

Earth Science/ Geoscience/ Environment
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Early Life

Speaker:

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Title: Origin of photosynthesis and its evolutionary pathway

1. Introduction

Prokaryotic phototrophs, cyanobacteria, can oxidize water using light energy, and which causes evolving oxygen molecules. In the history of life on the Earth, the origin of cyanobacteria is not so old. Prior to the first appearance of oxygenic photosynthesis, photosynthesis without oxygen production, namely anoxygenic photosynthesis, has been established in the bacterial lineage. Such anoxygenic phototrophic bacteria still survive up to now and are frequently found in various environments. They have been taxonomically divided into four groups: filamentous anoxygenic phototrophic bacteria (FAPB), purple bacteria, green sulfur bacteria, and heliobacteria. In addition to them, a new phototrophic bacterium, designated 'Chloracidobacterium' was recently proposed as a representative of the fifth group among anoxygenic phototrophs. Cyanobacteria are known to use two different types of photopigment-containing protein complex, i.e., photosystem I (PS I) and photosystem II (PS II), in their oxygenic photosynthesis, whereas anoxygenic phototrophs possess only one of two photosystems¹⁾. Green sulfur bacteria, heliobacteria and 'Chloracidobacterium' contain a PS I-type photosystem, while FAPB and purple bacteria contain a PS II-type photosystem. In this presentation, I would like to show an evolutionary pathway suggested by phylogenetic analyses based on several gene sequences and comparison of the photochemical structure among the phototrophic bacteria and discuss the origins of anoxygenic and oxygenic photosynthesis.

2. Differential characteristics and distribution of photosystems (PSs)

In cyanobacteria (and also chloroplasts in plants and algae), an electron is pumped up twice by two separate photosystems (PS II and PS I). Although two photosystems are involved in the oxygenic photosynthesis, anoxygenic phototrophic bacteria contain only one of two photosystems. The photosystem found in filamentous anoxygenic phototrophic bacteria (FAPB) and purple bacteria resembles PS II because it contains pheophytins and quinones as electron carriers. However, there is an obvious difference between these photosystems: The oxygen evolving subunit including manganese atoms found in the cyanobacterial PS II is absent in the anoxygenic photosystem²⁾. On the other hand, green sulfur bacteria, heliobacteria and 'Chloracidobacterium' possess a photosystem closely similar to PS I. Iron-sulfur (Fe-S) centers are included as electron transport elements in the photosystem³⁾. This type can directly reduce NADP⁺ (or NAD⁺), because its redox potential is low enough to do it.

3. Evolutionary pathway of photosynthesis inferred from phylogenetic analyses

The following evolutionary pathway is suggested by the phylogenetic analysis based on several gene sequences^{4,5)} and structural comparison of their photosystems:

1) The first appearance of photosynthesis. The ability of photosynthesis has been acquired in the very early evolutionary stage of life. The initial photosystem seems to resemble PS II and is considered as “a photosynthetic system that is sufficient to produce energy but has not been completely adapted to the reductive conditions,” because it cannot directly reduce NAD⁺;

2) The new photosystem that completely adapt to reductive environments. As time went by, a new type of photosynthetic system, PS I-type photosystem, was developed. This type had the advantage of direct reduction of NAD⁺ and efficient flow of electrons, and which probably caused the dominance of PS I-type phototrophs in the ancient microbial ecosystem;

3) Acquisition of oxygenic photosynthesis. To gain oxygenic photosynthesis, it is necessary that two events occurred successively, i.e., establishing coexistence of PS II and PS I in a single cell, and acquiring an oxygen evolving subunit in PS II-type photosystem. The coexistence of two different photosystems was possibly caused by transfer of the photosynthetic genes or fusion of cells. Next to the coexistence of two photosystems, an oxygen evolving subunit was acquired in a PS II-type photosystem. It is quite likely that the cyanobacterial ancestor can afford to evolve the PS II, because the more efficient PSI can support the growth by itself;

4) The influence of evolved oxygen on anoxygenic photosynthetic bacteria. Cyanobacteria have gotten an ability to use water as an electron donor, and were widely distributed all over the world. Consequently, their waste product, oxygen, had been constantly discharged on a global scale, and environments in the early Earth gradually went aerobic. One group of anoxygenic phototrophs, PS II-type phototrophs, could stand the increase of oxygen tension, because their photosynthetic system was not so sensitive to oxygen. The majority of PS II-type phototrophs eventually acquired capacity to respire with oxygen. In contrast, PS I-type phototrophs have never acquired the tolerance to oxygen due to their complete adaptation to reductive environments. They have been still running away from oxygen up to the present.

4. Conclusions

The origin of anoxygenic photosynthesis is clearly much older than that of oxygenic photosynthesis, and a photosynthetic core complex in the first phototroph appeared to be similar to a PS II-type photosystem. In the evolutionary pathway of photosynthesis, a PS II-type phototroph firstly emerged, and then a PS I-type phototroph came out. Oxygenic photosynthesis that appeared next to anoxygenic photosynthesis originated from incorporation of these two different types of photosystems. However, a precise period when the photosynthesis emerged in the early Earth is still controversial.

References

- 1) Olson, J. M. and Pierson, B. K. Evolution of reaction centers in photosynthetic prokaryotes, *International Review of Cytology* 108, 209-248 (1987).
- 2) Michel, H. and Deisenhofer, J. Relevance of the photosynthetic reaction center from purple bacteria to the structure of photosystem II, *Biochemistry* 27, 1-7 (1988)
- 3) Krauss, N., Hinrichs, W., Witt, I., Fromme, P., Pritzkow, W., Dauter, Z., Betzel, C., Wilson, K. S., Witt, H. T. and Saenger, W. 3-dimensional structure of system I of photosynthesis at 6 angstrom resolution, *Nature* 361, 326-331 (1993).
- 4) Xiong, J., Fischer, W. M., Inoue, K., Nakahara, M. and Bauer, C. E. Molecular evidence for the early evolution of photosynthesis, *Science* 289, 724-730 (2000).
- 5) Raymond, J., Zhaxybayeva, O., Gogarten, J. P., Gerdes, S. Y. and Blankenship, R. E. Whole-genome analysis of photosynthetic prokaryotes, *Science* 298, 1616-1620 (2002).