

The Evolution of Anoxygenic Photosynthesis

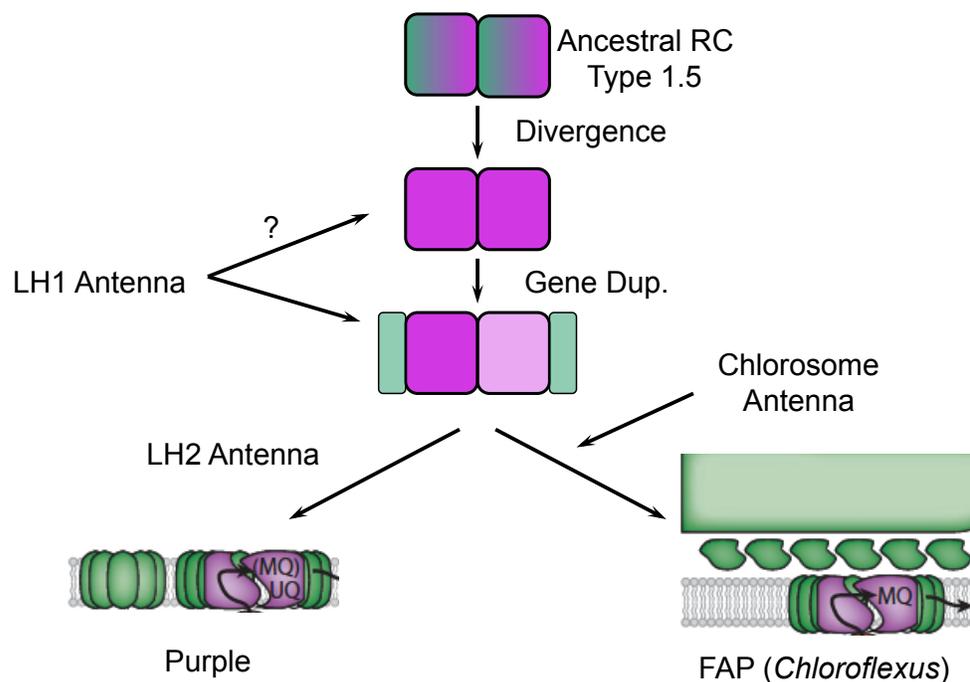
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Energy conversion of sunlight by photosynthetic organisms has changed Earth and life on it. Photosynthesis arose early in Earth's history, and the earliest forms of photosynthetic life were almost certainly anoxygenic (non-oxygen evolving). Multiple lines of evidence strongly suggests that all photosynthetic reaction centers derive from a common ancestor that was a homodimeric protein complex. The evolutionary history of photosynthetic organisms is further complicated by lateral gene transfer that involved photosynthetic components as well as by endosymbiotic events. The complexity of the evolutionary development of photosynthesis is manifested in novel biosynthetic pathways of photosynthetic cofactors and the modification of electron carriers, pigments, and existing and alternative modes of photosynthetic carbon fixation. The invention of oxygenic photosynthesis and the subsequent rise of atmospheric oxygen approximately 2.4 billion years ago revolutionized the energetic and enzymatic fundamentals of life. An expanding wealth of genetic information, together with biochemical, biophysical, and physiological data, reveals a mosaic of photosynthetic features. In combination, these data provide an increasingly robust framework to formulate and evaluate hypotheses concerning the origin and evolution of photosynthesis.

Hohmann-Marriott, MF and Blankenship RE (2011) Evolution of photosynthesis. *Annual Review of Plant Biology* **62**: 515-548.



Microscale sulfur cycling in the phototrophic pink berry consortia of the Sippewissett Salt Marsh

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Abstract: Microbial metabolism is the engine that drives global biogeochemical cycles, yet many key transformations are carried out by microbial consortia over short spatiotemporal scales that elude detection by traditional analytical approaches. We investigate syntrophic sulfur cycling in the ‘pink berry’ consortia of the Sippewissett Salt Marsh through an integrative study at the microbial scale. The pink berries are macroscopic, photosynthetic microbial aggregates composed primarily of two closely associated species: sulfide-oxidizing purple sulfur bacteria (PB-PSB1) and sulfate-reducing bacteria (PB-SRB1). Metagenomic sequencing was conducted using both the standard Illumina platform and novel long read sequencing approaches (Moleculo and Pacbio). The complete genomes for PB-PSB1 and PB-SRB1 demonstrate the genetic potential for sulfur cycling within the berries. Furthermore, the genome of PB-SRB1 encodes several putatively horizontally transferred, light-responsive proteins that are unique among known sulfate reducing bacteria, a finding that suggests this species is specifically adapted to life in the photic zone.

We demonstrate nanometer scale interspecies transfer of reduced sulfur metabolites from PB-SRB1 to PB-PSB1 using ^{34}S -enriched sulfate stable isotope probing coupled with nanoSIMS. The pink berries catalyze net sulfide oxidation and maintain internal sulfide concentrations of 0–500 μM . Sulfide within the berries, captured on silver wires and analyzed using SIMS, increased in abundance towards the berry interior while $\delta^{34}\text{S}_{\text{-sulfide}}$ decreased from 6‰ to -31‰ from the exterior to interior of the berry. These values correspond to sulfate-sulfide isotopic fractionations (15-53‰) consistent with either sulfate reduction or a mixture of reductive and oxidative metabolisms. Together this combined metagenomic and high-resolution isotopic analysis demonstrates active sulfur cycling at the microscale within well-structured macroscopic consortia consisting of sulfide-oxidizing anoxygenic phototrophs and sulfate-reducing bacteria.

