*** | | | | | | |
| **Class:** *Chlorobia* **Order:** *Chlorobiales* **Family:** *Chlorobiaceae* | *Chlorobium tepidum* (AE006470) | 2245 | RCI | Reverse TCA | Yes | (Eisen et al., 2002; Imhoff, 2003; Li, Sawaya, Tabita, & Eisenberg, 2005; Wahlund, Woese, Castenholz, & Madigan, 1991) |
| | *Chlorobaculum parvum* (CP001099) | 2043 | RCI | Reverse TCA | Yes | |
| | *Chlorobium limicola* (CP001097) | 2434 | RCI | Reverse TCA | Yes | |
| | *Chloroherpeton thalassium* (CP001100) | 2710 | RCI | Reverse TCA | Yes | |
| | *Prosthecochloris aestuarii* (CP001108) | 2327 | RCI | Reverse TCA | Yes | |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Class:** *Ignavibacteriae* | *Ignavibacterium album* (CP003418) | 3195 | – | N/A | No | (Iino et al., 2010; Liu et al., 2012; Podosokorskaya et al., in press) |
| **Phylum: *Chloroflexi*** | | | | | | |
| **Class:** *Chloroflexi* | *Chloroflexus aurantiacus* (CP000909) | 3853 | RCII | 3-Hydroxypropionate cycle | Yes | (Klatt, Bryant, & Ward, 2007) |
| **Order:** *Chloroflexales* | *Roseiflexus castenholzii* (CP000804) | 4330 | RCII | 3-Hydroxypropionate cycle | No | (Tang et al., 2011) |
| **Family:** *Chloroflexaceae* | | | | | | (Gupta, Chander, & George, in press; Hanada et al., 2002; Herter et al., 2001; Klatt et al., 2007) |
| **Family:** *Oscillochloridaceae* | *Oscillochloris trichoides* (ADVR00000000) | 3231 | RCII | CBB cycle | Yes | (Berg, Keppen, Krasil'nikova, Ugol'kova, & Ivanovskii, 2005; Keppen, Baulina, Lysenko, & Kondratieva, 1993; Kuznetsov et al., 2011) |
| **Order:** *Herpetosiphonales* | *Herpetosiphon aurantiacus* (CP000875) | 5279 | – | N/A | No | (Kiss et al., 2011; Klatt et al., 2007) |

*Continued*

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**Table 1.3** Phototrophic bacteria with completely sequenced genomes and their heterotrophic relatives—cont'd

| Taxonomy* | Representative organism (GenBank genome entry) | Proteins | Photo-system | $CO_2$ assimilation | Photoautotrophic growth | References |
|---|---|---|---|---|---|---|
| **Phylum: *Firmicutes*** | | | | | | |
| Class: *Clostridia*<br>Order: *Clostridiales*<br>Family: *Heliobacteriaceae* | *Heliobacterium modesticaldum* (CP000930) | 2999 | RCI | PEP carboxykinase | No | (Kimble, Mandelco, Woese, & Madigan, 1995; Sarrou et al., 2012; Sattley et al., 2008; Tang, Yue, & Blankenship, 2010) |
| Family: *Peptococcaceae* | *Desulfotomaculum reducens* (CP000612) | 3276 | – | N/A | No | (Junier et al., 2010) |
| **Phylum: *Proteobacteria*** | | | | | | |
| Class: *α-Proteobacteria* | *Rhodobacter capsulatus* (CP001312) | 3642 | RCII | CBB cycle | Yes | (Imhoff, Truper, & Pfennig, 1984) |
| Order: *Rhodobacterales* | *Rhodobacter sphaeroides* (CP000143) | 4242 | RCII | CBB cycle | Yes | |
| Family: *Rhodobacteraceae* | *Paracoccus denitrificans* (CP000490) | 5077 | – | CBB cycle | No | |
| Order: *Rhodospirillales* | *Rhodospirillum rubrum* (CP000230) | 3838 | RCII | CBB cycle | Yes | |
| Family *Rhodospirillaceae* | *Magnetospirillum magneticum* (AP007255) | 4561 | – | CBB cycle | No | (Geelhoed, Kleerebezem, Sorokin, Stams, & van Loosdrecht, 2010) |

