## Correlations of magnetosome-related genes in Nitrospirae genomes to magnetosome geometry and redox stratification in deep-sea environments

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Biogenic magnetic particles are ubiquitously found in deep-sea sediments and important carriers of rock magnetism for reconstructing the Earth' s past regarding sediment age and geomagnetic field. However, microorganisms responsible for the formation of magnetic particles are largely unknown in the deep-sea environment, because of the difficulty in sampling, cultivation, and magnetic separation of magnetotactic cells for single-cell genomics. In this study, deep-sea sediments from Japan Sea and a metal sulfide chimney from South Mariana Trough were subjected to magnetic separation and subsequent electron microscopic observations. Although teardrop-shaped magnetite (Fe<sub>3</sub>O<sub>4</sub>) particles without microbial cells and 16S rRNA gene sequences related to magnetotactic Nitrospirae species were previously obtained from Japan Sea sediments with a redox zonation enriched with dissolved Fe(II) (the iron boundary), no magnetotactic cells were observed after the magnetic separation. From the metal sulfide chimney, magnetotactic cells were observed with teardrop-shaped magnetite particles. Metagenomic analysis of the chimney sample revealed that contig sequences encoding genes involved in the formation of magnetosome, membrane-bound magnetic particles, were mostly affiliated within Nitrospirae based on sequence similarity. Previous studies have reported that magnetosome-related genes are clustered together as the magnetosome island (MAI) in known magnetotactic bacteria. However, those genes were scattered in a near-complete Nitrospirae genome reconstructed from the chimney sample. Although magnetotactic bacteria are generally considered to align magnetic particles into a chain for efficiently moving in a vertical redox zonation by orienting the cell along the geomagnetic filed, Nitrospirae-affiliated genes involved in chain formation were not found in the near-complete Nitrospirae genome from the chimney with a horizontal redox zonation. Comparative analysis of near-complete Nitrospirae genomes available from public databases revealed that the chain-related genes were found in the genomes from terrestrial deep aquifers and deep-sea sediments with a vertical redox zonation. As the Nitrospirae species associated with teardrop magnetite and the iron boundary in Japan Sea was closely related to Nitrospirae species with the chain-related genes, the presence of the chain-related genes appears to be correlated with a vertical redox zonation. In addition, our results suggest that the Nitrospirae species without MAI are responsible for the production of teardrop magnetite in deep-sea environment, and that teardrop magnetite is a paleoredox indicator especially for the iron boundary.

Keywords: magnetotactic bacteria, metal sulfide chimney, magnetofossil, remnant magnetization