Characterization of uncultured giant rod-shaped magnetotactic *Gammaproteobacteria* from a freshwater pond in Kanazawa, Japan

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Magnetotactic bacteria (MTB) are widespread aquatic bacteria, and are a phylogenetically, physiologically and morphologically heterogeneous group, but they all have the ability to orientate and move along the geomagnetic field using intracellular magnetic organelles called magnetosomes. Isolation and cultivation of novel MTB are necessary for a comprehensive understanding of magnetosome formation and function in divergent MTB. In this study, we enriched a giant rod-shaped magnetotactic bacterium (strain GRS-1) from a freshwater pond in Kanazawa, Japan. Cells of strain GRS-1 were unusually large (~13 μm). They swam in a helical trajectory towards the south pole of a bar magnet by means of a polar bundle of flagella. Another striking feature of GRS-1 was the presence of two distinct intracellular biomineralized structures: large electron-dense granules composed of calcium and long chains of magnetosomes that surround the large calcium granules. Phylogenetic analysis based on the 16S rRNA gene sequence revealed that this strain belongs to the *Gammaproteobacteria* and represents a new genus of MTB.

INTRODUCTION

Magnetotactic bacteria (MTB) are a phylogenetically, morphologically and metabolically heterogeneous group of prokaryotes that synthesize regular-shaped, nano-sized, single-domain magnetic particles of either magnetite (Fe₃O₄) or greigite (Fe₃S₄) in unique prokaryotic organelles called magnetosomes (Bazylinski & Frankel, 2004; Blakemore, 1975; Fairev & Schuler, 2008; Komeili, 2012). These magnetosomes function as a cellular magnetic compass in magnetotaxis motility that is directed along the geomagnetic field or in an applied magnetic field. Other intracellular structures that have been found in MTB are inclusions composed of elements such as phosphorus (Lins & Farina, 1999), iron–phosphorus (Byrne et al., 2010), sulfur (Keim et al., 2005), calcium (Isambert et al., 2007) or polyhydroxybutyrate (Gorby et al., 1988). Because of their involvement with these various ions, MTB probably play a significant role in geochemical cycling (Simmons et al., 2007).

MTB are globally distributed in aquatic systems where there is an oxygen gradient, such as lacustrine sediments or stratified water columns (Lefèvre & Bazylinski, 2013; Lefèvre & Wu, 2013; Lin et al., 2013), where they can represent up to 30% of the natural bacterial communities (Spring & Bazylinski, 2006). The model for magnetotaxis is built on the idea that MTB use their magnetosomes to navigate the oxic–anoxic interface to find the ideal oxygen concentration (Spring et al., 1993). The model for magnetotaxis is built on the idea that MTB use their magnetosomes to navigate the oxic–anoxic interface to find the ideal oxygen concentration (Spring & Bazylinski, 2006). They are phylogenetically diverse with members across three phyla, the *Proteobacteria*, *Nitrospirae* and Candidate division OP3. Most MTB in the *Proteobacteria* belong to the *Alphaproteobacteria*, *Gammaproteobacteria* and *Deltaproteobacteria* classes (Lefèvre & Bazylinski, 2013). However, there are just four strains...
reported within the *Gammaproteobacteria*, two cultured (Lefèvre et al., 2012) and two uncultured (Wang et al., 2013). MTB can be found in many different types of aquatic environments and their identification is restricted to those cells that can be isolated using the racetrack method (Wolfe et al., 1987), which suggests that their diversity is underestimated. This is particularly true for the magnetotactic members of the *Gammaproteobacteria*, which were only discovered in 2012.

In this study, we isolated and characterized the largest known single-celled MTB (strain GRS-1). The organism’s unusually large rod-shaped cells, ~13 × 8 μm, are not its only outstanding trait. It also contains more magnetosomes (hundreds per cell) than most other MTB, and also possesses unusually large calcium-rich granules that occupy most of the interior volume of the cell. The organism was isolated from a freshwater pond and was determined to be a member of the *Gammaproteobacteria*. All of these traits distinguish it from the other two characterized gammaproteobacterial MTB, which possess typical MTB characteristics, but were isolated from inland saline systems in the USA (strain BW-2 from Badwater Basin, Death Valley National Park, and strain SS-5 from the Salton Sea) (Lefèvre et al., 2012). The uncommon features of our newly discovered MTB push the boundaries of the limits of MTB diversity and precisely highlight the need to continue to pursue the identification of new MTB in the natural environment.

