Dating the Origins of Cyanobacteria: Solving Stem Lineage Problems using Reticulate Evolution

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Cyanobacteria are one of the most important microbial groups in planetary history, as the originators of oxygenic photosynthesis, and the source of biogenic O_2 production leading up to the Great Oxygenation Event (GOE) ~2.33 Ga. Additional geochemical and physical evidence further suggests that cyanobacterial O_2 production may have been present much earlier, possibly as early as 3.2 Ga. As oxygenic photosynthesis is a shared character among all members of Cyanobacteria, it must have evolved before the diversification of extant (crown) cyanobacteria, at some point within the ancestral stem lineage. Dating the emergence of characters within a lineage in the absence of clear fossil stem groups is a notoriously hard problem in paleontology. Previous efforts to date the diversification of crown Cyanobacteria using calibrated molecular clocks have resulted in poorly constrained estimates, typically between 3.5 and 2.5 Ga. We present a new estimate using three methodological improvements with relation to the cyanobacterial stem: (1) inclusion of bacterial outgroups containing additional age constraints and permitting more precise root prior mapping; (2) re-assessment of the cyanobacterial microfossil record via simulations testing the internal consistency with root prior distributions from (1); and (3) the inclusion of proxy outgroups via HGT events to the cyanobacterial stem from methanogens and chloroflexi, respectively. Using these methods, we consistently recover an age for crown Cyanobacteria close to the time of the GOE itself, with a most likely age within 2.3 – 2.7 Ga, and almost certainly younger than 3.1 Ga. These dates indicate a substantial interval of geological time elapsing between the invention of oxygenic photosynthesis and the diversification of extant Cyanobacteria. These dates are also consistent with a scenario in which early diversification of Cyanobacteria is coincident with the GOE itself, and may explain the rapid increase of atmospheric oxygen via ecological and physiological expansion of cyanobacterial metabolic activity. We highlight that these age estimates were reached without the use of GOE-based geochemical date calibrations, and argue that using such calibrations is problematic. Finally, we speculate on the plausibility of the evolution of thylakoid membranes and circadian clock proteins between the divergence of *Gloeobacter* and other extant cyanobacterial groups being key innovations driving the rise of oxygen at the GOE.