## The Rise of Algae in Cryogenian oceans and the emergence of animals

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Molecular clocks place the origin of primary endosymbiotic algae (Archaeplastida) into the time range ~1,700 to 1,400 million years (Ma) ago. Yet, as phytoplankton rarely leaves a fossil record, it remains unknown when Archaeplastida, comprising the green (Chlorophyta), red (Rhodophyta) and glaucophyte algae, started to play an important ecological role in the open marine realm. Yet, the transition from dominant bacterial to eukaryotic marine primary productivity was one of the most profound ecological revolutions in Earth's history, reorganizing the distribution of carbon and nutrients in the water column and increasing energy flow to higher trophic levels. The causes and geological timing of this transition, as well as possible links with rising atmospheric oxygen levels and the evolution of animals remain obscure.

We present a molecular fossils record of eukaryotic steroids demonstrating that bacteria were the only significant primary producers in the oceans prior to the Cryogenian (720-635 Ma). Increasing steroid diversity and abundance mark the rapid rise of primary endosymbiotic algae in the narrow time interval between the Sturtian and Marinoan Snowball Earth glaciations, 659-645 Ma ago. We propose that the incumbency of cyanobacteria was broken by a surge of nutrients supplied by the Sturtian deglaciation. The 'Rise of Algae' created shorter food webs with more efficient nutrient and energy transfers, driving an escalatory arms race towards larger and increasingly complex organisms, an effect recorded by the concomitant appearance of biomarkers for sponges and predatory rhizarians, and the subsequent radiation of eumetazoans in the Ediacaran.

The corrected record of fossil steroids demonstrates that algae only broke the incumbency of phototrophic bacteria as the principal marine primary producers during the inter-Snowball period of the Cryogenian. This new timeframe offers a network of explanations for a Neoproterozoic / Palaeozoic rise in atmospheric oxygen levels, establishment of more modern nutrient and carbon cycles, and the evolution of an increasingly complex biota. We propose that the radiation of algae in late Cryogenian and early Ediacaran marine ecosystems was the bottom-up driver for the evolution of eumetazoan animals.