



# Morphological features of elongated-anisotropic magnetosome crystals in magnetotactic bacteria of the *Nitrospirae* phylum and the *Deltaproteobacteria* class

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## ABSTRACT

High resolution transmission electron microscopy was used to study the crystallographic habits of the elongated magnetite crystals, variously described as bullet-, tooth- or arrowhead-shaped, in two recently described, uncultured, magnetotactic bacteria belonging to the *Nitrospirae* phylum designated *Candidatus Magnetovum mohavensis* strain LO-1, and *Candidatus Thermomagnetovibrio paiutensis* strain HSMV-1; and a cultured sulfate-reducing magnetotactic bacterium of the *Deltaproteobacteria* class of the *Proteobacteria* phylum designated strain AV-1. The elongation axes of the magnetosomes do not coincide with the easy magnetization axis (which is [111]) but they are parallel to [100] in LO-1 and AV-1 and parallel to [110] in HSMV-1. In all three strains, magnetosome magnetite crystals appear to elongate at constant width, resulting in asymmetric shapes. Idealized crystal morphologies are proposed. Neither the control mechanism over crystal growth, nor the adaptiveness, if any, of such unusual crystal habits are known at the moment. Since similar elongated and asymmetric morphologies are unknown in inorganically-formed magnetite crystals, these forms of magnetosome magnetite appear to be excellent biomarkers.

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## 1. Introduction

Magnetotactic bacteria (MTB) biomineralize magnetosomes comprising nano-scale magnetic-iron-mineral crystals enclosed in lipid bi-layer membranes (Bazylinski and Frankel, 2004). The iron minerals are magnetite,  $\text{Fe}_3\text{O}_4$ , and greigite,  $\text{Fe}_3\text{S}_4$ . A striking feature of magnetosome magnetite crystals is that they have different, consistent, two-dimensional (2D) projected shapes in different bacterial species or strains when observed by transmission electron microscopy (TEM). The 2D projected shapes include cuboidal, quasi-rectangular and asymmetric (arrowhead-, tooth-, or bullet-shaped). The asymmetric crystal morphologies appear to be inconsistent with the cubic point symmetry (m3m) of the spinel-type structure of magnetite.

While three-dimensional (3D) crystal habits cannot be determined from 2D projected images alone, idealized 3D crystal habits, based on low-index crystallographic forms, have been proposed (e.g., Lins et al., 2005; Mann et al., 1984; Matsuda et al., 1983; Meldrum et al., 1993a, 1993b). These habits include cuboctahedral, elongated-prismatic and elongated-anisotropic, for the corresponding cuboidal, quasi-rectangular and asymmetric 2D projected shapes, respectively. In this context, anisotropic means a crystal habit lacking a center of inversion symmetry. The overall sizes of the crystals, the width/length ratios, and the relative sizes of corner faces can vary from one species or strain of MTB to another, resulting in the distinctive projected shapes.

All MTB known to date are affiliated with the *Alpha*-, *Gamma*- and *Deltaproteobacteria* classes of the *Proteobacteria* phylum, or the *Nitrospirae* phylum. While magnetite-bearing MTB occur in all four taxa, greigite-bearing bacteria examined to date are phylogenetically affiliated with only the *Deltaproteobacteria*. Of the magnetite-bearing MTB, magnetosomes with cuboctahedral and elongated-prismatic idealized habits, respectively, occur only in those phylogenetically affiliated with the *Alpha*- and *Gammaproteobacteria*, (e.g., *Magnetospirillum* species, and *Candidatus Magnetococcus marinus* strain MC-1). On the other hand, magnetosomes with elongated-anisotropic habits have been found in MTB affiliated only with the *Nitrospirae* and the *Deltaproteobacteria*, (e.g., *Candidatus Magnetobacterium bavaricum* and *Desulfovibrio magneticus* strain RS-1, respectively).

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The most common 2D projected image of elongated-anisotropic crystals is the bullet or flat-top shape (fts), with one flat end and one narrower, rounded, end (Blakemore et al., 1980; Mann et al., 1987a, 1987b; Thornhill et al., 1994). Sometimes the magnetosome crystals with fts projections are bent in one direction along their length (Hanzlik et al., 2002). Fts magnetosome crystals in an uncharacterized MTB from the Exeter River (ER) in New Hampshire, USA were proposed to have an idealized, six-sided prismatic, magnetosome habit comprising four {111} and two {100} faces capped by two faces of {111} with associated {111} and {100} corner faces. Crystal growth of a nascent cuboctahedron supposedly commences via nucleation on the magnetosome membrane and continues until the width of the crystal is about 40 nm. Subsequent elongation then occurs parallel to  $\langle 112 \rangle$  while the crystal width remains relatively constant (Mann et al., 1987a, 1987b).

Some elongated-anisotropic magnetosomes have distinctive projected images with double-triangle shape (dts), two isosceles triangles sharing a common base. These dts magnetosomes occur in some MTB phylogenetically affiliated with the *Nitrospirae* and with the *Deltaproteobacteria* (Li et al., 2010; Lins et al., 2007; Pósfai et al., 2006; Vali and Kirschvink, 1990). Both projected triangles have the same width, but in mature crystals one triangle is longer than the other. Until now, no idealized habit for dts magnetosomes has been proposed.