**METHODS**

**Sampling and enrichment of GRS-1 cells.** Samples of sediment (0–3 cm deep) and surface water were collected from near the edge of a shallow freshwater pond in Kanazawa, Japan (36° 54’ N 136° 93’ E), and placed into tightly capped 0.5 l glass bottles. Isolation was begun immediately on return to the laboratory. The MTB were magnetically concentrated by attaching the south pole of neodymium magnets (10 mm × 5 mm) to the outside of sample bottles just above the sediment–water interface. The bottles were kept in the dark for up to 3 h to allow the magnetotactic cells to swim towards the magnet. A pipette was used to remove ~1.5 ml of sample from the inside of the bottle near the magnet and then placed into a 1.5 ml plastic tube. To isolate large MTB, we did not use the capillary racetrack method (Wolfe et al., 1987) that is commonly used to isolate MTB, because the large cell-sized MTB could not pass through the cotton filter. Instead, a neodymium magnet was placed on one end of the 1.5 ml plastic tube and incubated for 3 h and then a ~0.25 ml aliquot of fluid was collected near the magnet. This sample was observed by phase-contrast microscopy on an Olympus CKX41 microscope. While viewing the sample in the microscope, individual GRS-1 cells were collected using a very fine-tipped glass pipette. After collecting many GRS-1 cells, they were further purified by centrifuging at 2000 × g for 1 min, and then suspending the pellet in 150 μl sterilized water. The centrifugation step was repeated three times and the enriched GRS-1 cells were used for further analysis. All isolation steps were performed at room temperature.

**Optical microscopy.** Cell morphology was observed using phase-contrast microscopy on a Nikon Eclipse Ti microscope, equipped with an iXon3 EMCCD camera (Andor Technology). A video of cell motility was recorded using phase-contrast microscopy on an Olympus CKX41 microscope, equipped with a Moticam 2000 digital camera (Shimadzu) using Motic Images Plus 2.1S software (Shimadzu). The swimming speed of GRS-1 cells was calculated by measuring the distance travelled between successive frames of the recorded movie (elapsed time between each frame 0.1 s). The motility of a cell was traced and coloured using Adobe Photoshop software.

**Electron microscopy.** To prepare the specimen for observation in the scanning electron microscope (SEM), the samples were fixed in 0.1 M phosphate buffer (pH 7.4) containing 2% glutaraldehyde, post-fixed with 0.1 M phosphate buffer (pH 7.4) containing 2% osmium tetroxide, dehydrated in a graded series of ethanol (30–100%), critical point dried and sputter coated with gold according to standard procedures. The cells were observed using a JSM-6320F SEM (JEOL) operating at 5 kV.

Whole cells for observation in the transmission electron microscope (TEM) were prepared by placing a drop of cell suspension onto a Formvar- and carbon-coated copper grid and then allowed to air dry. The grids were examined using a JEM 2000EX TEM (JEOL) operating at 120 kV. For preparation of ultrathin sections of GRS-1 cells, the samples were fixed in 0.1 M phosphate buffer (pH 7.4) containing 2% glutaraldehyde, post-fixed with 0.1 M phosphate buffer (pH 7.4) containing 2% osmium tetroxide, dehydrated in a graded series of ethanol (30–100%) and embedded in Quetol 812. Ultrathin sections 80–90 nm thick were observed using an ultramicrotome (Leica Ultracut R), and mounted on 200-mesh Formvar- and carbon-coated copper grids, stained with lead citrate and 2% uranyl acetate, and observed as described above. The elemental distribution within the cells was analysed by electron dispersive spectroscopy (EDX) using a JEM-2010FF (JEOL) operating at 200 kV equipped with a JED-2300 EDX detector (JEOL). High-resolution transmission electron microscopy (HRTEM) analysis of the crystals in the ultrathin sections was performed using a JEM-2010FF operating at 200 kV.

