Magnetic foraminifera thrive in the Mariana Trench

H. Yang1,2, X. Peng1*, A.J. Gooday3,4, B. Jones5, J. Li1, S. Liu6, W. Huang7, Z. Sun8, S. Chen1, S. Dasgupta1, H. Xu1, S. Liu1, W. Xu1, K. Ta1

Abstract

Unicellular magnetic microorganisms include magnetotactic bacteria and some protist species. Although magnetosome magnetite in bacteria (prokaryotes) is well studied, little is known regarding the characteristics and origin of magnetic minerals in protists (eukaryotes). Stercomata stored within tests of the hadal foraminifera R. bilocularis from the Mariana Trench (6980–10,911 m depth), contain magnetite crystals. As a result, this species can orient in accordance with magnetic fields. The magnetite differs chemically and physically from that in the surrounding sediments. The crystals also differ from bacterial magnetosomes in being of variable size, porous structure, not arranged in chains, and encapsulated in a lipid membrane. Putting available evidence together indicates a biological origin of the magnetite, although a sedimentary source cannot be eliminated. This is the first record of a magnetic protist from hadal depths, opening a new window for the biomagnetism in the Earth’s extreme environment.

Introduction

Biogenic magnetite occurs inside magnetotactic bacteria (Mann et al., 1984) and some protists (algae and protozoa) (Bazylinski et al., 2012; Leão et al., 2020; Monteil and Lelevre, 2020), the latter including a number of biflagellates, dinoflagellates, and ciliates, as well as multicellular animals (insects, molluscs, fish, birds, and mammals) (Frankel, 1984; Kirschvink et al., 2001). In these organisms, magnetite facilitates magnetic field detection, making it possible for them to orientate and navigate (Maugh, 1982; Andrews et al., 2003). Bacteria and protists are particularly important in this regard, because their simple structure and wide distribution in various aquatic environments facilitates the study of biogenic magnetic formation and magnetotaxis (Bazylinski and Frankel, 2004; Bazylinski et al., 2012; Leão et al., 2020). Although the synthesis of magnetite nanoparticles in magnetotactic bacteria is well studied (Uebe and Schüler, 2016), the formation mechanisms of magnetite and its physiological functions in eukaryotic protists remain largely unknown.

Several protistan taxa, including diplomnemids, kinetoplastids, ciliates, and foraminifera (Todo et al., 2005; Schoenle et al., 2021), have been reported from abyssal plains and hadal trenches, where they probably play a critical role in carbon cycling (Schoenle et al., 2021). Foraminifera are among the most common meiofauna-sized organisms at hadal depths greater than 6000 m. Between 2016 and 2019, exploration by the R/V TANSLUOYIHAO (Table S-1) at 11 stations in the southern Mariana Trench at water depths between 6980 and 10,911 m, recovered numerous specimens of the organic walled species R. bilocularis from the surface sediments. This species, which had been described earlier from the Mariana Trench (Gooday et al., 2008) and is currently classified within the foraminifer class Monothalamidae (‘monothalamids’), was found to be highly magnetic (Fig. 1a,b).

Results

Response of foraminifera to magnetic fields. All R. bilocularis specimens in a sample of 1000 observed in this study showed varying degrees of passive response to the applied magnetic field (Video S-1). A magnetite enrichment experiment based on 1000 R. bilocularis showed that each specimen contained an average of 1020 ng of magnetite. Analyses of the single cell magnetic dipole moment of 31 R. bilocularis using a miniaturised atomic magnetometer revealed that their magnetic response is based on a permanent magnetic dipole moment (M) per cell, which ranged from $1.10 \times 10^{-14}$ to $1.51 \times 10^{-11}$ J/T. The ratio of magnetic to thermal energy, $MB/k_B T$, calculated from the average upper limit