| | | | | | | |
|---|---|---|---|---|---|---|
| Class: *β-Proteobacteria* | *Rubrivivax gelatinosus* (AP012320) | 4693 | RCII | CBB cycle | No | (Nagashima et al., 2012) |
| Order: *Burkholderiales* | *Methylibium petroleiphilum* (CP000555) | | – | N/A | No | (Kane et al., 2007) |
| Class: *γ-Proteobacteria* | *Allochromatium vinosum* (CP001896) | 3220 | RCII | CBB cycle | Yes | (Imhoff, Suling, & Petri, 1998; Weissgerber et al., 2011) |
| Order: *Chromatiales* | *Thiocystis violascens* (CP003154) | 4330 | RCII | CBB cycle | Yes | |
| Order: *Methylococcales* | *Methylococcus capsulatus* (AE017282) | 2956 | – | N/A | No | (Ward et al., 2004) |
| **Phylum: *Cyanobacteria*** | | | | | | |
| Order: *Chroococcales* | *Acaryochloris marina* (CP000828) | 8383 | RCI and II | CBB cycle | Yes | (Pfreundt, Stal, Voss, & Hess, 2012) |
| | *Microcystis aeruginosa* (AP009552) | 6312 | RCI and II | CBB cycle | Yes | (Kaneko et al., 2007) |
| | *Synechococcus elongatus* (CP000100) | 2662 | RCI and II | CBB cycle | Yes | |
| | *Synechococcus* sp. PCC 7002 (CP000951) | 3187 | RCI and II | CBB cycle | Yes | |
| | *Synechocystis* sp. PCC 6803 (BA000022) | 3575 | RCI and II | CBB cycle | Yes | (Kaneko et al., 1996) |
| | *Candidatus Atelocyanobacterium thalassa* (UCYN-A, CP001842) | 1199 | RCI | N/A | No | (Thompson et al., 2012; Tripp et al., 2010; Zehr et al., 2008) |
| Order: *Gloeobacterales* | *Gloeobacter violaceus* (BA000045) | 4430 | RCI and II | CBB cycle | Yes | (Nakamura et al., 2003) |

*Continued*

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**Table 1.3** Phototrophic bacteria with completely sequenced genomes and their heterotrophic relatives—cont'd

| Taxonomy* | Representative organism (GenBank genome entry) | Proteins | Photo-system | $CO_2$ assimilation | Photoautotrophic growth | References |
|---|---|---|---|---|---|---|
| Order: *Nostocales* | *Anabaena variabilis* (CP000117) | 5710 | RCI and II | CBB cycle | Yes | |
| | *Nostoc* sp. PCC 7120 (BA000019) | 6129 | RCI and II | CBB cycle | Yes | |
| Order: *Oscillatoriales* | *Arthrospira platensis* (CM001632) | 6108 | RCI and II | CBB cycle | Yes | |
| Order: *Prochlorales* | *Prochlorococcus marinus* (AE017126) | 1883 | RCI and II | CBB cycle | Yes | (Chisholm et al., 1992; Dufresne et al., 2003; Rocap et al., 2003) |

*Taxonomy of phototrophic strains, according to the List of Prokaryotic Names with Standing in Nomenclature (Munoz et al., 2011) and the NCBI Taxonomy database (Federhen, 2012). Closely related non-phototrophic bacteria (selected based on the 16S rRNA sequence similarity) are listed with the highest taxon that is distinct from that of the respective phototroph(s).

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p0075 The existence of free-living heterotrophic relatives of known phototrophs in Acidobacteria, Chlorobi, Chloroflexi, Firmicutes, and Proteobacteria (Table 1.3) can be contrasted with the secondary loss of the photosynthetic ability among degenerate plastids, e.g. in apicomplexans, which lack both [AU1] RCI and RCII. A symbiotic cyanobacterium, UCYN-A (*Candidatus Atelocyanobacterium thalassa*), with streamlined metabolism has been described that lacks the RCII but still retains a functional RCI (Thompson et al., 2012; Tripp et al., 2010; Zehr et al., 2008). In contrast, the free-living heterotrophic members of the other five phyla typically encode relatively large protein sets (Table 1.3) and do not display any signs of genome degradation.

p0080 The 'patchy' distribution of the ability to conduct photosynthesis could be explained either by a massive loss of photosynthesis genes by non-photosynthetic members of the respective phyla or by a relatively late acquisition of this ability by a handful of selected genera (Table 1.3) through lateral gene transfer of certain photosynthesis genes. Given the obvious evolutionary advantage of having solar radiation as a source of energy, the first scenario appears extremely unlikely. As a result, there is a general consensus that photosynthesis genes are being spread through lateral gene transfer (Blankenship, 1992; Bryant & Frigaard, 2006; Bryant et al., 2012; Gupta, 2012; Hohmann-Marriott & Blankenship, 2011; Mulkidjanian et al., 2006; Olson & Blankenship, 2004). This consensus has been further supported by the findings that photosynthesis genes could be transduced by phages (Alperovitch-Lavy et al., 2011; Mann, Cook, Millard, Bailey, & Clokie, 2003; Sharon et al., 2009; Sullivan et al., 2006) and expressed in the infected host cells (Lindell et al., 2004).