Here we report on the idealized crystal habits and crystal size distributions for elongated-anisotropic magnetosome crystals in a newly cultivated MTB affiliated with the *Deltaproteobacteria*, and in two newly described, uncultured MTB affiliated with the *Nitrospirae*. The former organism, designated strain AV-1, appears to be a magnetotactic strain of *Desulfonatronum thiodismutans* (Pikuta et al., 2003) and was isolated from an ambient-temperature, alkaline spring in the Amaragosa Valley, near Death Valley Junction, California. The organism is helical in shape and possesses a single polar flagellum. Strain AV-1 contains dts magnetosomes arranged in single, or in some cells double, chains that traverse the length of the cell (Lefèvre et al., 2011a). One of the *Nitrospirae*, designated *Candidatus Magnetovibrio mohavensis* strain LO-1, was collected from sediments of Lake Mead, Nevada, and contains dts magnetosomes arranged in three chains that resemble twisted braids (Lefèvre et al., 2011b). Since dts magnetosomes occur in strains AV-1 and LO-1, the idealized crystal habit for strain AV-1 also applies to strain LO-1. The other *Nitrospirae*, designated *Candidatus Thermomagnetovibrio paiutensis* strain HSMV-1, is a moderately thermophilic vibrio that was collected from a series of thermal springs in northern Nevada. Each cell contains fts magnetosomes arranged in a single chain (Lefèvre et al., 2010).

## 2. Methods

Details of the collection of cells of strains HSMV-1 and LO-1 from the environment and the isolation of strain AV-1 in pure culture are discussed in Lefèvre et al. (2010, 2011a and 2011b, respectively). Living cells of each type from cultures in late exponential to early stationary phase were deposited on carbon-coated grids and dried in air. The grids were examined as soon as possible after drying. Typically this time period ranged from an hour or two to several days. Grids were stored in small plastic vials under oxygen-free nitrogen to prevent oxidation of magnetite. Low magnification images and high resolution TEM (HRTEM) images were taken with a JEOL Model 3010 TEM at 300 kV. Tilt series of low magnification images and selected-area electron diffraction patterns (SAED) were taken with a Philips Model CM20 at 200 kV. To obtain SAED patterns we used a projected aperture with a diameter of 250 nm in the image plane.

Crystal habits were modeled with KrystalShaper software. We used the cubic point group  $m\bar{3}m$ , and variables included the faces present (with specific Miller-indices) and their distances from the center of the crystal. Magnetosome sizes were measured with ImageJ software (U.S. National Institutes of Health).

## 3. Results

### 3.1. Idealized crystal habits for dts magnetosomes in strains AV-1 and LO-1

TEM images of magnetosome chains in cells of strains AV-1, LO-1, and HSMV-1 are shown in Figs. 1A–1C, respectively. The dts magnetosomes in strain AV-1 appear to consist of two triangles: a short “base” triangle and an elongated triangle, with a common side. In small crystals (<45 nm) the two triangles are congruent. Whereas the sides of the base triangle are low-index crystal faces (see below), the sides of the elongated triangle are slightly curved. Such curved sides can only result from either the presence of a large number of high-index faces or some irregular surfaces that cannot be described by crystallographic faces (and thus by Miller-indices). In fact, the former case converges into the latter, since the more high-index faces appear on a crystal, the less regular the shape becomes.

Concerning the base triangle, the interpretation of the 3D shape is straightforward. The measured angle between the two sides that meet to form the tip in the projected image ranges from 70 to 90° (Fig. 1A), exactly the two extreme values obtained by tilting a regular octahedron from [110] into [100] orientation, respectively. In other words, the projection of any two sides that join in the same vertex of a regular octahedron must be between 70 and 90°, as long as the octahedron is tilted about a  $\langle 100 \rangle$  axis. This also applies to slightly “distorted” or “elongated” octahedra in which the different {111} faces are not equally developed, because the sizes of the faces do not affect the angles between them.

The above reasoning is confirmed by HRTEM images. The crystallographic directions in the HRTEM image of a single crystal in Fig. 2 can be clearly identified from both the Fourier transform and the lattice spacings. The magnetosomes are elongated along [100]. Since the sides of the projected base triangle coincide with {111} octahedral faces, the base section of each magnetosome crystal is just half a regular octahedron. The presence of narrow (110)-type faces between the octahedral faces cannot be excluded on the basis of the HRTEM images. In strain LO-1, dts magnetosomes crystals are also elongated along [100] (Fig. 1B).

In order to understand the 3D shape of the elongated section of the dts magnetosome, images of a magnetosome chain in strain AV-1 were sequentially acquired as the microscope stage was tilted as far as possible ( $\pm 45^\circ$ ). Although no magnetosome chain was entirely parallel to one of the tilt axes, the one shown in Fig. 3 was close. The approximate direction of the tilt axis is marked in the third panel. This tilt series indicates that the elongated section essentially has  $\infty$ -fold symmetry about the [100] elongation axis. This means that the habits of dts magnetosomes can be modeled simply on the basis of any two-dimensional projection. As discussed above, the base section is either a regular or a slightly distorted half-octahedron (four-sided pyramid). The elongated, pointed section consists of a series of high-index faces, mostly of {hh1}- and {h01}-type forms (Fig. 4B). If faces of several such forms are present, the outline of the projected crystal appears to be curved. While there are many variations of forms that can be used to approach the curved outline of the crystals, the sizes of these faces cannot be varied randomly (if some are enlarged, faces of other forms disappear), so the length of the crystal is almost fixed for a given curvature. On the very elongated magnetosomes, {110} and {100}-type faces, which are parallel to the elongation axis, are prominent close to the base. In this case, the crystal can be of any length. Of course, the model shown in Fig. 4 is an idealization of the magnetosome habit. In reality, it is possible that the surfaces of the elongated section are really curved and do not exactly correspond to crystallographic faces.

In addition to the dts magnetosomes, there are some magnetosomes with unusually curved 2D projections in strain AV-1 (see the arrowed magnetosomes in Fig. 1A). These crystals invariably show heterogeneous contrast in bright-field images, suggesting that they

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