Final Technical Report

Sponsoring Agency: Department of Energy

Award no.: DE-FG02-94ER20137

Project Title: Light Energy Transduction in Green Sulfur Bacteria

Institution: Pennsylvania State University

Principal Investigator: Donald A. Bryant

Project Period: 04/01/1994 through 10/31/2020

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Final Scientific Report for DE-FG02-94ER20137

Period Covered: April 1, 1994 to October 31, 2020

Introduction

In 1988, I chaired a session at a meeting on light-harvesting antenna structures in phototrophic bacteria, and two of the speakers in my session nearly engaged in fisticuffs over the issue of the roles—and even the presence—of proteins in chlorosomes. After convincing the would-be combatants to stand down, I thought to myself that any subject that could bring seemingly reasonable men to such excessive behavior was a subject that I would be interested in studying as a way of expanding the scope of the research in my laboratory. I had an upcoming sabbatical at the ETH in 1989-1990 in Zürich in Herbert Zuber's lab, which studied light-harvesting proteins in purple and green sulfur bacteria (GSB) as well as cyanobacteria, I decided that I would learn how to grow GSB and initiate a research program aimed at characterizing the role(s) of proteins in chlorosomes, using a combination of biochemistry and molecular genetics. After my year in Zürich and my return to Penn State, I recruited a graduate student to work on this topic in 1991, and by 1992 we already had begun to identify proteins and had cloned a few genes—including the *csmA* genes from *Chlorobium vibrioforme* 8327d and *Chlorobaculum tepidum*. At about this time, I received an invitation to attend a small gathering of scientists hosted by Bob Rabson, which served as my introduction to the Energy Biosciences leadership at DOE, and the rest is history. Encouraged by Bob and with growing preliminary results, I submitted a proposal to DOE to study the photosynthetic apparatus of these two GSB strains, both of which could grow on thiosulfate, and which had been shown to offer possibilities for genetic manipulation. The proposal was funded in 1994 and we began our studies in earnest. This project would have continuous support from DOE over the ensuing 26 years, resulting in about 140 publications. It supported the research of 13 postdoctoral associates (7 male, 6 female) and 8 graduate students (1 male and 6 female Ph. D. students; 1 female M. Sc. student). Additionally, this project supported the training of many undergraduate students, several of whom were authors on our publications and/or who wrote honors theses for their B. Sc. degrees. Obviously, it will not be possible to describe in this 5000-word report the details included in all those publications. Therefore, this report will present a very high-level overview of some of the notable findings we made over the course of this project.

Chlorosomes

Chlorosomes are very large structures produced by green bacteria that can contain up to 250,000 BChl *c/d/e/f* molecules enclosed in a lipid monolayer envelope membrane. These massive, irregular organelles were the last light-harvesting structures in photosynthesis to have their structures determined. We quickly learned that there are indeed proteins in chlorosomes, but relative to the vast amounts of bacteriochlorophyll (BChl) *c/d/e/f*, proteins make up only a minor component of their structures. In fact, there are no proteins in the chlorosome interior at all. The chlorosomes of *Chlorobaculum* (*Cba.*) *tepidum* contain 10 proteins; all occur in the chlorosome

envelope except CsmA, which forms the baseplate for membrane attachment. CsmA was initially believed to be involved in binding BChl *c* by Zuber and coworkers, but in fact this protein binds BChl *a*. Each CsmA subunit binds a single BChl *a*, and the baseplate is essentially a two-dimensional, paracrystalline array of CsmA and BChl *a* that interacts with the Fenna-Mathews-Olson (FMO) BChl *a*-binding protein on the cytoplasmic membrane. In addition to BChl *c*, chlorosomes of *Cba. tepidum* contain quinones, carotenoids, and lipids. CsmA is essential, but any one of the remaining nine proteins can be deleted with little discernable phenotype. Even when as many as four or five proteins were deleted, only the size and shape of the chlorosomes changed, but they still retained functionality in light harvesting. Chemical cross-linking followed by immunoblotting analyses revealed nearest neighbors for all proteins in the chlorosome envelope. We showed that three proteins, CsmI, CsmJ, and CsmX, bound [2Fe-2S] clusters. These proteins control the oxidation of reduced quinones and the reduction of oxidized quinones that act as quenchers of energy transfer, which provides protection against lethal exposure to oxygen. The combination of light and oxygen is especially lethal to GSB, but oxidizing conditions rapidly quench energy transfer by more than 90%. We identified several factors that help to protect GSB from oxidative damage.