p0085 Despite the obvious propensity of photosynthesis genes to lateral gene transfer, a direct comparison of the completely sequenced genomes of phototrophic bacteria from different lineages revealed a surprisingly little overlap between the respective gene sets (Table 1.4). This circumstance greatly affected the evolutionary analyses of photosynthesis genes. Indeed, the typical approaches to such analyses involve identification of shared traits and construction of phylogenetic trees from sequences of the genes (proteins) that are responsible for these shared traits. In this case, several attempts at delineation of the 'photosynthesis gene set' of the genes shared by all photosynthetic organisms revealed that: (1) there are very few such genes and (2) most of these genes are involved in biosynthesis of (bacterio)chlorophyll and related processes, rather than in photosynthesis per se (Mulkidjanian et al., 2006; Raymond, Zhaxybayeva, Gogarten, & Blankenship, 2003; Raymond, Zhaxybayeva, Gogarten, Gerdes, & Blankenship, 2002; Sato, 2002;

t0025 **Table 1.4** Distribution of the core photosynthesis genes in various phototrophic lineages*

| | | Anoxygenic phototrophs | | | | | Oxygenic phototrophs | |
|---|---|---|---|---|---|---|---|---|
| **System or pathway** | **Genes** | **Acido** | **Chlorobium** | **Chloroflexus** | **Helio** | **Purple** | **Cyano** | **Plants** |
| **Chlorophyll biosynthesis** | *chlB, chlD, chlG, chlH, chlI, chlL, chlM, chlN, chlP* | + | + | + | + | + | + | + |
| ***Photosystem I*** | | | | | | | | |
| Core RC1 subunit | *psaB/pshA* | + | + | – | + | – | + | + |
| Iron–sulfur subunit | *psaC* | + | ±[†] | – | + | – | + | + |
| Photosystem I subunits | *psaD, psaE, psaF, psaI, psaJ, psaK, psaL, psaM* | – | – | – | – | – | + | + |
| ***Photosystem II*** | | | | | | | | |
| Core RC2 subunit D1/D2 | *psbA/psbD* | – | – | + | – | + | + | + |
| Photosystem II subunits | *psbB, psbC, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbM, psbN, psbO, psbP, psbQ, psbT, psbU, psbV, psbW, psbX, psbY(Ycf32), psbZ(Ycf9), psb27* | – | – | – | – | – | + | + |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| ***Cytochrome $b_6f$ complex*** | | | | | | | | | |
| Cytochrome $b_6$ with fused or separate subunit IV, Rieske iron–sulfur protein | *petB* (±*petD*), *petC* | + | + | – | + | + | + | | + |
| Cytochrome f, other subunits | *petA*, *petD*, *petG*, *petL*, *petM*, *petN* | – | – | – | – | – | + | | + |
| Cytochrome *c* ($c_6$, $c_{553}$) | *petJ*, *cytM* | + | + | + | + | + | + | | + |
| Plastocyanin | *petE* | – | – | ± | – | – | + | | + |
| ***CBB cycle*** | | | | | | | | | |
| RuBisCO | *rbcS*, *rbcL* | – | –/+ | – | – | + | + | | + |
| Common enzymes | *pgk*, *gapA*, *rpe*, *tpiA*, *tktA* | + | + | + | + | + | + | | + |

*Presence or absence of orthologs of the respective cyanobacterial genes in the genomes of phototrophic representatives of Acidobacteria (*Candidatus Chloracidobacterium thermophilum*, Genbank entry CP002514, CP002515), Chlorobi (*Chlorobium tepidum* TLS, AE006470), Chloroflexi (*Chloroflexus aurantiacus* J-10-fl, CP000909), Firmicutes (*Heliobacterium modesticaldum* Ice1, CP000930), Proteobacteria (*Rhodopseudomonas palustris* CGA009, BX571963), Cyanobacteria (*Synechocystis* sp. PCC 6803, BA000022), and plants (*Arabidopsis thaliana*, NC_003070, NC_003076, NC_000932). This table has been originally compiled for reference Mulkidjanian et al. (2006) and updated based on the analysis of the complete genomes of *Candidatus* Chloracidobacterium thermophilum and *H. modesticaldum* (Garcia Costas et al., 2012; Sattley et al., 2008).
†Iron–sulfur protein PscB of *C. tepidum* is not homologous to PsaC-like FeS-subunits of other groups of phototrophs.

