

## The pattern and timing of cyanobacterial diversification: Molecular-phylogenetic and paleontological perspectives.

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Cyanobacteria have played a significant role in earth's history as primary producers and the ultimate sources of atmospheric oxygen. Accordingly, an understanding of the cyanobacterial evolution provides a key to the elucidation of early biological and environmental history. In tandem, paleontology and molecular phylogeny provide constraints on the timing and pattern of cyanobacterial diversification.

16S rRNA, rbcL and hetR genes were isolated from 21 strains of cyanobacteria distributed among 16 genera, with particular care taken to represent the known diversity of filamentous taxa. Phylogenetic trees constructed by multiple methods support the hypothesis that cyanobacteria capable of cell differentiation (heterocysts and akinetes) form a monophyletic clade among undifferentiated filaments and coccoid forms. The phylogenies also support the view that the Stigonematales, traditionally recognized as heterocystous cyanobacteria with complex branching patterns, are nested within the broader grouping of heterocyst- and akinete-bearing taxa.

The geological record may provide both upper and lower boundaries on the origin of heterocystous cyanobacteria. Akinetes are common in ca. 1,500 Ma cherts from tidal flat carbonates of the Billyakh Group, Siberia. Rare but probable akinetes have been identified here in silicified carbonates of the ca. 1,650 Ma Amelia Dolomite, northern Australia, where they occur with other microfossils representing a broad cross-section of cyanobacterial diversity. The earliest possible akinetes yet known are preserved in 2000 Ma Francevillian cherts from West Africa. Geochemical evidence suggests that oxygen first reached levels that would compromise nitrogen-fixation (and hence select for heterocyst differentiation) 2,400-2,200 Ma. Taking the molecular phylogenies into consideration, the origination of heterocyst- and akinete-bearing cyanobacteria might have occurred once between 2,400 Ma and 2,000Ma.