Initial reverse genetics were performed in *C. vibrioforme*, the only strain that had been shown to be naturally transformable at that time. Conjugation-based introduction of DNA into *Cba. tepidum* would be demonstrated by Wahlund and Madigan, and this prompted us to test whether transformation of *Cba. tepidum* was possible. When we successfully demonstrated that *Cba. tepidum* was naturally transformable with linear or circular DNA, we shifted all effort to studying this organism that became the model organism for most studies on GSB. This demonstration of transformability occurred contemporaneously with the complete sequencing of the *Cba. tepidum* genome in 2000. The genome sequence supercharged our research effort on *Cba. tepidum* (and that of some other labs as well). The genomic data allowed us to expand our research effort to study the biosynthesis of carotenoids and BChls *c/d/e/f*. It turned out that being able to manipulate the BChl *c* biosynthetic pathway genetically would be the key to solving the conundrum of how BChls are organized in chlorosomes.

The BChl *c* molecules in the chlorosomes of *Cba. tepidum* are a complex mixture of homologs that differ in multiple ways. Up to three methyl groups can be added at the $C8^2$ position of BChl *c*; one methyl group can also be added to the $C12^1$ methyl group of BChl *c*; the $C3^1$ carbon is chiral with both *R*- and *S*- stereoisomers occurring in chlorosomes; and methylation at C20 occurs in BChls *c* and *e* but not in BChls *d* and *f*. This remarkable heterogeneity leads to inhomogeneous broadening of the BChl absorbance band by producing a continuum of local site energies for the BChls. We demonstrated that this is advantageous to the organism by allowing light harvesting to occur over a broader range of wavelengths than when this heterogeneity is absent. However, chlorosome assembly is not dependent upon these modifications, and chlorosomes lacking methylation at $C8^2$, $C12^1$, and C20 are much more structurally homogeneous than those from the wild type. The upshot of this finding was that for the first time, solid-state NMR data from chlorosomes of a *bchQRU* mutant lacking methylation could be correctly interpreted. In combination with information gained from cryo-EM studies of the same chlorosomes, a structural model for the organization of the BChl *d* molecules in chlorosomes of the *bchQRU* mutant was attained. The model showed that the BChls were arranged in *syn-anti* pairs, with the farnesol tail of one BChl pointing upward relative to the tetrapyrrole ring and that of the other pointing downward. The BChls were further arranged in shallow helices of variable diameter, thereby forming concentric nanotubes of BChl *d*. In essence, the tetrapyrrole rings of the

BChls form sheet-like surfaces that are folded into tubes of different diameters, somewhat like a jellyroll. The sheets fit together by forming bilayer-like interactions of the hydrophobic farnesol tails of the BChls. At the outermost layer adjacent to the envelope, the BChl *c* tails extending outward interact with the fatty acyl groups of the lipids of the envelope, providing an explanation for the asymmetric, monolayer lipid membrane of the envelope. Modeling showed that this was indeed the structure, and at long last the structural model was published in 2009. In subsequent studies of a *bchQR* mutant, we learned that BChl *c* molecules stack in a slightly different manner than BChl *d* but still retain the basic *syn-anti* dimeric unit as the basic structural element. Spectroscopic studies on single chlorosomes led to some further refinement of the structure, mostly involving some subtle adjustments of the angles between individual BChl molecules in the chlorsome.

