Magnetovibrio blakemorei gen. nov., sp. nov., a magnetotactic bacterium (Alphaproteobacteria: Rhodospirillaceae) isolated from a salt marsh

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A magnetotactic bacterium, designated strain MV-1T, was isolated from sulfide-rich sediments in a salt marsh near Boston, MA, USA. Cells of strain MV-1T were Gram-negative, and vibrioid to helicoid in morphology. Cells were motile by means of a single polar flagellum. The cells appeared to display a transitional state between axial and polar magnetotaxis: cells swam in both directions, but generally had longer excursions in one direction than the other. Cells possessed a single chain of magnetosomes containing truncated hexaoctahedral crystals of magnetite, positioned along the long axis of the cell. Strain MV-1T was a microaerophile that was also capable of anaerobic growth on some nitrogen oxides. Salinities greater than 10% seawater were required for growth. Strain MV-1T exhibited chemolithoautotrophic growth on thiosulfate and sulfide with oxygen as the terminal electron acceptor (microaerobic growth) and on thiosulfate using nitrous oxide (N2O) as the terminal electron acceptor (anaerobic growth). Chemo-organoheterotrophic and methylotrophic growth was supported by various organic acids and amino acids, under microaerobic and anaerobic conditions. Optimal growth occurred at pH 7.0 and 26–28 °C. The genome of strain MV-1T consisted of a single, circular chromosome, about 3.7 Mb in size, with a G+C content of 52.9–53.5 mol%.

†Deceased.

Abbreviations: CBB, Calvin–Benson–Bassham; RubisCO, ribulose bisphosphate carboxylase/oxygenase.

Three supplementary figures, three supplementary tables and supplementary methods are available with the online version of this paper.
Magnetotactic bacteria were described first by Salvatore Bellini in 1963 (Bellini, 2009), and then independently by Richard Blakemore in 1975, when micro-organisms were observed to migrate rapidly within freshwater-mud samples on microscope slides in response to magnetism (Blakemore, 1975). The term ‘magnetotaxis’ was coined for this behaviour (Blakemore, 1975), and it was found to be the result of a permanent magnetic dipole moment conferred by internal magnetite (Fe₃O₄) or greigite (Fe₃S₄) crystals, which causes the cell to be orientated along geomagnetic field lines as it swims (Bazylinski & Frankel, 2004). Magnetotaxis is hypothesized to expedite the search for optimal concentrations of certain nutrients within water columns and sediments, by simplifying a three-dimensional search to a linear search (Frankel et al., 1997; Bazylinski & Frankel, 2004). The first magnetotactic bacterium to be isolated in pure culture and cultivated was the magnetite-producing strain Magnetospirillum magnetotacticum (basonym *Aqua-
spirillum magnetotacticum*) MS-1T (Blakemore et al., 1979; Maratea & Blakemore, 1981; Schleifer et al., 1991). Cells of MS-1T were found to require molecular oxygen for growth and magnetite biosynthesis (Blakemore et al., 1985). Biogenic, single-magnetic-domain magnetite crystals in magnetosomes were therefore assumed to be formed only under microaerobic conditions and were indicative of oxygenated sediments at the time of deposition. This was refuted by the discovery and axenic cultivation of the magnetotactic bacterium strain MV-1T (‘magnetic vibrio 1’), which is capable of growth and magnetite production under strictly anoxic conditions (Bazylinski et al., 1988). This was an important discovery, because strain MV-1T demonstrated that magnetite biosynthesis was not dependent upon the availability of molecular oxygen, and therefore anaerobic magnetotactic bacteria could be important contributors to the magnetic remanence in sediments (Bazylinski et al., 1988). Since then, other magnetotactic bacteria have been demonstrated to grow anaerobically, including the obligate anaerobe Desulfovibrio magneticus RS-
1T, *Candidatus Desulfamplus magnetomortis* BW-1 and the obligately alkaliphilic strains ML-1, ZZ-1 and AV-1, using sulfate (Sakaguchi et al., 1993, 2002; Lefèvre et al., 2011a, b), and the facultative anaerobes Magnetospirillum sp. strain AMB-1 and Magnetospirillum gryphiswaldense MSR-
1T, using nitrate (Matsunaga et al., 2005; D. Schüler, personal communication).

Strain MV-1T was originally isolated from sulfide-rich sediments from a salt marsh pool at the Neponset River estuary near Boston, MA, USA (Bazylinski et al., 1988). Strain MV-1T has been the subject of several previous studies, centred mostly on the production and morphology of magnetite by this strain in culture (Bazylinski et al., 1988, 1995; Thomas-Keprta et al., 2001; Dubbels et al., 2004), including the generation of spontaneous non-
magnetotactic mutants (Dubbels et al., 2004), and autotrophic growth of strain MV-1T via the Calvin–Benson–Bassham (CBB) cycle (Bazylinski et al., 2004). Nevertheless, this important magnetotactic strain has not yet been characterized in the literature. The aim of the current study is to characterize and formally name the magnetivibrio strain MV-1T.