Zhaxybayeva, Hamel, Raymond, & Gogarten, 2004). The major additions to the genomic analysis after 2006, as included in Table 1.4, was the discovery of photosynthetic apparata, namely a type I RC and the accompanying set of protein-coding genes in a representative of *Acidobacteria*, *Candidatus Chloracidobacterium thermophilum* (Bryant et al., 2007; Garcia Costas et al., 2012; Tsukatani, Romberger, Golbeck, & Bryant, 2012). Another important new result was the discovery of a cytochrome $b_6f$ complex in a non-phototrophic (Table 1.3) representative of Chloroflexi, *Herpetosiphon aurantiacus* (Kiss et al., 2011). Before that, in Chloroflexi, only the alternative complex III had been identified as an oxidoreductase that would connect the membrane menaquinol pool with high-potential electron acceptors (Yanyushin, 2002; Yanyushin, del Rosario, Brune, & Blankenship, 2005). Thus, cytochrome *bc* complexes have now been found in all phototroph-containing phyla. Still, the principal observation that the shared set of photosynthesis genes is related to the (bacterio)chlorophyll biosynthesis and not to the photosynthetic machinery per se still stands.

s0030 ## 3.2. Who Were the Ancestral Phototrophs?

p0090 The inability to draw conclusions on the evolution of photosynthesis and the nature of ancestral form of the RC from genome comparisons alone prompted us to bring the genomic results into a broader context.

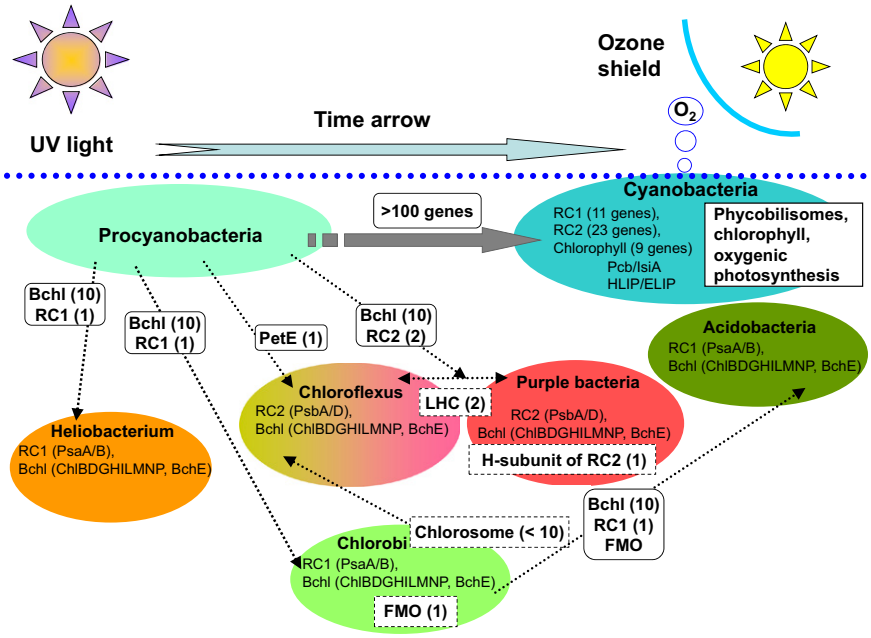
p0095 Previously, we have argued that since all free-living cyanobacteria contain almost 100 photosynthesis-related genes and are obligate autotrophs, their anoxygenic ancestors, procyanobacteria, could be the first phototrophic organisms. In support, we have invoked the geological evidence, as obtained by Tice and Lowe at Buck Reef Chert, a 250–400 m-thick rock running along the South African coast (Tice & Lowe, 2004, 2006). Tice and Lowe have identified traces of a primordial phototrophic community within this >3.4 Gy-old chert and defined the inhabitants of this community as partially filamentous phototrophs, which, according to the carbon isotopic composition, used the Calvin–Benson–Bassham (CBB) cycle to fix $CO_2$. Overall, this set of features most closely resembles cyanobacteria, so that the Buck Reef Chert may have been inhabited by their direct ancestors. We have suggested that phototrophic organisms belonging to phyla other than cyanobacteria could have obtained their photosynthesis genes via lateral gene transfer from the (pro)cyanobacterial lineage at different steps of evolution.

