Goldschmidt 2024 Abstract
https://doi.org/10.46247/gold2024.22863

Impacts of Ancient Iron-Rich Environments on Methanogenesis of the Methanogen *Methanococcus maripaludis*

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Methanogens, the most ancient group of extant organisms, require Fe-S clusters for their metabolism, more so than other organisms, but their growth is more dependent on S than on Fe. Methanogens witnessed a transition from the Archaean ferruginous ocean (Fe^{2+}-rich) to the Late Proterozoic and Neoproterozoic sulfidic ocean (HS^--rich). This raises a question as to how methanogens coped with high Fe levels in the Archaean oceans and maintained a high CH_4 productivity. In this study, we synthesized Mackinawite under rich-Fe^{2+}&low-HS^- (i.e., all S in mackinawite with some aqueous Fe^{2+}) and low-Fe^{2+}&rich-HS^- (i.e., all Fe in mackinawite with excess aqueous S) conditions, which is readily formed by meeting Fe^{2+} and HS^-, as the Fe and S sources of a presentative methanogen *Methanococcus maripaludis*. These two conditions did not result in any difference in methane production. Under transmission electron microscopy (TEM), black nanoparticles were only observed inside the cells under rich-Fe^{2+}&low-HS^- condition, hinting the cells may have assimilated S from mackinawite nanoparticles. TEM-EDS and Nano-SIMS analyses confirmed that the composition of these particles is Fe and S. Transcriptome results showed that transmembrane transport related genes were downregulated, including genes associated with iron (III), ammonia, molybdenum, and other transport proteins. Proteomic results revealed energy metabolism related proteins were upregulated, including oxidoreductases such as methyl coenzyme M reductase (Mcr), Fe-S flavoprotein and hydrogenase, which are iron-sulfur proteins. These findings suggest that methane production was unaffected by the relative concentrations of Fe^{2+} and HS^- concentrations. In the Fe^{2+}-rich Archean oceans, methanogens can acquire S from mackinawite nanoparticles. Transcriptomic and proteomic data suggest that transmembrane genes were downregulated to impede excess nanoparticle uptake, while upregulation of energy-related proteins ensured growth and metabolism. These findings elucidate the adaptive strategies of methanogens to ancient Earth environments and the biological mechanisms that sustain methane production under iron-rich condition.