Cells of strain MV-1T were isolated from a natural enrichment of magnetotactic bacteria at the oxic–anoxic interface within a bottle containing water and sediment (Fig. S1, available in IJSEM Online). A complete description of the collection, enrichment and isolation procedure is given in Supplementary Methods (available in IJSEM Online). After isolation, cells were grown routinely in oxygen-free liquid cultures of diluted artificial seawater (ASW) medium containing (per litre diluted ASW) 16.4 g NaCl, 3.5 g MgCl₂·6H₂O, 2.7 g Na₂SO₄, 0.47 g KCl, 0.39 g CaCl₂·2H₂O, 5 ml modified Wolfe’s mineral elixir (Frankel et al., 1997), 0.5 ml vitamin solution (Frankel et al., 1997), 0.5 g sodium succinate, 0.5 g Casamino acids, 0.2 g sodium acetate trihydrate, 0.2 g NH₄Cl, 2 ml freshly prepared, filter-sterilized, neutralized 0.43 M cysteine hydrochloride hydrolyzed as the reducing agent, 1.8 ml 0.5 M KHPO₄ buffer, pH 6.9, and 2.4 ml 0.8 M NaHCO₃. Nitrous oxide (N₂O) at 1 atm (101.3 kPa) was used as the terminal electron acceptor.

Analytical electron microscopy was performed on cells using a VG Microscopes model HB-5 scanning transmission electron microscope (Fisons Instrument Surface Systems) operating at 100 kV linked to a field-emission electron gun, a Link LZ-5 X-ray detector (Link Analytical) and an AN10000 X-ray analysis system. Motility of strain MV-1T was determined using a Zeiss Axiolab M1 light microscope (Carl Zeiss MicroImaging Inc.) equipped with phase-contrast and differential interference contrast capabilities. Cells of strain MV-1T were vibrioid to helicoid, 1–
3 µm long by 0.2–0.4 µm wide (Figs 1a and S2) and motile by means of a single polar flagellum (monotrichous; Fig. 1a). Cells had a more vibrioid (comma-shaped) than helicoid morphology when grown microaerobiocally (Fig. S2). They possessed a typical Gram-negative cell wall and some cells had a polar membrane or organelle (Fig. 1c) that has been associated with the flagellar apparatus and ATPases, and cytochrome oxidase activities in other bacteria (Tauschel, 1985). Cells contained sulfur-rich inclusions when grown on sulfide (Bazylinski et al., 2004). Some cells also contained intracellular inclusions.
that were rich in phosphorus, and probably represent deposits of polyphosphate (Bazylinski et al., 2004). The parallelepipedal-shaped magnetite crystals were arranged as a single chain of around 10 crystals positioned along the long axis of the cell, which sometimes had large gaps between them (Fig. 1b).

Cells of strain MV-1T appear to display aspects of both polar and axial magnetotaxis (Frankel et al., 1997); that is, they swim in both directions, changing direction spontaneously without turning around, similar to magnetotactic species of Magnetospirillum (Bazylinski et al., 1988). However, in hanging-drop assays, many cells appeared to accumulate at the edge of the drop, suggesting that some cells have a polar preference in their swimming direction and that they swim longer distances in one direction than another (Bazylinski & Williams, 2007). Thus, cells of strain MV-1T appear to display a transitional state between axial and polar magnetotaxis.

Anaerobic growth (using sodium succinate, sodium acetate and Casamino acids as electron donors) was tested in liquid medium using the following as terminal electron acceptors (sodium salts, where appropriate): nitrate (2, 5 and 10 mM), nitrite (1, 2 and 5 mM), N2O (1 atm; 101.3 kPa), fumarate (20 mM), sulfate (5 and 10 mM), trimethylamine oxide (15 mM) and DMSO (15 mM). Cells grew anaerobically with nitrate, at 2 and 5 but not 10 mM, nitrite and N2O, but none of the other tested terminal electron acceptors supported anaerobic growth.

During growth on N2O, oxidation of completely reduced resazurin to resorufin in the growth medium caused the colour of the medium to change from initially colourless to pink. This did not occur during anaerobic growth with...
nitrate or nitrite. Growth and N₂O reduction appeared to be necessary for the oxidation of resazurin, because the addition of 1% acetylene to these cultures, a known inhibitor of N₂O reduction (Yoshinari et al., 1977), inhibited growth, N₂O reduction and resazurin oxidation completely. This suggests that, under these conditions, the completely reduced form of resazurin acts as an electron donor during N₂O reduction, although it is not necessary for growth on this terminal electron acceptor. To our knowledge, reduced resazurin has never been shown to act as an electron donor in nitrogen oxide reduction, although a method was developed that utilized this reaction to detect NO- or N₂O-producing bacteria in solid or liquid medium (Jenneman et al., 1986). Alternatively, the oxidation of Fe(II) might support N₂O reduction during growth and the resulting Fe(III) could, in turn, cause the oxidation of resazurin and the change from colourless to pink. Strain MV-1ᵀ is known to possess an Fe(II) oxidase (Dubbels et al., 2004). Our results show that strain MV-1ᵀ is a facultatively anaerobic microaerophile.

