Microbiological Research 186–187 (2016) 99–118

Contents lists available at ScienceDirect

Microbiological Research

journal homepage: www.elsevier.com/locate/micres

Powered by light: Phototrophy and photosynthesis in prokaryotes and its evolution

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ARTICLE INFO

Article history:
Received 21 December 2015
Received in revised form 12 February 2016
Accepted 1 April 2016
Available online 2 April 2016

Keywords:
Carbon fixation
Lateral gene transfer
Phototrophy
Photosynthesis
Photosynthetic bacteria
Photosystems

ABSTRACT

Photosynthesis is a complex metabolic process enabling photosynthetic organisms to use solar energy for the reduction of carbon dioxide into biomass. This ancient pathway has revolutionized life on Earth. The most important event was the development of oxygenic photosynthesis. It had a tremendous impact on the Earth's geochemistry and the evolution of living beings, as the rise of atmospheric molecular oxygen enabled the development of a highly efficient aerobic metabolism, which later led to the evolution of complex multicellular organisms. The mechanism of photosynthesis has been the subject of intensive research and a great body of data has been accumulated. However, the evolution of this process is not fully understood, and the development of photosynthesis in prokaryota in particular remains an unresolved question. This review is devoted to the occurrence and main features of phototrophy and photosynthesis in prokaryotes. Hypotheses concerning the origin and spread of photosynthetic traits in bacteria are also discussed.

Contents

Abbreviations: BChl, bacteriochlorophyll; BPhe, bacteriopheophytin; CBB cycle, Calvin-Benson-Bassham cycle; Chl, chlorophyll; CoA, coenzyme A; cyt, cytochrome; DXP pathway, 1-deoxy-D-xylulose-5-phosphate pathway; FMO protein, Fenna-Matthews-Olson protein; LGT, lateral gene transfer; MK, menaquinone; MVA pathway, mevalonate pathway; PQ, plastoquinone; PSI, photosystem I; PSII, photosystem II; RC, reaction center; RLPs, Rubisco-like proteins; RQ, rhodoquinone; rTCA cycle, reductive tricarboxylic acid cycle; UQ, ubiquinone.

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http://dx.doi.org/10.1016/j.micres.2016.04.001
0944-5013/

1. Introduction

Photosynthesis is a complex metabolic process, in which the energy of light, captured by an elaborate system of pigment-containing proteins, is used for the reduction of CO_2, which is an essential step in the biosynthesis of organic compounds. As photosynthesis uses the most abundant energy source available on Earth, it is the most important biochemical process in biological production on our planet (Bryant and Frigaard, 2006). The first living organisms used organic compounds supplied by meteorites or produced by chemical reactions. Chemosynthetic processes enabled biochemical carbon fixation, but they are strictly dependent on specific substrates and their efficiency is low (Sleep and Bird, 2008; Sleep, 2010). Photosynthesis allowed living organisms to exceed these limitations, the Sun supported energy, whereas reduced compounds needed as electron donors were available in primeval oceans (Sleep and Bird, 2008). The most pronounced event was the development of oxygenic photosynthesis, where water is an electron donor and molecular oxygen is formed as a byproduct. Over millions of years, oxygenic phototrophs dramatically changed the composition of the Earth's atmosphere and geochemistry (Dismukes et al., 2001). The rise in atmospheric O_2 created a niche for the development of the aerobic metabolism. Highly efficient aerobic processes enabled the evolution of complex multicellular organisms (Grula, 2005). Photosynthetic organisms have introduced biomass into ecosystems, created an environment not only for themselves, but also for heterotrophic ones. Life on Earth has been shaped and powered by photosynthesis.

Photosynthesis has been widely examined and its molecular mechanism is well known, especially in the case of oxygenic photosynthesis. Nevertheless, the origin and evolution of this process is not yet fully understood. Due to geological processes, rocks older than 3.8 Ga (giga-annum 1×10^9 years ago) have not been preserved unchanged (Sleep, 2010). Moreover, the available microfossils are not easy to interpret (Xiong, 2007). Modern bioinformatics provides us a useful tool for gene and genome comparisons, which could help us to elucidate the evolution of photosynthetic organisms. However, lateral gene transfer (LGT) is a major complicating factor. The image we got is blurred and very difficult to interpret (Xiong, 2007). The ability to perform photosynthesis is a trait present in distinct phyla of bacteria and eukaryotes (Hohmann-Marriott and Blankenship, 2011). The evolution of prokaryotic photosynthesis is a controversial question and there are a lot of contradictory hypotheses (Xiong, 2007). In this article we concentrate on prokaryotic organisms, present and compare information about prokaryotic photosynthesis and phototrophy and discuss recent hypotheses concerning its evolution in bacteria.