One of the team of collaborators that solved the structure spent nearly 25 years working toward this goal. The structure, long believed to be impossible to determine, came 15 years after the initiation of this project. It is certainly one of the highlights of my research career, and yet it probably could not have happened had DOE not provided the long-term support required to achieve this goal and supported our studies on the biosynthesis of BChls *c/d/e/f*. It has subsequently been shown that some artifical antenna systems employ the same basic assembly principles to self-organize light-harvesting molecules into chlorosome-like structures. The information derived from our structure has been used to design other artificial self-organizing, light-harvesting molecular arrays.

Comparative studies have shown that all chlorosomes contain CsmA and are structurally similar. However, the chlorosome envelope proteins of members of the *Chloroflexota* and *Acidobacteriota* are either completely unrelated to, or only very distantly related to, the chlorosome envelope proteins of GSB. Because of this, the chlorosomes of these other organisms differ in size and shape compared to those of *Cba. tepidum.*

Genomics of chlorophototrophs

My experience in sequencing the genome of *Cba. tepidum* and the model cyanobacterium, *Synechococcus* sp. PCC 7002, convinced me in 2000 that there would soon be only two types of bacteria: those with sequenced genomes and those without, and one did not want to work with the latter. It also seemed obvious that one could gain lots of insights from comparative genomics. Thus, I decided that it would be wise to sequence the genomes of many GSB representing the full diversity of organisms in the phylum *Chlorobi*. Later, our sequencing efforts included a diversity of *Chloroflexota*, purple bacteria, and cyanobacteria. Some of the sequencing was done by writing proposals to the Joint Genome Institute, and some by obtaining support from NSF. The real beneficiary of these efforts, however, was DOE, because having many genomes for comparative analyses helped to identify novel genes involved in BChl and carotenoid biosynthesis that were important for our functional studies. Over the years since 2000, we sequenced about 100 bacterial genomes, most of which were closed and complete. As predicted, those data became a valuable resource for comparative genomics and functional studies for the entire photosynthesis research community.

As a result of one of the genome sequencing projects, in 2004 I contacted David Ward of Montana State University. This led to a collaboration that is still ongoing some 17 years later. In the summer of 2005, I spent a three-month, mini-sabbatical in the Ward lab in Bozeman, MT, where I hoped to determine whether there were any unknown chlorophototrophs in the hot spring

microbial communities that he was studying. On the very first day I spent time sifting through his metagenomic data for Octopus and Mushroom Springs, I discovered sequence signatures for a novel chlorophototroph, which we would soon determine to be a member of the phylum *Acidobacteriota*, named *Chloracidobacterium* (*Cab.*) *thermophilum*. I correctly predicted that day in the summer of 2005 that this finding would be published in *Science* (it was in 2007), and that started a 15-year period during which we characterized this organism in detail (see section on *Cab. thermophilum*). This was followed by another three-month stay in summer of 2007, a 13-month sabbatical in 2010-2011, and another year-long sabbatical in 2017-2018. Ward is microbial ecologist, and his skills matched up well with my own interests and skills in microbial biochemistry and physiology.

Our collaboration with the Ward lab led to deeper characterization of the chlorophototrophs in the microbial mats of Yellowstone through multi-omics analyses. My lab mainly contributed by studying *in situ* transcription across the diel cycle in mats. These studies have helped to answer long-standing questions about the physiology and metabolism of multiple chlorophototrophs, as they exist in nature.

In addition to molecular methods, we pursued traditional cultivation approaches informed by information gleaned from the metagenome analysis and our experience with cultivating *Cab. thermophilum*. These studies provided evidence for 17 different chlorophototrophs in the mats, most of which had never been detected previously. This included five different purple bacteria, none of which had been detected previously. Most of these were isolated as axenic cultures, and some of their genomes were sequenced. Analyses of the metagenomic data also provided evidence for other previously unknown bacteria with interesting metabolic traits, e.g., "*Candidatus* Thermonerobacter thiotrophicus,". This early-diverging member of the *Chlorobi* is capable of sulfate reduction, a remarkable finding considering the relationships between sulfur oxidizers and sulfur reducers in microbial mats and in evolution.