Further reading:

- Wilbanks EG, Jaekel U, Salman V, Humphrey PT, Eisen JA, Facciotti MT, Zinder SH, Buckley DH, Druschel GK, Fike DA, Orphan VJ. (2014). Microscale sulfur cycling in the phototrophic pink berry consortia of the Sippewissett Salt Marsh. *Environmental Microbiology*. Early online, doi: 10.1111/1462-2920.12388
- Canfield, D.E., Stewart, F.J., Thamdrup, B., De Brabandere, L., Dalsgaard, T., Delong, E.F. et al. (2010) A cryptic sulfur cycle in oxygen-minimum-zone waters off the Chilean coast. *Science* **330**: 1375-1378.

Sulfur and beyond: Energy sources of sulfur-oxidizing symbionts

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Chemosynthetic symbioses between sulfur-oxidizing bacteria and marine invertebrates were first discovered in 1977 at deep-sea hydrothermal vents but are now known to occur in a wide range of habitats including coral reef sediments, seagrass beds, cold seeps and sunken whale carcasses. In the hosts of chemosynthetic symbionts, these associations have evolved multiple times in convergent evolution in at least 9 animal groups such as flatworms, annelids, nematodes, mussels, clams, and snails. Similarly, chemosynthetic symbionts have evolved – and are continuing to evolve - from numerous bacterial lineages in convergent evolution, and many are so closely related to free-living chemosynthetic bacteria that at the 16S rRNA level, they can be considered to belong to the same genus or even species (Dubilier et al. 2008).

It is generally assumed that sulfur-oxidizing symbionts use reduced sulfur compounds as their sole energy sources, but only a few studies have examined the genomic potential for other energy sources and even fewer have investigated which energy sources are used in situ. We recently discovered that chemosynthetic symbionts use a surprisingly wide range of energy and carbon sources that includes hydrogen, carbon monoxide, and organic carbon compounds (Kleiner et al. 2012 PNAS, Petersen et al. 2011. Nature). In my talk, I will present an overview of the research in my lab in this area and discuss if the metabolic versatility of both symbiotic and free-living sulfur-oxidizing bacteria may be much greater than currently recognized.

Dubilier N, Bergin C, Lott C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology* 6: 725-740

Kleiner M, Wentrup C, Lott C, Teeling H, Wetzel S, Young J, Chang Y-J, Shah M, VerBerkmoes NC, Zarzycki J, Fuchs G, Markert S, Hempel K, Voigt B, Becher D, Liebeke M, Lalk M, Albrecht D, Hecker M, Schweder T, Dubilier N. 2012. Metaproteomics of a gutless marine worm and its symbiotic microbial community reveal unusual pathways for carbon and energy use. *Proc. Natl. Acad. Sci. USA*. 109: E1173-E1182.

Petersen JM, Zielinski FU, Pape T, Seifert R, Moraru C, Amann R, Hourdez S, Girguis PR, Wankel SD, Barbe V, Pelletier E, Fink D, Borowski C, Bach W, Dubilier N. 2011. Hydrogen is an energy source for hydrothermal vent symbioses. *Nature* 476: 176-180.

Title: Oxidative sulfur biomineralization and preservation in a “sulfidic ice” system

Authors: Alexis Templeton¹, Graham Lau¹, Chris Trivedi², Julie Cosmidis¹, Damhnait Gleeson¹, Katherine Wright¹, Robert Pappalardo³, and John Spear² (¹Department of Geological Sciences, University of Colorado; ²Civil and Environmental Engineering, Colorado School of Mines; ³Jet Propulsion Laboratory).

Microbial activity can control the abundance and distribution of sulfur species in environments far from chemical equilibrium, including the precipitation of intracellular and extracellular elemental sulfur in association with organic structures such as surface coatings, cell surfaces, filaments and sheaths. However, the potential for generation and preservation of biologically-influenced large-scale S⁰ mineral deposits has not been extensively investigated. Thus our team is currently engaged in a long-term project that takes advantage of the annually recurring and aerially-extensive formation of an icy elemental sulfur deposit at Borup Fiord Pass in the Canadian High Arctic to define direct feedbacks between the aqueous geochemistry of cold sulfide springs, microbial community composition, genetic potential and the chemical speciation and preservation of cryogenic S⁰ minerals.

We will present a conceptual model for the ecology and mineralogy of terrestrial cold S springs that sustain consortia of *Flavobacteria* and S-oxidizing bacteria (e.g. *Sulfurovum* and *Sulfuricurvum*). In particular, we will focus on how microbial activity gives rise to the production of enormous volumes of elemental sulfur and gypsum at a subsurface/surface interfacial environment dominated by sulfidic ices, and then link our field observations to biomineralization experiments conducted with pure cultures of Borup organisms in the laboratory. This talk will include a significant amount of unpublished data from field work and spectroscopic experiments all conducted in the Summer of 2014; our most recent publications, which will also be referenced to provide a framework for discussion, include a metagenomic analysis of the Borup Sulfur deposits (Wright et al., 2013) and initial investigations of sulfur biomineralization in both our field and laboratory systems (Gleeson et al., 2011).

References:

Wright, K.E., Williamson, C., Grasby, S.E., Spear, J.S., and **Templeton, A.S.**, 2013, Metagenomic evidence for sulfur lithotrophy by Epsilonproteobacteria as the major energy source for primary productivity in a sub-aerial arctic glacial deposit, Borup Fiord Pass. *Frontiers in Extreme Microbiology*, v4, Article 63.

Gleeson, D.F., Williamson C.H.D., Grasby S.E., Spear J.R., Pappalardo R.T., **Templeton A.S.**, 2011, Low temperature S⁰ biomineralization at a supraglacial spring system in the Canadian High Arctic, *Geobiology Journal*, v. 9, p. 360-375.