p0100 According to the proposed scenario, the ancestors of *Chlorobium, Heliobacterium*, and *Chloracidobacterium* must have acquired the primordial, homodimeric form of the RC1, whereas proteobacterial phototrophic

lineages and *Chloroflexus* acquired their RC2 before it 'learned' to oxidize water. Anoxygenic phototrophs usually dwell in the depth of microbial mats. Perhaps therefore they were subject to a weaker selective pressure from light and oxygen than those (ancestors of modern cyanobacteria) that remained on the surface, resulting in preservation of ancestral features of their photosynthetic machinery. Thus, photosynthetic enzymes of anaerobic bacteria can be considered snapshots of the ancient RCs: the homodimeric RC1 of *Heliobacillus mobilis* (PshA) and *Chlorobium tepidum* (PscA) are probably more similar to the ancient homodimeric RC1 than the highly evolved heterodimeric PSI (PsaA/PsaB) of modern cyanobacteria.

p0105 This scenario is in a good correspondence with the most recent work of Gupta (2012), who has analysed conserved signature insertions and deletions in key proteins involved in bacteriochlorophyll biosynthesis. In this work the bacteriochlorophyll synthesis enzymes from Heliobacteriaceae were identified as primitive in comparison to all other photosynthetic lineages, and some ancient Firmicutes were suggested as first phototrophic organisms (Gupta, 2012). Heliobacteriaceae, however, form a very narrow group of phototrophs within the Firmicutes phylum. Furthermore, the photosynthetic apparata of *Heliobacillus mobilis* and *Heliobacterium modesticaldum* are harboured on large operons (Sattley et al., 2008; Xiong, Inoue, & Bauer, 1998), potential subjects of lateral gene transfer. Hence, it seems very likely that heliobacteria, indeed, obtained their photosynthesis genes via lateral gene transfer. The same operon in *H. modesticaldum* also carries the genes of a menaquinone-dependent cytochrome $b_6f$ complex, which, arguably, also represents a primitive form of cytochrome *bc* complexes (Dibrova, Cherepanov, et al., submitted for publication; Dibrova, Chudetsky, et al., in press). Most likely, all these proteins emerged and were shaped not within Heliobacteriaceae, but within some other anoxygenic, menaquinone-containing phototrophic lineage, which, we believe, directly preceded cyanobacteria. This lineage later also invented oxygenic photosynthesis, and underwent dramatic changes in response to the oxygenation of the biosphere (Mulkidjanian et al., 2006; Raymond & Blankenship, 2004; Rutherford, Osyczka, & Rappaport, 2012), which they could not evade. In contrast, the strictly anaerobic heliobacteria retained the low-potential menaquinone and, correspondingly, the ancestral versions of the homodimeric photosynthetic reaction complex and of the cytochrome $b_6f$ complex.

p0110 The proposed scenario is illustrated in Fig. 1.1, which we have upgraded as compared to a previous publication (Mulkidjanian et al., 2006). Here, the phototrophic phyla are depicted in accordance with the depth of their




f0010

**Figure 1.1** Distribution of the photosynthesis gene contents in different lineages of phototrophs and the directions of proposed lateral gene transfer. *(Modified from Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin (2012), Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin (in press), see text for details).* (For colour version of this figure, the reader is referred to the online version of this book.)

location in modern (and, perhaps, primordial) microbial mats (Nisbet & Sleep, 2001). Rounded text boxes show the extent of photosynthesis gene lateral transfer between the phyla; the numbers of CyOGs transferred are indicated in parentheses. Rectangular text boxes show major photosynthesis-relevant 'inventions' that occurred inside (solid box) or outside (dashed boxes) the (pro)cyanobacterial lineage. The colouring of the Chloroflexi reflects the presence in this group of both green chlorosome-containing organisms (Pierson & Castenholz, 1974) and the pink ones, lacking the chlorosomes (Hanada, Takaichi, Matsuura, & Nakamura, 2002). The chlorosome-less Chloroflexi carries its photosynthesis genes in an operon that is similar in gene content and even in the gene order to the RC2-encoding operon of purple bacteria (Yamada et al., 2005). Since the RC2 of Chloroflexi is menaquinone-dependent and operates at lower redox potentials than the ubiquinone-dependent RC2 of proteobacteria, we suggest that the latter have attained their RC2 and, perhaps, the light-harvesting proteins via Chloroflexi. In proteobacteria, a new protein was recruited, the 'heavy'

H-subunit that cups/protects RC2 from the cytoplasmic side. In other phototrophs, the RCs are cupped either by phycobilisomes (cyanobacteria) or by chlorosomes (Chlorobi, Chloroflexi, and *Ca*. Chloracidobacterium), so
[AU2] that part of the light excitation energy pours into the RC2 through this interface. The gene for the H-subunit, although present in the photosynthesis gene cluster, is located separately from the genes of the other two RC subunits (Suwanto & Kaplan, 1989). In Chlorobi and *Ca*. Chloracidobacterium, a bacteriochlorophyll-binding Fenna–Matthews–Olson protein (FMO) protein (Matthews, Fenna, Bolognesi, Schmid, & Olson, 1979) is used to mediate the excitation transfer from the chlorosome to the RC1.

p0115 The picture emphasizes that while the surface phototrophs, moving along the time arrow from the anoxic into the self-made oxygenated world, underwent a major transformation from anoxygenic procyanobacteria to cyanobacteria (Raymond & Segre, 2006; Rutherford et al., 2012), the inhabitants of the lower layers of microbial communities (mats), better protected from oxygen, could retain their traits in the course of evolution.