Biosynthesis of bacteriochlorophylls *c*, *d*, *e,* and *f*

The genome of *Chlorobium* (now *Chlorobaculum*) *tepidum* became available to us in 2000, and we immediately began to analyze the genome for genes involved in the biogenesis of the photosynthetic apparatus. This included an analysis of genes that could account for the synthesis of Chl *a*, BChl *a*, and BChl *c*. Homologs of all genes encoding enzymes for BChl *a* biosynthesis in purple bacteria known at that time were identified in the genome, and paralogs for some of these genes were also identified. Using the transformation system we had developed for *Cba. tepidum*, we began to inactivate genes to identify enzymes involved in BChl *c* biosynthesis, because this pathway was completely unknown. A paralog of BchG and ChlG, which encode BChl and Chl synthase, respectively, could no longer synthesize BChl *c*. This *bchK* mutant revealed the identity of the BChl *c* synthase, but importantly it showed that *Cba. tepidum* could grow in the absence of chlorosomes. This meant that all mutants in the BChl *c* biosynthetic pathway would be viable and that mutants unable to produce chlorosomes should also be viable.

The next gene we identified was *bchU*, a methyltransferase that had a homolog encoded in an operon together with *bchK* in *Chloroflexus aurantiacus*. This gene encoded the C20 methyltransferase, and we showed that a spontaneous frameshift mutation had naturally inactivated this gene in a spontaneous mutant of *C. vibrioforme* 8327d. An expanded family of radical SAM methyltransferases was identified, and when these two genes, *bchQ* and *bchR*, were inactivated, methylation of BChl *c* at $C8^2$ and $C12^1$ was eliminated, respectively. A homolog of

bchF, named *bchV*, was identified, and the deletion of this gene caused the accumulation of some Chls with vinyl side chains at C3, but only when the C8 and C12 sidechains were more methylated. Moreover, the stereochemistry of those Chls with a hydroxyl group at $C3^1$ were *R* chirality. This indicated that BchV was involved in hydroxylating BChls which carried extensive methylation and produced chlorophylls of mixed chirality (both *R* and *S*; i.e., BchV preferred substrates with extensive methylation and produced predominantly *S* chirality but BchF preferred substrates without methylation and produced molecules with *R*-chirality). The search for the enzyme that catalyzes the first committed step in BChl *c* biosynthesis went on for several years. Twelve GSB genomes were sequenced, but in no case could a good candidate be identified in operons with other genes for BChl biosynthesis. Finally, when the genome of *Cab. thermophilum* was sequenced, a small gene was identified amid several other genes involved in BChl biosynthesis. Homologs of this gene were only found in genomes of organisms that could synthesize BChl *c*. Inactivation of the homolog of this gene in *Cba. tepidum* produced a strain that could no longer synthesize BChl *c* and that accumulated excess chlorophyllide *a* as expected. This gene, named *bciC,* completed the pathway leading to biosynthesis of BChl *c*.

We next initiated studies in *Chlorobaculum limnaeum*, a brown-colored GSB that synthesizes BChl *e*, in hopes of identifying the gene(s) involved in the synthesis of BChl *e*. Comparative genomic analysis of strains producing BChl *c* or BChl *e* were performed, and a cluster of genes was identified that colocalized with *cruB*, a gene required for for isorenieratene biosynthesis, a carotenoid that co-occurs with BChl *e* in chlorosomes. Inactivation of a gene encoding a member of the radical SAM family within that cluster led to the identification of *bciD*, the gene that encodes an enzyme that can hydroxylate the C7 methyl group of bacteriochlorophyllide *c* (and *d*). When this gene was deleted, no BChl *e* was formed. Heterologous expression of this gene in *E. coli* was successful, and the purified enzyme was able to hydroxylate bacteriochlorophyllide *c* as predicted when SAM was provided. The enzyme mechanism was shown to proceed via two rounds of hydroxylation on the same methyl group to produce a *gem*-diol, leading to a spontaneous dehydration that yields the C7 formyl group of BChl *e* (or BChl *f* if bacteriochlorophyllide *d* was provided as the substrate). With the characterization of BciD, the full complement of enzymes sufficient for BChl *c/d/e/f* biosynthesis had been identified.