2. History of photosynthesis

In research into the history of photosynthesis, the most important approaches are the analysis of the fossil record, biochemical markers, also called biomarkers, and isotopes present in ancient rocks. Fossil records of microorganisms are rather poor and difficult to interpret, especially when it comes to speculation on the type of metabolism harbored by ancient bacteria (Buick, 2008). The analysis of carbon isotopes can be used to discriminate between biological carbon fixation and inorganic processes leading to the accumulation of sediments enriched in carbon, whereas the analysis of sulfur isotopes is used for the determination of oxygenation events (Buick, 2008; Olson and Blankenship, 2004). Geological analyses of deposited minerals are also useful as indicators of the presence of O_2 in the environment, because some metals, such as Fe and Mn, in the oxidized state form insoluble minerals. The appearance of significant amounts of O_2 in the environment caused a massive deposition of such minerals (Buick, 2008). Molecular biomarkers are compounds typical of known systematic groups of modern organisms (Knoll et al., 2007). Hydrocarbon skeletons of lipids in particular can be preserved over long periods of time (Falkowski et al., 2004).

The oldest sedimentary rocks have undergone a metamorphosis which has led to a significant alteration and destruction of fossil records. Rocks harboring carbon signatures typical of biological carbon fixation have been found in Greenland and dated to 3.8 Ga. However, other scientists claim that such a composition of carbon isotopes could result from abiotic processes (McCollom and Seewald, 2006). What is more, different carbon fixation pathways differently influence the composition of organic carbon. A well known preference for ^{12}C is typical of carbon assimilation via the Calvin cycle, whereas the 3-hydroxypropionate pathway, present in green filamentous bacteria, produces organic carbon enriched in ^{13}C when compared to that fixed by Rubisco (van der Meer et al., 2000). Interestingly, recent studies on nitrogen isotopes in sedimentary rocks indicate the early emergence of another process crucial for the evolution of life, biological N_2-fixation, at 3.2 Ga (Stüeken et al., 2015).

In the fossil record, stromatolites are very important structures. Extant "living" stromatolites consist of alternate layers of mat-forming microorganisms and sediment. They are almost always formed by both cyanobacteria and green filamentous bacteria (Olson and Blankenship, 2004). However, it is not certain if ancient stromatolites were formed by oxygenic phototrophs. Fossil stromatolites, occurring in 3.5 Ga and 3.2 Ga old rocks, have been thought to be of cyanobacterial origin, but the dating of some has been questioned and there is controversy about their origin being truly biotic (Buick, 2008; Grotzinger and Knoll, 1999; Schopf, 2006). Other fossils, 3.4 Ga-old cherts are thought to be remnants of microbial mats formed by filamentous anoxygenic photosynthetic organisms, probably using hydrogen as an electron donor (Tice and Lowe, 2006). The more convincing fossil stromatolites are 2.8 Ga old. Since that time there is a continuous record of these structures (Olson and Blankenship, 2004). Stromatolites from 2.7 Ga were postulated to have been built by oxygenic phototrophs, as they developed in an environment lacking hydrothermal activity, which would have supplied substrates for anoxygenic photosynthesis (Buick, 1992). The specific structure of so called conical stromatolites, contorted or discontinuous laminae in the crestal zone and the presence of fossil bubbles, was postulated to result from O_2 production by stromatolite-forming microorganisms. There are conical fossil stromatolites dating to 2.7 Ga (Bosak et al., 2009). Large stromatolitic reefs dating to 2.5 Ga are thought to have been created by microorganisms performing oxygenic photosynthesis. There are also cyanobacterial microfossils dating back to 2.5-2.6 Ga and older, but more putative sedimentary structures from 2.9 Ga (Butterfield, 2015; Posth et al., 2013).

Biomarker analysis seems to support the presence of cyanobacteria 2.7 Ga ago as 2-methylhopanoids typical of this phylum were found in 2.5-2.7 Ga-old rocks (Brocks et al., 1999; Summons et al., 1999). However, the specificity of hopanoids for cyanobacteria and dating of the samples have been questioned (Blank and Sánchez-Baracaldo, 2010; Posth et al., 2013). Other important biomarkers are steranes, because their modern biosynthetic pathways demand O_2. The presence of steranes in the geological record is thus considered a sign of the presence of O_2 in the environment. However, it was hypothesized that ancient microorganisms could use an alternative O_2-independent sterane biosynthetic pathway. On the other hand, there is no current organism known to use such a pathway (Buick, 2008; Knoll et al., 2007). Biomarkers typical of green sulfur bacteria (chlorobactene and isorenieratene) and purple bacteria (okenone) have been found in materials dating back to 1.64 Ga (Brocks et al., 2005). Abundant isorenieratene and aryl isoprenoids were found in rocks deposited at the Permian-Triassic boundary