## s0035 4. PHOTOSYNTHESIS AND THE EMERGENCE OF LIFE

p0120 The evolutionary scenario, as put forward in the previous section, implies that the first phototrophic organisms depended on solar light and dwelled in illuminated habitats. An alternative hypothesis, proposed by Nisbet and co-workers (Nisbet, Cann, & Dover, 1995), has suggested that anoxygenic photosynthesis could have evolved from the infrared phototaxis systems of bacteria that dwelled around deep-sea hydrothermal vents. Geologically, this hypothesis joined the popular line of thinking, according to which life emerged around deep-sea hydrothermal vents, where it was protected from the damaging impact of the solar UV radiation, which had been orders of magnitude stronger in the absence of ozone layer (Russell, Hall, Cairns-Smith, & Braterman, 1988; Sagan, 1973). Biochemically, this hypothesis provided backing to the phylogenetic reconstruction, according to which the proteobacterial bacteriochlorophylls, which absorb in the infrared part of the solar spectrum, were the first photosynthetic pigments and proteobacteria, accordingly, could be the first phototrophs (Xiong, Fischer, Inoue, Nakahara, & Bauer, 2000).

p0125 The scenario of proteobacteria as first phototrophs, as well as the underlying phylogenetic analysis, has been criticized by many authors and from different viewpoints (Bryant et al., 2012; Green & Gantt, 2000; Gupta, 2012; Mix, Haig, & Cavanaugh, 2005). As one more argument against the ancestral

status of phototrophic proteobacteria, it could be noted that high-potential quinones are found exactly in those lineages of proteobacteria that harbour photosynthetic enzymes, i.e. α-, β-, and γ-proteobacteria. As argued by Nitschke and co-workers, the replacement of menaquinone by a high-potential ubiquinone took place in these lineages (Schoepp-Cothenet et al., 2009; Schoepp-Cothenet et al., in press); accordingly, the very emergence of α-, β-, and γ-proteobacteria should have followed the oxygenation of the atmosphere only some 2.5 Gy ago (Hazen et al., 2011).

p0130 The geological viewpoint on the emergence of life around deep-sea hydrothermal vents has also been challenged. It has gradually become clear that the emergence of the first biopolymers could hardly happen without the participation of solar UV radiation as a selective factor. The common property of native nucleobases, which discriminates them from other molecules of comparable complexity, is their exceptional photostability (Mulkidjanian, Cherepanov, & Galperin, 2003; Serrano-Andres & Merchan, 2009; Sobolewski & Domcke, 2006). We have argued earlier that because of this property, nucleotides could have been photo-selected by solar UV radiation – in the absence of an ozone layer – from a plethora of abiotically (photo)synthesized organic compounds (Mulkidjanian et al., 2003). It has been shown that nucleobases and nucleotides can specifically form in formamide-containing solutions, particularly under UV irradiation and in the presence of phosphorous compounds (Barks et al., 2010; Costanzo, Saladino, Crestini, Ciciriello, & Di Mauro, 2007; Schoffstall, 1976). More recently, it has been found that after a prolonged UV illumination of complex mixtures of ribonucleotides and diverse by-products of nucleotide synthesis, only 2′,3′-cyclic nucleotides remained in the solution as the most photostable of the produced molecules (Powner, Gerland, & Sutherland, 2009). The 2′,3′-cyclic ribonucleotides can polymerize into oligomers even in the absence of templates (Verlander, Lohrmann, & Orgel, 1973); this polymerization is driven by the cleavage of one of the two phosphoester bonds (transesterification). Hence, cyclic nucleotides, which could form abiotically at high concentrations of formamide and phosphate (Costanzo, Pino, Botta, Saladino, & Di Mauro, 2011; Costanzo et al., 2007; Saladino, Botta, Pino, Costanzo, & Di Mauro, 2012; Saladino, Crestini, Pino, Costanzo, & Di Mauro, 2012), could serve as both monomers and the energy source for the abiotic formation of RNA replicators and ribozymes.

p0135 Independently, the 'hatcheries' of the first cells were reconstructed by combining a geochemical analysis with phylogenomic scrutiny of the inorganic ion requirements of universal components of modern cells

(Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press). These ubiquitous, and by inference primordial, proteins and functional systems show affinity to and functional requirement for $K^+$, $Zn^{2+}$, $Mn^{2+}$, and phosphate. Thus, protocells must have evolved in habitats with a high $K^+/Na^+$ ratio and relatively high concentrations of Zn, Mn, and phosphorous compounds. Geochemical reconstruction shows that the ionic composition conducive to the origin of cells is compatible with emissions of vapour-dominated zones of inland geothermal systems. A major distinctive feature of such systems is the separation of the vapour phase from the liquid phase due to the boiling of the ascending hot hydrothermal fluids. The ascending vapour, after reaching the surface of the rock, discharges via numerous fumaroles and mud pots, which make a geothermal field. The chemical composition of the two phases differs dramatically: the liquid phase contains large amounts of Na and Cl whereas the vapour phase is specifically enriched in $H_2S$, $CO_2$, and $NH_3$ (Aver'ev, 1961; Fournier, 2004; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press; White, Muffler, & Truesdell, 1971).

p0140 As argued elsewhere, anoxic geothermal fields should have been particularly conducive for abiogenic synthesis of ribonucleotides and their polymerization (Dibrova, Cherepanov, et al., submitted for publication; Dibrova, Chudetsky, et al., in press; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press), unlike any marine habitats that could never been enriched in simple amides, phosphorous compounds and borate, all of which are needed for abiotic formation of nucleobases and nucleotides (Benner, Carrigan, Ricardo, & Frye, 2006; Saladino, Botta, et al., 2012; Saladino, Crestini, et al., 2012). Two types of environments relevant for the early stages of evolution can be expected at anoxic geothermal fields, namely: (1) periodically wetted, illuminated mineral surfaces that could serve as templates and (photo)catalysts for diverse abiotic syntheses and (2) puddles and pools of cooled, condensed vapour that would function as concentrators of prebiotic organic molecules. Each such pool would 'harvest' substrates from its catchment area and should have contained mixture of water, simple amides, silica, metal sulfides, and amphiphilic molecules (which could be present as micelles). These pools could have served as hatcheries of the first replicating organisms. Under anoxic, $CO_2$-dominated atmosphere, the ionic composition of pools of cool, condensed vapour at anoxic geothermal fields would resemble the internal milieu of modern cells. Such pools would be lined

with porous silicate minerals mixed with metal sulfides, and enriched in $K^+$ ions and phosphorous compounds.

p0145 Concerning the mentioned clear preference of the ancient proteins for Zn and Mn as transition metal cofactors (Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press; Mulkidjanian & Galperin, 2009), it is noteworthy that these two metals precipitate together at the outlets of the hydrothermal and geothermal systems, forming Zn- and Mn-enriched, ring-like deposits around them (Reed & Palandri, 2006; Tivey, 2007). Currently, these metals can precipitate both as sulfides (at the sea floor) and oxides (at terrestrial systems). At the primordial Earth, however, only sulfides could precipitate at inland geothermal fields. Sulfides of Zn and Mn are among the most potent photocatalysts (Fox & Dulay, 1993; Henglein, 1984; Mulkidjanian, 2009 and references therein). Under solar light that contained an essential UV component and in the presence of high levels of $CO_2$ in the primordial atmosphere (Sleep, 2010), ZnS and MnS would reduce carbon dioxide to diverse organic molecules. Numerous experiments have shown that this kind of photosynthesis proceeds with a high yield, reaching 80% in the case of ZnS particles (Guzman & Martin, 2009, 2010; Henglein, 1984; Kisch & Twardzik, 1991; Reber & Meier, 1984; Yanagida, Azuma, Midori, Pac, & Sakurai, 1985; Yanagida, Kizumoto, Ishimaru, Pac, & Sakurai, 1985; Zhang et al., 2004, 2007). Hence, the preference of the ancient cellular systems for Zn and Mn as transition metal cofactors might simply reflect the fact that the first life forms dwelled among ZnS and MnS-enriched photosynthesizing precipitates and recruited the Zn and Mn ions, which were released upon photosynthesis, for stabilizing their proteins and RNA polymers (Mulkidjanian, 2009; Mulkidjanian & Galperin, 2009).

p0150 Hence, the porous sediments, enriched in sulfides of Zn and Mn, could serve as photosynthesizing habitats of first heterotrophic cells (Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press). Apparently, such organisms did not initially need photosynthetic systems of their own, because they could get organic molecules for free, from abiotic photosynthesis (Zhang et al., 2004, 2007) and also from geothermal vapour, which carries diverse organic molecules (Sleep, Meibom, Fridriksson, Coleman, & Bird, 2004).