Mutant strains in the BChl *c/d/e/f* biosynthetic pathway provided a very interesting set of strains for characterization by biophysical methods. By studying the properties of chlorosomes from these strains together with growth rate studies under appropriate conditions, we were able to largely recapitulate the selective pressures that led to the extension of this pathway. The product of BciC is already capable of producing functional chlorosomes when combined with *bchF* and *bchK*. The other steps in this pathway were introduced to improve upon the light-harvesting characteristics and would naturally be under positive selection in most natural settings. This pathway nicely fulfills the Granick hypothesis that posits that pathways evolve as organisms evolve within their light niche.

Biosynthesis of carotenoids

Analysis of the *Cba. tepidum* genome identified several genes that were homologous to enzymes of carotenoid biosynthesis in other bacteria. However, homologs for several expected genes could not be identified. Notable among these was the gene for lycopene cyclase. A complementation study in *E. coli* identified a gene fragment that encoded a novel lycopene cyclase,

and characterization of this gene, *cruA*, led to the identification of a fourth family of lycopene cyclases that occur in GSB and cyanobacteria. Other unusual aspects of carotenoid biosynthesis were found. For example, the pathway was like that in cyanobacteria and plants in requiring an isomerase and two desaturases to convert phytoene into lycopene. Genes for the glycosyl and acyl transferases involved in carotenoid biosynthesis were also identified. Frustratingly, for many years, only one gene eluded identification—the 1,2 reductase. This gene was finally identified by a postdoc about five years ago. All genes required for the biosynthesis of the carotenoids in *Cba. tepidum* are now known. Interestingly, carotenoids are not required for viability and functionality of the photosynthetic apparatus in *Cba. tepidum*. However, carotenoids improve survival when cells are exposed to oxygen, with different carotenoids contributing to various degrees to protection against oxidative stress. We were able to extend our studies on carotenoid biosynthesis to determine the pathway of the important biomarker carotenoid, okenone, solving its complete biosynthetic pathway. We have also had a very productive collaboration with the laboratory of Roger Summons at MIT, with whom we have investigated the origins of biomarkers in the fossil record by studying the carotenoids of extant chlorophototrophs. A remarkable finding has been that cyanobacteria that produce synechoxanthin also make small amounts of isorenieratene. This discovery has major implications for correctly interpreting carotenoid biomarkers in the rock record.

Chloracidobacterium thermophilum strain B^T (2015)

As noted above, evidence for the existence of a new phototroph was obtained from metagenomic data from Octopus and Mushroom Springs in Yellowstone National Park in 2005. We were fortunate to be able to link the *pscA* gene, encoding the subunit of a type-1 homodimeric reaction center, to a 16S rRNA gene, which told us that the organism belonged to the phylum *Acidobacteriota*. In a second fortunate occurrence, the organism was found lurking in a supposedly axenic culture of *Synechococcus* sp. B′, which also contained the new chlorophototroph and two hetertrophic bacteria, *Anoxybacillus* sp. and *Meiothermus ruber*. It was relatively easy to eliminate the cyanobacterium by simply adding a mixture of potential carbon sources and DCMU. This enrichment with "*Ca*. Cab. thermophilum" as the only phototroph was maintained for several years, but we repeatedly failed in attempts to render the culture axenic. We were able to sequence the genome of the organism by removing most of the contaminating bacteria by differential centrifugation. Analysis of the genome proved to be highly illuminating. The organism was clearly a heterotroph, was unable to synthesize branched chain amino acids and lysine but could take up and degrade branched chain amino acids. It was unable to synthesize vitamin B_{12} but could probably salvage derivatives of vitamin B_{12}. Finally, the organism was unable to reduce nitrate and sulfate. These inferences from the genome were shown to be correct experimentally, and systematic testing of amino acids, vitamins, and nitrogen carbon and sulfur sources showed that the organism preferred to grow with amino acids as carbon and nitrogen sources; several compounds could be used to provide reduced sulfur, but thioglycolyate and cysteine were preferred. No sugars stimulated growth, and only vitamin B_{12} was required among vitamins. The organism required oxygen but could not grow in the presence of air levels of oxygen. Finally, we showed that "*Ca*. Cab. thermophilum" was an oligotroph that was easily killed by excessive amounts of nutrients. Armed with all this information, an axenic culture was fially obtained in late 2014, and its description was published in 2015.

