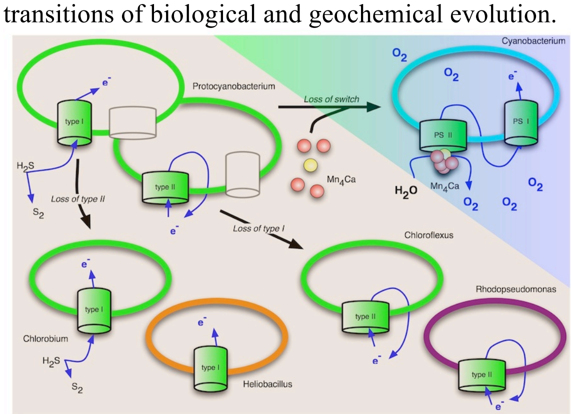
ON THE EVOLUTIONARY ORIGIN OF OXYGENIC PHOTOSYNTHESIS. John F. Allen, Research Department of Genetics, Evolution and Environment, University College London, Gower Street, London, WC1E 6BT, U.K. j.f.allen@ucl.ac.uk

Hypothesis: The redox switch hypothesis for the first cyanobacterium proposes that the immediate antecedent of cyanobacteria was an anoxygenic photosynthetic bacterium containing genes for both type I and type II photochemical reaction centres [1]. These genes were never expressed at the same time. Instead, they were switched on and off by redox state, permitting growth either with or without H_2S as the electron donor for photosynthesis.

Such a bacterium may have flourished in the Archean eon, prior to the origin of the cyanobacteria to which it gave rise. Photosynthetic oxygen evolution then resulted of the coincidence of two unusual events: (i) failure, by mutation, of the redox genetic switch; (ii) acquisition of outer-membrane-bound manganese and calcium, with manganese oxidation coupled to re-reduction of photooxidised chlorophyll [2,3]. These events complemented each other, conferring a novel and unstoppable selective advantage — water as the source of electrons for photosynthesis.

The reaction product, free molecular oxygen, is inhibitory to carbon and nitrogen fixation. Oxygen nevertheless became the respiratory electron acceptor of choice for subsequent life. Its advent drove major transitions of biological and geochemical evolution.



The proposed protocyanobacterium (top left) retains the ability to switch between a *Chlorobium*-like, type-I photosynthetic reaction center, and a *Rhodopseudomonas*-like, type-II photosynthetic reaction center. If either reaction center becomes permanently switched off, its genes are lost. This process may have given rise to the familiar, anoxygenic species, represented in the diagram by *Chlorobium* and *Heliobacillus* (type I), and *Chloroflexus* and *Rhodopseudomonas* (type II). A mutation in the redox switch allows the two photosystems to co-exist in the same membrane at the same time. With a catalyst that oxidizes water to oxygen, the two photosystems become complementary, and together begin to use light to drive oxygen evolution by the first true cyanobacterium (top right).

Prediction: The proposed protocyanobacterium, an anoxygenic bacterium with genes for both type I and type II reaction centers, may have identifiable living descendants [4]. Their modern habitat is predicted to be:

- freshwater
- anoxic
- low light intensity, where the lower quantum yield of oxygenic photosynthesis confers a selective disadvantage
- one with fluctuating concentrations of H_2S.
- one with a solid substrate for growth of sequential layers of photoautotrophic and photoheterotrophic cells or biofilms.

References: [1] Allen J. F. (2005) *FEBS Lett. 579,* 963-968. [2] Allen J. F. and Martin W. (2007) *Nature 445,* 610-612. [3] Russell M. J. et al. (2008) *In: Allen J. F. et al. (eds) Photosynthesis. Proc 14th Intl. Congr. Photosynth. Springer.* pp. 1187–1192. [4] Allen J. F. (2014) *In: Golbeck J. H. and van der Est, A. (eds) Biophysics of Photosynthesis. Biophysics for the Life Sciences, Vol.11, Part V.* Springer. pp. 433-450.