

Bacteria as the powerhouse of mid-Proterozoic ecosystems

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The oceans of the mid-Proterozoic, 1.8 to 0.8 Ga ago, were devoid of animal-like life. According to some models, this lack of large multicellular heterotrophs may be connected to a global limitation of nutrients, and thus lack of efficient food sources at the base of the food chain [1,2]. Here we present evidence based on fossil chlorophylls and other biomarkers that mid-Proterozoic marine ecosystems were dominated by oxygenic and anoxygenic phototrophic bacteria. By contrast, larger eukaryotic algae, representing a more efficient carbon and energy source, remained ecologically insignificant well into the Neoproterozoic.

Porphyrins are the molecular fossils of chlorophylls, light capturing pigments in phototrophs. Using a 9.4 Tesla FT-ICR mass spectrometer, we detected porphyrins in 1,100 Ma old marine black shales from Mauritania, 600 million years older than previous findings [3]. Notably, compound-specific porphyrin nitrogen isotopic compositions ($\delta^{15}\text{N}_{\text{por}} = 5.6$ to 10.2‰) were heavier than in most modern sediments, and the isotopic offset ϵ_{por} between sedimentary bulk nitrogen and porphyrins (-5.1 to -0.5‰) was lower than in any other ancient sedimentary sequence. The low ϵ_{por} values point to predominantly cyanobacterial primary production, while fossil carotenoid pigments highlight a notable contribution by anoxygenic phototrophic bacteria. Moreover, sterane/hopane ratios were beneath the detection limit of $\text{S/H} < 0.001$ to 0.0002 , demonstrating that algae did not play a detectable role in this ancient ecosystem. The data, in combination with S/H ratios across the mid-Proterozoic, support the view that low particle size, and thus inefficient energy transfer from the base of the food web to higher trophic levels, contributed to a low evolutionary drive towards complex multicellularity and large size.

[1] Brocks, J.J. (2018) *Emerging Topics in Life Sciences*, 10.1042/etls20180039. [2] Brocks, J.J., Jarrett, A.J.M., Sirantoine, E., Hallmann, C., Hoshino, Y., Liyanage, T., (2017) *Nature* 548, 578–581. [3] Gueneli, N., McKenna, A.M., Ohkouchi, N., Boreham, C.J., Beghin, J., Javaux, E.J., Brocks, J.J. (2018) PNAS, 10.1073/pnas.1803866115.