Evolutionary origin of the eukaryotic cellular membrane and its geobiological implications

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The emergence of the modern eukaryotic cellular membrane system was a crucial step for a proto-eukaryotic cell to perform endocytosis and hence acquire organelles such as mitochondria and chloroplasts during eukaryogenesis. Steroids are indispensable components of the eukaryotic cellular membrane and have important roles in the process of endocytosis. Steroids are characteristic of eukaryotic organisms and hence have been utilized as biomarkers for eukaryotes in the Precambrian geological record. It had generally been considered that steroids were invented by eukaryotes and the steroid production in several bacteria is a result of horizontal gene transfers from eukaryotes. However, more bacteria have been found to possess the steroid biosynthesis pathway and the traditional understanding of the steroid evolution is now called into question.

Our genomic analysis suggests that the entire eukaryotic isoprenoid biosynthesis pathway, including the steroid biosynthesis, is derived from bacteria. Almost all genes that are involved in the steroid biosynthesis up to cholesterol are inferred to have evolved within the bacterial domain. However, the evolutionary trajectory for individual genes seems to be different from one another. Hence, the evolution of the eukaryotic isoprenoid biosynthesis pathway is inferred to have been a multi-step process. Further, the evolution of eukaryotic-type isoprenoid biosynthesis pathway may have been an adaptation towards aerobic environments that emerged after the Great Oxidation Event. An aerobic group of δ-proteobacteria (myxobacteria) and eukaryotes have recently been suggested to have an evolutionary link in terms of the steroid biosynthesis [1]. Our current analysis suggests that part of the eukaryotic-type isoprenoid biosynthesis pathway may already have evolved before the emergence of myxobacteria within δ-proteobacteria in response to the rise of oxygen.

[1] Lee et al. (2018) *PNAS* **115**, 5884-5889.