In the period before an axenic culture was obtained, we were able to use the enrichment culture to learn a lot about the photosynthetic apparatus of *Cab. thermophilum*. We analyzed in detail the (B)Chls, carotenoids, and lipids of this novel phototroph. We characterized its chlorosomes and FMO proteins, which were quite divergent from those of GSB. We were able to describe highly purified reaction centers for the first time in 2012. These reaction centers did not contain any cytochrome subunits and at that time did not contain the PscB subunit or FMO as well. They were clearly quite different from the reaction centers of GSB. Most surprisingly of all, these reaction centers contained three types of Chls: BChl *a* esterified with phytol; Chl *a* esterified with phytodienol; and Zn-BChl *a′* esterified with phytol. ^{15}N-Photo-CIDNP MAS NMR experiments showed that Chl *a* was the primary electron acceptor in these reaction centers. Considering the amount and stereochemistry of Zn-BChl *a′*, it seemed highly likely that this highly unusual BChl would likely form the special pair, which had maximal photobleaching at 840 nm. Together with K. V. Lakshmi and John Golbeck, we used ^{67}Zn-HYSCORE spectroscopy to demonstrate that this was indeed the case. To our best knowledge, this is the first application of this method to the study of an enzyme/protein.

Most recently, we compared the genome sequences of nine axenic isolates of *Chloracidobacterium* spp. Eight isolates came from different temperatures in the microbial mats of Mushroom Spring in Yellowstone National Park, and one came from Rupite hot spring in Bulgaria. Comparative analyses indicate that these nine strains represent at least three species, which we have named *Cab. thermophilum, Cab. aggregatum,* and *Cab. validum*. The photosynthetic apparatuses in these three species are very similar, and the metabolic characteristics of the three species are likewise quite similar. *Cab. thermophilum* produces BChl *c* with a wide range of esterifying alcohols, and the amounts of these tailing molecules and of the carotenoids are distinctive in the various strains. The strains differ with respect to growth temperature and to some extent to oxygen levels. Further studies will be required to determine specifically how they differ physiologically and metabolically. Perhaps surprisingly, none of the isolates can synthesize branched chain amino acids or lysine, but all strains can degrade branched amino acids as well as other amino acids. We have recently learned as well that there is still another species in the mats in Yellowstone that grows at ~68°C. We can tentatively call this species "*Ca*. Cab. extremum."

Concluding Remarks

This report touches on the highlights of a 26-year project that led to the structural characterization of chlorosomes, the elucidation of the pathways for the synthesis of carotenoids and BChls *c/d/e/f*, and the in-depth characterization of a novel chlorophototroph, *Chloracidobacterium thermophilum*. In combination with the recent structure of the reaction center of *Cba. tepidum* and FMO, the photosynthetic apparatus of GSB is now very well characterized. Given the strong similarities between the photosynthetic apparatus in GSB and *Cab. thermophilum*, and the analyses we performed on the latter, it is likely that fairly accurate models can developed for the *Cab. thermophilum* as well.

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Lab Personnel: PostdocsLab Personnel: Postdocs
(13 total: 7 male, 6 female)

Christiane Jakobs	07/94—07/96	Research associate, University of Bonn
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Zhenfeng Liu	02/12—10/12	Bioinformatics Scientist, Quantgene, Berkeley, CA
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