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1. Laboratory of Deep-Sea Geology and Geochemistry, Institute of Deep-Sea Science and Engineering, Chinese Academy of Sciences, Sanya, 572000, China
2. University of Chinese Academy of Sciences, Chinese Academy of Sciences, Beijing, 100049, China
3. National Oceanography Centre, European Way, Southampton SO14 3ZH, UK
4. Life Sciences Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK
5. Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada
6. State Key Laboratory of Lithospheric Evolution, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China
7. Beijing Synchrotron Radiation Facility, Institute of High Energy Physics, Chinese Academy of Sciences, Beijing, China
8. Jiangsu Key Laboratory of Medical Optics, Suzhou Institute of Biomedical Engineering and Technology, Chinese Academy of Sciences

* Corresponding author (email: xtpeng@idsse.ac.cn)

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of M for the foraminifera, is $9.974 \times 10^4$ (Table S-2). The magnetic energy of *R. bilocularis* is therefore obviously much greater than the thermal energy.

**Characteristics of magnetite in foraminifera.** Tests of *Resigella bilocularis* contain numerous stercomata (Fig. 1a,b), waste pellets that are also present in many other hadal monothalamid foraminifera (Gooday et al., 2008). Scanning electron microscopy (SEM), light microscopy and confocal laser scanning microscopy (CLSM) observations revealed multiple particles contained in the stercomata, but absent in the cytoplasm (Fig. 1c,d; Fig. S-1a,b; Fig. S-2; Fig. S-3a,b; Fig. S-4a). They are of variable size (0.15–12 μm) and not arranged in chains (Video S-2, Fig. 2c). These euhedral magnetite particles are octahedral and exhibit a porous structure (Fig. 1g–i). Secondary ion mass spectrometry (NanoSIMS) and SEM-based energy dispersive X-ray spectroscopy (EDX) revealed that they are mainly composed of Fe and O (Fig. 1e; Fig. S-4c; Fig. S-5b). Raman spectroscopy analyses further showed that they are magnetite particles (Fig. S-4b; Fig. S-6a; Fig. S-7f–h), which are commonly encapsulated by lipid membranes (Fig. 1g,j;k; Fig. 3; Fig. S-3). This is consistent with the results of synchrotron phase contrast analysis experiments showing intact porous magnetite inside stercomata (Fig. 2e; Fig. S-1e–l). The magnetic properties of the foraminifera therefore clearly originate from these micron-sized magnetite particles.

**Comparison of magnetite within foraminifera with that from sediments.** The magnetite crystals in the stercomata of *R.
bilocularis differ in a number of respects from magnetite found in the surrounding hadal sediments. First, they commonly have an octahedral and porous structure (Fig. 1g–i), whereas magnetite in the environmental sediment has an irregular shape, smooth surfaces (Fig. S-8a) and a larger particle size (Fig. S-9; Fig. S-10). Second, magnetite particles within the foraminifera are wrapped in an organic envelope, in contrast to those from surrounding sediments, which lack this feature (Fig. 1e–k; Fig. S-3). Third, EDX analyses of magnetite particles from foraminifera demonstrated that they contain no inclusions, whereas silicate-like, magnesium oxide-like, and chrome-aluminum oxide-like inclusions are present in the magnetite from sediments, a feature shared with hydrothermal and magmatic magnetite (Ciobanu et al., 2019)(Fig. S-11; Fig. S-12). Fourth, a magnetic property measurement system (MPMS) yielded a lower transition temperature (104 K) for the foraminiferal magnetite than the magnetite from sediments (111 K) (Fig. S-13).

**Discussion**

**Origin of magnetite in R. bilocularis.** The porous structure in non-biogenic magnetite generally occurs during the terrestrial weathering of magnetite to hematite (Anand and Gilkes, 1984), or as a result of the formation of magnetite during the reduction of hematite in the solid phase (Deo et al., 1989). The magnetite in R. bilocularis did not contain any hematite that would be produced during the weathering of magnetite or left as a residue during the reduction of hematite. Hence, it is not likely that the porous structure associated with magnetite in R. bilocularis originates from the weathering (i.e. corrosion) of magnetite or the reduction of
hematite. The euhedral structure of magnetite from *R. bilocularis*, which distinctly differs from the irregular shape of magnetite from sediments, also indicates that they might have different origins. The porous structure is possibly formed due to the incorporation of organic matter into the magnetite during the formation process, as indicated by SEM-EDX analyses (Fig. S-5). The formation of minerals with porous structures due to the involvement of organic matter is also a common feature of biologically induced mineralisation (Sanz-Montero et al., 2009).