**Sequence analysis of the 16S rDNA gene.** The genomic DNA of bacterial cells was extracted using Lyse and Go Reagent (Thermo Scientific). The 16S rDNA genes from the concentrated solution of large MTB were amplified by PCR using the universal primers 27f (5′-AGAGTTTGTATCCTGCCAGC-3′) and 1525r (5′-AAAGAGGTGTATTCCAGGCC-3′) (Lane, 1991). For amplification of the gammaproteobacterial 16S rRNA genes, a *Gammaproteobacteria*-specific primer gamma1 (5′-GTTCCCGAAGGCCACR-3′, nucleotide positions 1024–1038 according to the Escherichia coli 16S rDNA gene numbering) was used as the reverse primer. PCR products were cloned into a pMD20-T vector using the Mighty TA-cloning Reagent Set for *Escherichia coli* (Promega). Sequence analysis of the 16S rRNA gene products was performed using the BLAST algorithm in GenBank (http://www.ncbi.nlm.nih.gov). 16S rDNA gene sequences, including isolated MTB, reference cultures and environmental clones, were aligned using the CLUSTALW multiple alignment accessory application (Thompson et al., 1994) in the BioEdit sequence alignment editor (Hall, 1999). A phylogenetic tree was reconstructed using the neighbour-joining method (Saitou & Nei, 1987) in MEGA software (v. 4.0) (Tamura et al., 2007) using bootstrap values based on 1000 replicates.

**Fluorescence in situ hybridization (FISH).** Based on the newly obtained 16S rDNA gene sequence of GRS-1, two oligonucleotide probes were designed, Big-1 (5′-GCTCACTCATATAGGACG-3′; nucleotide positions 217–233, E. coli 16S rDNA gene numbering) and negative probe CBIG (5′-CTGCTGTCAGAGTGACC-3′). Three types of controls were used; the bacterial universal probe EUB338 (5′-GCTGCTCCCTCCCGTAA-3′; nucleotide positions 338–355), the *Bacterioproteobacteria*-specific probe BET42a (5′-GCTTCTCACCTCGTTT-3′; nucleotide positions 1027–1043, E. coli 23S rDNA gene number).
numbering) (Manz et al., 1992) and the Gammaproteobacteria-specific probe GAM42a (5'-GCCCTCACCACATCGTTT-3'; nucleotide positions 1027–1043, E. coli 23S rRNA gene numbering) (Manz et al., 1992). The oligonucleotides BIG-1, BET42a and GAM42a were labelled with Alexa561, while the oligonucleotide EUB338 was labelled with Alexa488. In the hybridization experiments, Burkholderia oxyphila NBRC 105797 (Otsuka et al., 2011) and E. coli cells were used as controls for Betaproteobacteria and Gammaproteobacteria, respectively. FISH was carried out according to protocols reported by Pernthaler et al. (2002). After hybridization, the samples were observed using a Nikon ECLIPSE Ti microscope.

**Nucleotide sequence accession number.** The sequence of the 16S rRNA gene of strain GRS-1 was deposited in the DNA Data Bank of Japan under accession number AB897514.

## RESULTS AND DISCUSSION

### Purification of giant rod-shaped MTB

Most MTB have been isolated from freshwater habitats and can be easily separated from sediment samples using a simple magnet and enriched using a capillary racetrack (Wolfe et al., 1987). In this study, most of the collected MTB were magnetotactic cocci (~1 μm in diameter), although we also observed unusually large rod-shaped MTB, which we designated GRS-1 [Fig. 1(a) and Movie S1 (available in the online Supplementary Material)]. These larger cells required an extra step of enrichment to separate them from the smaller MTB. GRS-1 cells were isolated and purified from smaller MTB using a customized glass capillary pipette and then centrifuged at low speed to further enrich the large rod-shaped cells (Fig. 1b). Even with these extra enrichment steps, other MTB still remained that could be seen using the light and electron microscopes.

