What do studies of photosynthetic bacteria, algae and plants tell us about the evolution of photosynthesis?

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The intricate nature of the photosynthetic pathway found in modern plants has spurred extensive debate and investigation into its origins and evolutionary history. By delving into the integration of chloroplasts into eukaryotic organisms and using this as a foundation for exploring the evolution of photosystems (PSs), we can unravel the intriguing evolutionary journey of photosynthesis.

When first considering where to look to gain an evolutionary history of photosynthesis, we should examine the origin of the chloroplasts to aid us in finding the nearest relative. Our current model of endosymbiosis is formed from a large array of evidence for a bacterial origin of the chloroplast from both the features of the chloroplast that are common across all of the Plant Kingdom as well as remnant evidence of the endosymbiosis that is present in a few organisms. Expressed features, such as the 70s ribosomes used within the chloroplast as well as the double membrane and similar division mechanisms to bacteria provided the initial evidence for the bacterial origin. However, now with advanced genetic tools, the sequencing of the double stranded circular DNA, reminiscent of bacteria DNA, has revealed that there are prokaryote-like promoters and the DNA sequences are similar to those sequenced in cyanobacteria. This was further verified by the confirmation that E. coli promoters work and have similar functions within the chloroplast. When looking at remnant features, for example the plastocyanin, Reaction Centres (RCs), Light Harvesting Complexes (LHCs) and the primary photosynthetic enzymes (such as RuBisCo) that are retained across the Plant Kingdom. However, there is also evidence gained from looking at specific species where there are features that have not been lost, such as in the glaucophytes where the cell wall has not been lost in chloroplasts, and we can examine its peptidoglycan composition to confirm its lineage. A common feature within the algae group is the evidence for secondary and tertiary endosymbiosis events, where the cell membrane from the endocytosed eukaryote is still visible with a nucleomorph formed from the engulfed redundant nucleus. Upon examining the replication controls within the chloroplast, we can further confirm this hypothesis, as analogous mutations in the same genes cause similar inhibitions to the replication cycle. This is exemplified such as in FtsZ which causes the inhibition in the chloroplast in similar ways to the bacteria and has a similar mechanism within E. coli.

Using this bacterial origin as our basis for our examination of the origins of Plantae photosynthesis, we are able to look to the groups of the photosynthesising bacteria to aid in our understanding of the evolution of the photosystems. The two different pathways and cofactors, combined with phylogenetic analysis, has led to the hypothesis that there are two different lineages of the photosystems that were subsequently linked in the cyanobacteria before the endosymbiosis. The Photosystem II-like (PSII) lineage can be categorised by its use of pheophytin-quinone RCs as seen in the purple bacteria. Similarly to what is seen in PSII, the purple bacteria contain multiple LHCs (LHII proteins) used to capture light energy and pass this on to the primary LHC (LHI) which channels this energy to the central RC. The protein-cofactor pathway that exists within these purple bacteria appears to be conserved, with little modification to the pathway in PSII, with the end effect of the pathway, driving the generation of a proton gradient, being also conserved. The Photosystem I-like (PSI) lineage is also categorised based on its type of RC, with the core components being made from Iron-Sulphur (Fe-S) complexes. One of the relatives to the cyanobacteria that utilise the Fe-S RCs are the green sulphur bacteria, which contain membrane extrinsic proteins which aid in the light harvesting process. There are a few interesting points of note with the green sulfurs however, such as the electron donor is via H2S rather than H2O, and also the metabolic choice between production of reducing power via NAD and ATP synthesis via a proton gradient. These two groups are able to give us an understanding of the likely origins of the two pathways, as well as a model for the linking of the two PSs within the cyanobacteria (the PSII end electron being passed to P870/680 in PSI instead of being cycled back to start of PSII). Looking further back in the phylogenetic history of photosynthesis, we are able to see a very simple form of photosynthesis in halobacteria, where a proton gradient is formed using light energy causing a conformational change in Bacteriorhodopsin which then drives an ATP synthase. This has been suggested to be a precursor for the pathways seen in purple and green sulphur bacteria, where more complexity and efficiency is added via evolutionary change.

In conclusion, the analysis of chloroplast origins and photosystems provides valuable insights into the evolution of photosynthesis, offering a clear evolutionary link between modern plants and photosynthetic bacteria and highlighting the complex journey of photosynthetic pathway development throughout evolutionary history.

Feedback:

- *Overall, I appreciated the general structure of your essay, starting with the endosymbiotic point and tracing back to the origins of PSI and PSII. It* *seems like you grasp the core principles and aim to illustrate them through your narrative.*

- *Your overall structure is somewhat diluted by excessive descriptive and unnecessary words. If you trim down some of the verbose language and aim for precision, your reader will have an easier time understanding your arguments.*
- *In some sections of the essay, I felt there was a lack of depth in understanding the key points about the evolution of photosynthesis. Evolution revolves around adaptation, so it's crucial to explore major adaptive innovations driven by changes in niches and environments.*
- *The final paragraph lacks some impact in demonstrating the tangible benefits of this knowledge, as mentioned in my comments in my last paragraph.*
- *Overall, I would categorise this essay as falling somewhere between a 2i and 2ii, with a slight tendency towards a 2ii, from my perspective.*