The differences between the magnetite in *R. bilocularis* stercomata and the magnetite from surrounding sediments further suggests that the former may be produced within the foraminifera, as also reported for certain other protists (Leão et al., 2020). Foraminiferal magnetite is encapsulated by a lipid membrane, which is also more consistent with a biogenic origin. Moreover, the relatively low transition temperature (104 K) of the foraminiferal magnetite is similar to that of biogenic magnetite produced by magnetotactic bacteria (Li et al., 2010; Jackson and Bruce, 2021), perhaps providing additional indirect evidence for biogenic origin.

High throughput sequencing of *R. bilocularis* failed to reveal the presence of any associated magnetotactic bacteria, although about 0.09% of sequences were attached to the iron reducing bacterium *Shewanella* sp. (Fig. S-14). The sequences had 94.47% similarity with *Shewanella piezotolerans* WP3 which was isolated from deep sea sediments (Wang et al., 2004). The magnetite synthesised by *S. piezotolerans* WP3 is commonly 4–8 nm in diameter and significantly smaller than that found in *R. bilocularis* (Vu et al., 2013). Thus, a purely bacterial origin for the magnetite particles found in *R. bilocularis* is unlikely.

Biologically controlled mineralisation typically generates magnetite crystals with a uniform morphology, high chemical purity and arranged in chains, whereas biologically induced mineralisation (BIM) generates magnetite crystals of variable size and morphology that are not arranged in chains (Bazylinski et al., 2007). The presence of a lipid membrane, together with the morphological and chemical characteristics of the *R. bilocularis* crystals, favours the hypothesis that they are most likely formed through BIM in microenvironments within stercomata. However, the collection of mineral grains is typical of foraminifera and therefore we cannot completely rule out the possibility that magnetite may be derived from surrounding sediments.

The iron reducing bacterium *Shewanella* sp. detected in *R. bilocularis* may be involved in magnetite biominalisation within *R. bilocularis* via providing a Fe$^{2+}$ source. We develop the following conceptual model for the formation of magnetite in foraminifera (Fig. 4). The foraminifera first feed on the iron oxides that are commonly present in the surface sediments. The semi-enclosed environment within the foraminiferal test provides conditions that permit *Shewanella* sp. to reduce Fe$^{3+}$ in iron oxides to Fe$^{2+}$. Generated Fe$^{2+}$ within the foraminiferal test then is transported into the stercomata where micron-sized magnetite is formed in the presence of organic matter (Fig. S-5a).

### Implications

Regardless of whether magnetite in *R. bilocularis* has a biological origin or is derived from surrounding sediments, their passive response to the magnetic field make them the first example of magnetic protist at hadal depths. In magnetotactic bacteria and algae, the magnetic energy is sufficient to overcome the irregular motion induced by external thermal energy, allowing these microorganisms to exhibit magnetotactic behaviour (Araujo et al., 1986; Pan et al., 2005). Although the magnetic energy in *R. bilocularis* is also larger than external thermal energy, this does not mean that these foraminifera must have magnetotactic capability, because larger particles, such as foraminifera 100–200 μm in size are less affected by the Brownian motion than much smaller microbial organisms (Russel, 1981). Whether the magnetite in *R. bilocularis* fulfills any physiological function remains unknown. Perhaps, these foraminifera may take advantage of the magnetite to sense the Earth’s magnetic field, like some ciliates and flagellates (Monteil and Lefèvre, 2020) or adjust the iron balance within the test (Andrews et al., 2003). *In situ* experiments are needed to test these possibilities and better understand the origin of the magnetite crystals and other aspects of the biology of these very common but enigmatic hadal protists.

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