### Morphology and motility of GRS-1

There are many morphotypes of MTB, including cocci, vibrios, spirilla, rods and clusters of cells. Cells of GRS-1

![Fig. 1. Morphology and motility of GRS-1. (a) Phase-contrast microscopy images of north-seeking MTB at the edge of a drop that were magnetically collected from sediment. The double-headed arrow indicates a layer of smaller MTB (mainly cocci). The yellow arrowheads show examples of GRS-1 cells. (b) Purified GRS-1 cells that were separated from other magnetic cells. The white arrows in (a) and (b) indicate the direction of the magnetic field. (c) Tracing the motility of a GRS-1 cell by colouring sequential images. Bars, 10 μm (a, b); 5 μm (c).](image)

![Fig. 2. SEM observation of GRS-1 cells. (a) Micrograph of a whole GRS-1 cell showing the bundle of flagella emanating from one end of the cell. The flagella are bundled immediately adjacent to the cell, but then splay out showing a large number of filaments. (b) Bundle of polar flagella with a twist in the bundle (arrow). (c) Magnified image of the boxed area in (b) showing the area where the filaments begin to separate from one another. Bars, 2 μm (a); 1 μm (b); 0.5 μm (c).](image)
were rod-shaped having a mean (±SD) length of 12.9±
2.7 μm and width of 7.8±1.0 μm (n=100), and a maxi-
mum length of 20 μm and width of 11 μm. These dimen-
sions show that these cells are the largest single-celled MTB
reported to date. Recently, large rod-shaped MTB were
isolated from a freshwater source in the Yellow Sea (Zhang
et al., 2013). These MTB were similar in length (mean
10.07±1.87 μm) to GRS-1, but they were much narrower
(mean width of 3.51±0.49 μm).

GRS-1 cells swam towards the south pole of a bar magnet
in a helical trajectory at rates up to 32 μm s⁻¹ (n=4) [Fig.
1(c) and Movie S2]. This speed was lower than for other

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**Fig. 3.** TEM observation of a GRS-1 cell. (a) Image of a whole GRS-1 cell illustrating several magnetosome chains near the
periphery of the cell, and a large electron-dense granule occupying most of the volume within the cell. Inset: detail of one of the
magnetosome chains showing their slightly elongated shape. (b) The size distribution and (c) shape factor of the crystals.
Crystal size was determined as the mean of the short axis plus the long axis. (d) HRTEM image of a single crystal and its (e)
Fourier transform pattern. Bars, 5 μm (a); 100 nm (inset); 2 nm (d).
MTB, which swim at speeds greater than 100 μm s$^{-1}$ (Lefèvre et al., 2010; Lin et al., 2012). When viewed in the SEM, the oval shape of GRS-1 cells was discernible (Fig. 2a), albeit a little distorted from the dehydration step during sample preparation. A bundle of flagella emerged from the base of one end of the cell. These appear to be twisted near the base of the cell, but then splay out farther away from the cell (Fig. 2b, c). The width of each flagellum filament was 56 nm ($n=13$). These flagella were only visible in the SEM samples and not in the TEM samples. Perhaps this is because flagella are inadvertently removed during the sample preparation for TEM analysis.

**Ultrastructures of the interior of the cell**

TEM imaging revealed that the cells contain two distinct internal structures, long chains of crystalline structures and large electron-dense granules that occupy most internal space of the cells. The long chains of regularly spaced crystals, representing the magnetosomes, were clearly visible around the inside periphery of the cells, but were often obscured by the large opaque granules (Fig. 3a). The cells contained at least 300 crystals, but the exact number could not be determined because they were hidden by the granules. The mean length of the crystals was $54.6 \pm 4.8$ nm ($n=300$) and they had a mean shape factor (the short axis divided by the long axis) of $0.85 \pm 0.06$ ($n=300$) (Fig. 3b, c), indicating they were slightly elongated prisms. The size of the crystals falls within the single-domain size range (Butler & Banerjee, 1975), and the size and shape of the crystals indicate that they are similar to other MTB (Pósfai et al., 2013). EDX analysis clearly indicated a large iron K alpha peak and a very small sulfur K alpha peak (Fig. S1a–c). Elemental maps of an ultrathin section of the cells demonstrated that iron and oxygen are concentrated where the crystalline structures exist (Fig. 4a–d). Although there does appear to be very minor amounts of sulfur, we suggest this originates from the background of the cell. Analysis of the crystals using HRTEM unequivocally identified the magnetosome crystals as magnetite (Fig. 3d, e).