p0155 The ZnS- and MnS-containing sediments could also provide shelter from the UV irradiation for the first organisms. Even a thin, 5 μm-layer of ZnS would attenuate the UV light by a factor of $10^{10}$ (Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova,

Galperin, & Koonin, in press). A stratified system could have been established within geothermal ponds where the illuminated upper layers were involved in 'light harvesting' and production of reduced organic compounds, whereas the deeper, less productive but better protected layers would have provided shelter for the replicating organisms (Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, 2012; Mulkidjanian, Bychkov, Dibrova, Galperin, & Koonin, in press). The light gradient and the interlayer metabolite exchange are typical of modern stratified phototrophic microbial communities (Nold & Ward, 1996).

p0160 It is noteworthy that for a particular organism it might be beneficial to get closer to the surface of a sediment and, hence, closer to the source of abiotically produced organic molecules. Therefore organisms that could synthesize or recruit UV-absorbing compounds, such as porphyrins, might have an evolutionary advantage (Mulkidjanian & Junge, 1997). Porphyrin-carrying membrane proteins may have eventually evolved later into the first biogenic photosynthetic apparata.

p0165 Halmann and colleagues (Halmann, Aurian-Blajeni, & Bloch, 1980) have noted the similarity between physical mechanisms of chlorophyll-based and semiconductor-based photosyntheses, which both include light-induced charge separation followed by the stabilization of the low-energy, reduced states, as shown in Fig. 1.2, where the energy diagrams for a ZnS crystal and a sulfide-oxidizing RC1 of Chlorobi are compared. Even the

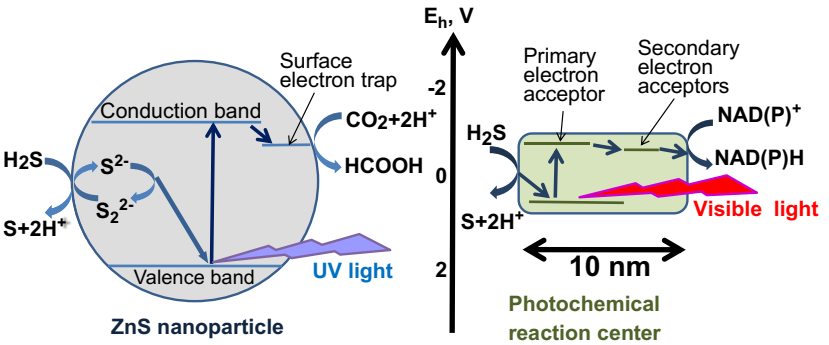



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**Figure 1.2** ***A comparison of energy diagrams for a photosynthesizing ZnS nanoparticle and a photosynthetic reaction centre.*** Left, the energy diagram for a ZnS crystal, based on references Henglein, Gutierrez, and Fischer (1984), Kisch and Künneth (1991), Yoneyama (1997). Right, an energy diagram for a simple, sulfide-oxidizing reaction centre complex of green sulfur bacteria is shown as an example, see Bryant et al. (2012), Frigaard and Bryant (2004), Jagannathan and Golbeck (2008) for reviews on this type of reaction centre. *(The figure is taken from Mulkidjanian and Galperin (2009)).* (For colour version of this figure, the reader is referred to the online version of this book.)

same reaction of sulfide oxidation is utilized to re-fill the photo-generated electron vacancies (holes).

p0170 The emergence of biogenic photosynthesis seems to have happened after the separation of bacteria from archaea, so it was not a very early event. Therefore it cannot be fully excluded that biogenic photosynthesis may have emerged after some ancestral bacteria, which possessed porphyrin-carrying membrane proteins, had colonized deep-sea hydrothermal vents.

p0175 Still, we consider it more plausible that porphyrin/chlorophyll photosynthesis was 'invented' by terrestrial life forms, which moved away from geothermal fields and invaded new habitats that were depleted in ZnS, MnS, and abiogenically produced organic molecules. Upon getting away from geothermal fields, the use of biogenic photosynthesis could have initially complemented the gradually diminishing ZnS-mediated photosynthesis; its contribution, however, should have increased with the departure from geothermal fields and invading, for example, terrestrial fresh-water basins. In this framework, the emergence of biogenic photosynthesis might represent a clear-cut case of functional takeover – with the primeval photochemical RCs and primordial CBB cycle accomplishing together the function that ZnS- and MnS-rich precipitates carried out at the geothermal fields: namely, utilization of solar and geothermal energy for producing organic compounds from $CO_2$.

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## Non-Print Items

**Keywords:** Genes; Photosynthesis; Bacteria; Genome sequencing