

論文の内容の要旨

論文題目 : **Theoretical modeling and phylogenetic analysis of cyanobacterial promoters regarding the rise of atmospheric oxygen in the Paleoproterozoic**

(原生代初期における大気酸素濃度上昇に関する理論研究と
シアノバクテリアのプロモーター分子系統解析)

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The early Palaeoproterozoic is a remarkable period in the Earth's history, marked by the rise of atmospheric oxygen, snowball glaciation, and the evolution of life. Geochemical studies suggest that the rise of oxygen was a transition from oxygen poor to oxygen rich steady states of the atmosphere, accompanied with an overshoot. However, the trigger for the transition has been unclear, leaving its linkage to the snowball glaciation and consequences to the biological evolution poorly understood.

In the first half this thesis (Chapter 2), the trigger for the rise of oxygen was discussed by numerical calculations using biogeochemical cycle models. In this study, I focus on the climate jump at the end of the snowball glaciation at ~2.2 Ga as a trigger for the rise of oxygen. Calculation results suggest that the super-greenhouse conditions after the deglaciation caused intense nutrient riverine input to the oceans via chemical weathering. In the nutrient-rich oceans, the bloom of cyanobacteria caused the massive release of oxygen into the atmosphere and the burial of organic carbon into the sediments. The large perturbations in the carbon cycles result in a rapid transition from oxygen-poor ($< 10^{-5}$ PAL, PAL: Present Atmospheric Levels) to oxygen-rich ($> 10^{-2}$ PAL) conditions within $\sim 10^4$ years after the deglaciation. The transition is followed by an overshoot of oxygen to 0.1–1 PAL lasting for 10^6 – 10^8 years. The magnitude and time scale of the overshoot vary depending on the initial and boundary conditions. However, only under the conditions assuming typical “hard snowball” Earth scenario, an extensive and long-term overshoot (~ 1 PAL lasting for $\sim 10^8$ years) occur. Such an extensive overshoot causes the oxidation of deep oceans and the long-term

accumulation of oceanic sulphate ions, which are in good agreement with the geochemical records. Therefore, in this study, I suggest that the oxygen transition in the Palaeoproterozoic was accompanied with an extensive overshoot to ~ 1 PAL, and the snowball glaciation would be a strong candidate as the trigger for the rise of oxygen.

In the second half of the thesis (Chapter 3), the phylogenetic analysis of cyanobacteria was performed in order to estimate the consequences of the rise of oxygen to the biological evolution. Contrary to previous studies that have mainly discussed the evolution of morphologies and habitat of cyanobacteria, this study focuses on the evolution of the gene expression levels of oxygen catalysing enzymes, which would be a good indicator that can be directly correlated to the changes in environmental oxygen levels. The ancestral sequences of DNA that regulates gene expression levels (i.e., promoter sequences) of RubiCO (ribulose 1,5-bisphosphate carboxylase/oxygenase) and Fe-SOD (Fe-superoxide dismutase) were obtained from phylogenetic analysis. In order to estimate the gene expression levels, the obtained sequences were compared to the promoters of genes that are highly expressed (rRNA and ribosomal proteins). The results show that the similarity between ancestral sequences of Fe-SOD promoters and the promoters of highly expressed genes have been low at the time of the emergence of cyanobacteria. The similarity increased at the branching nodes diverged at 2.5–2.0 Ga, which roughly coincided with the rise of atmospheric oxygen reported from geochemical records. This implies that the gene expression levels of Fe-SOD increased in response to the rise in atmospheric oxygen. In contrast, the results suggest that the gene expression levels of RubsiCO have been continuously high through history, independent on the changes in the oxygen levels. Such discrepancies imply that, regarding the carbon fixation catalysed by RubsiCO, the adaptation to the oxygen-rich conditions might have been compensated by the evolution of biochemical characteristics other than gene expression, such as the improvement of the activity of the enzyme. Though improvement would be required in future works, I suggest that methodologies of ancestral promoter analysis developed in this study will become novel tools that provide the evidence of the biological evolution in response to the environmental changes in the Earth's history.

In this dissertation, relationships among three major events in the Palaeoproterozoic: the rise of atmospheric oxygen, snowball glaciation, and the evolution of life were studied by numerical

calculation and phylogenetic analysis. I propose that the cyanobacterial bloom after the snowball deglaciation triggered the rise of oxygen and that the rise of oxygen caused the adaptive evolution of cyanobacteria. This would be the first study to provide a comprehensive view regarding the environmental and biological phase changes in the Palaeoproterozoic, suggesting the occurrence of interaction between the climate, chemical composition of atmosphere-ocean system, and biosphere.