The other internal structures are large, electron-dense granules that occupy a large proportion of the internal volume of the cell. The granules range from 2.5 to 4.5 μm in width. EDX spot analysis on one of the granules in a cell revealed it was composed mostly of calcium with very minor amounts of carbon, sodium, oxygen, phosphorus and silicon (Fig. S1d–f). The copper peak was generated from the copper grid used to support the sample in the microscope. We then analysed whole granules in a cell and made elemental maps of calcium and phosphorus, which demonstrated that they were composed predominantly of calcium (Fig. 4e–g). However, a minor amount of phosphorus was detected but we assume that this was from the background of the cell. It is common for MTB to contain internal granules, especially phosphorus (Lins & Farina, 1999) and sulfur (Keim et al., 2005), but calcium has been reported only once within MTB (Isambert et al., 2007). The role of calcium in GRS-1 cells remains undetermined.

There is no evidence to support the idea that GRS-1 is a magnetotactic multicellular prokaryote (MMP). The electron microscope images give no indication that GRS-1 is composed of multiple cells. For example, MMPs typically comprise dozens of individual cells, which can clearly be seen in cross-section in the TEM (Keim et al., 2007a). In Fig. 3(a), we show a whole cell, which does not demonstrate any indication of intracellular membranes or an interruption of the magnetosome chains, which is reported for the MMPs by Keim et al. (2007a). Moreover, Keim et al. (2007b) have shown SEM images of MMPs in which there is a regular pattern of clusters of ovoid structures (the ovoid structures
being individual cells). However, in our SEM image there is no indication of a regular pattern on the surface of GRS-1 cells (Fig. 2). Additionally, the swimming behaviour of GRS-1 does not mimic the 'ping-pong' motility of all recognized MMPs (Rodgers et al., 1990). Furthermore, our organism does not have peritrichous flagella characteristic of MMPs. GRS-1 was isolated from a freshwater environment, compared with the saline environments from which other MMPs have been isolated. Finally, GRS-1 swims much more slowly than MMPs (32 versus 90 μm s⁻¹, respectively). These individual points do not exclude GRS-1 from being an MMP, but taken together they clearly show that GRS-1 is not an MMP.

**FISH and phylogenetic analysis**

The phylogenetic and FISH analyses showed that GRS-1 belongs to the *Gammaproteobacteria*. First, we analysed 16S rRNA gene sequences that were amplified from the enriched GRS-1 sample by using eubacterial-specific primers. The 16S rRNA gene sequences obtained showed large variation, belonging to the *Betaproteobacteria*, *Gammaproteobacteria*, *Deltaproteobacteria* and *Firmicutes* (Table S1). We then performed FISH analyses using *Betaproteobacteria* and *Gammaproteobacteria*-specific probes and found that the *Gammaproteobacteria*-specific probe positively labelled the GRS-1 cells (Fig. 5a, b), indicating that GRS-1 belongs to the *Gammaproteobacteria*. We then amplified the 16S rRNA gene fragment from the enriched GRS-1 sample using the gammaproteobacterial 16S rRNA gene-specific primer. This resulted in 33 of the 42 clones having identical 16S rRNA gene sequences (Table S2). Finally, we generated a FISH probe (BIG-1) using the specific sequence obtained from the 16S rRNA gene sequence to confirm that the obtained 16S rRNA gene sequence originated from GRS-1. The BIG-1 probe specifically recognized GRS-1 cells (Fig. 5c), while the probe designed from the negative chain (CBIG-1) did not label the GRS-1 cells (Fig. 5d).

![Fig. 5](http://mic.sgmjournals.org)
A phylogenetic tree based on the 16S rRNA gene sequence from strain GRS-1 showed that this organism belongs to the class *Gammaproteobacteria* of the phylum *Proteobacteria* (Fig. 6). GRS-1 lies within the order *Thiotrichales*, which also contains the rod-shaped MTB BW-2 (Lefèvre et al., 2012) as well as the uncultured MTB operational taxonomic unit (OTU) 8 (Wang et al., 2013) (Fig. 6). GRS-1 showed 88–90% sequence identity to the other four known MTB belonging to the *Gammaproteobacteria* and was closest to the uncultured MTB OTU 8. This latter clone was also collected from a freshwater environment; however, no morphological information is known about this organism, so no morphological comparison can be made. The phylogenetic tree clearly indicates that GRS-1 represents a phylogenetically different group from previously known MTB in the *Gammaproteobacteria* (Lefèvre et al., 2012; Wang et al., 2013).

Only two of the four other MTB belonging to the *Gammaproteobacteria* have morphological information, SS-5 and BW-2. GRS-1 has phenotypic characteristics that are similar to and different from SS-5 and BW-2. All reported MTB *Gammaproteobacteria* cells are motile, but have different types of flagella. BW-2 and GRS-1 both have a polar bundle of flagella, but SS-5 has a single polar flagellum. All of the *Gammaproteobacteria* MTB contain magnetite crystals. SS-5 cells contain 20 ± 7 crystals per cell and have an octahedral habit, a shape factor of 0.74 ± 0.07, a mean length of 86 ± 27 nm and width of 63 ± 19 nm. BW-2 cells produce 30 ± 9 magnetite crystals per cell and have an octahedral structure with a shape factor of 0.94 ± 0.04, a mean length of 67 ± 16 nm and a mean width of 63 ± 15 nm. These are very similar to the size and shape of the crystals found in GRS-1, even though the environments from which they were isolated were different (GRS-1 from freshwater, SS-5 and BW-2 from saline environments). The biggest difference between GRS-1 and the other *Gammaproteobacteria* is the presence of calcium granules in strain GRS-1, whereas BW-2 contained phosphate.
inclusions and SS-5 contained phosphate and sulfur inclusions. Another difference that distinguishes GRS-1 from other known types of Gammaproteobacteria is cell size; GRS-1 cells are much longer and wider than those of BW-2 and SS-5. Table 1 compares the characteristics of strains BW-2, SS-5 and GRS-1.

**CONCLUSION**

The first MTB belonging to the Gammaproteobacteria (SS-5 and BW-2) were identified and described by Lefèvre et al. (2012). Since then, two other phyotypes have been identified, but not described (Wang et al., 2013). GRS-1 is the third MTB in the Gammaproteobacteria to be described, and it has unique characteristics that set it apart from SS-5 and BW-2, such as cell dimensions, number, size and organization of magnetosomes, speed of motility, type of flagellum, type of intracellular inclusion, and habitat. The most noteworthy characteristics are the cell size of GRS-1, which is the largest of all the MTB, and the presence of intracellular calcium inclusions. Together, these characteristics set this organism apart from all the other known MTB and increase the amount of diversity described within MTB.

GRS-1 has the unique ability to sequester large amounts of iron in the form of magnetosomes and large amounts of calcium in the form of intracellular inclusions. This ability makes this organism a unique model for the study of metal compartmentalization in unicellular organisms. To establish such models we first need to determine the genome of GRS-1 to understand the mechanisms of metal uptake and the synthesis of these metal-accumulating organelles. Once we understand this we could then investigate the use of GRS-1 in environmental applications such as bioaccumulation of metals such as calcium and iron.

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**REFERENCES**


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**Table 1.** Comparison of the characteristics of all known MTB belonging to the Gammaproteobacteria*

All sizes listed are mean values. Bold type in the GRS-1 row indicates differences between GRS-1 and the other two Gammaproteobacteria.

<table>
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<th>Strain</th>
<th>Order</th>
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<th>Cell size (length×width, μm)</th>
<th>Inclusion(s)</th>
<th>Crystal type</th>
<th>Crystal shape</th>
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<td>Octahedral</td>
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<td>Thiotrichales</td>
<td>Rod</td>
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<td>Calcium</td>
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<td>This paper</td>
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*There are no data on the characteristics of OTU 7 or OTU 8 from Zhang et al. (2013).


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