Carbon sources at a concentration of 0.1 % (w/v) were tested for microaerobic growth in semi-solid [1.5 g agar noble (Difco) 1⁻¹⁰⁷ [O₂] gradient medium as well as for anaerobic growth with N₂O as the terminal electron acceptor. Screw-capped test tubes were used to test for microaerobic growth. Each tube contained 10 ml growth medium and was inoculated with approximately 10⁵ cells ml⁻¹, distributed throughout the growth medium while the medium was still liquid (kept at about 44 °C). A carbon source was deemed positive for the support of aerobic growth of strain MV-1ᵀ if three conditions were met: (i) a band of cells formed in the tube, (ii) the cell count after growth was significantly greater than the control containing no carbon source and (iii) cells continued to grow in the same medium in three successive transfers. Anaerobic growth on specific carbon sources using N₂O as the terminal electron acceptor was determined in the same way, except that the test tubes had septum stoppers. After inoculation as described above, the headspace of these tubes was replaced quickly with 1.2 atm (121.6 kPa) N₂O. Growth was determined as described above, except that bands of cells did not form and N₂ formation as bubbles from the reduction of N₂O was monitored. The semi-solid agar tended to trap bubbles of N₂, thereby making them visible.

A range of compounds was tested as carbon sources; sodium salts were used for all acids, neutralized when appropriate. The organic acids, amino acids, alcohols, carbohydrates and complex substrates that were tested are listed in Table S1. Those compounds that resulted in growth indicate chemo-organoheterotrophic growth by strain MV-1ᵀ except for formate, which is interpreted as supporting chemo-organoaotrophic growth (see below).

Cells of strain MV-1ᵀ grown autotrophically under microaerobic conditions in semi-solid [O₂] gradient cultures using sulfide, thiosulfate and formate as electron donors but not tetrathionate or ferrous iron (as a sulfide or carbonate) (Bazylinski et al., 2004). However, in further studies of these electron donors, cells only grew on thiosulfate anaerobically with N₂O as the terminal electron acceptor. Strain MV-1ᵀ utilizes the CBB cycle for CO₂ fixation and autotrophy and possesses a form II ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) gene (cbbM) (GenBank accession no. AF442518; Bazylinski et al., 2004). Thus, strain MV-1ᵀ is capable of chemolithoautotrophic and chemo-organoaotrophic (with formate as electron donor) growth.

Because strain MV-1ᵀ was found in a brackish-to-marine environment, we examined whether concentrations of salts close to those of marine waters were required for growth. Cells were grown anaerobically with N₂O as the terminal electron acceptor as described above, except that different concentrations of Lyman and Fleming’s ASW (Lyman & Fleming, 1940), a formulation that has a salinity very close to that of natural seawater (~35 p.p.t.), was used as the diluent. Cells grew well in concentrations of this ASW ranging from 25 to 125 %, with the shortest doubling time during exponential growth, ~11 h, at a concentration of 50 %. Cells grew very poorly (1–2 doublings) at 10 and 150 % ASW and not at all with distilled water as the diluent or when the concentration of ASW was >150 %. Thus, like many marine bacteria (Kaye & Baross, 2004), strain MV-1ᵀ is euryhaline but has a growth requirement for salts, as it will not grow at very low concentrations of ASW or in freshwater media.

The magnetosomes of strain MV-1ᵀ contain crystals of magnetite surrounded by a membrane (Fig. 1b–d) (Bazylinski et al., 1988). Greigite was never observed in magnetosomes. The specific crystal habit of magnetite is truncated hexacahedron, with eight 111 octahedral faces, six 110 hexagonal faces and six 100 cubic faces (Thomas-Keptra et al., 2001). The dimensions of each crystal are approximately 35 × 35 × 53 nm, with the axis of elongation corresponding to the alignment of crystals within the chain (Fig. 1b, d) (Sparks et al., 1990).

Cells produced magnetosomes and were magnetotactic under both microaerobic and anaerobic conditions. When grown anaerobically with N₂O as the terminal electron acceptor, cells produced a mean of 10.4 ± 3.9 magnetosomes per cell (n=125), while 2.4 % of the cells did not contain magnetosomes. Interestingly, cells still produced magnetosomes even when the major source of iron (ferric quinate) was omitted from the growth medium, but with a mean of 4.9 ± 3.7 magnetosomes per cell (n=111). In this latter case, 10.8 % of the cells did not contain magnetosomes. However, the final cell yield of these cultures was only 23–28 % of the high-iron-containing culture, based on direct cell counts, which suggests that cells in these low-iron cultures continue to produce magnetosomes, thereby starving themselves of iron and limiting their growth yield. This further indicates that magnetosome iron in this strain is not biologically available for growth, and thus magnetosomes are not used for iron storage (Dubbels et al., 2004).
Further support for this notion comes from the fact that the addition of ferric quinate to these cultures resulted in continued growth and a final yield similar to that when ferric quinate was added prior to inoculation (data not shown). Cells of strain MV-1T grown anaerobically with nitrate produced fewer magnetosomes than those grown with N₂O, a mean of 6.7 ± 4.8 magnetosomes per cell (n = 150). When grown on nitrate, 10.5% of cells did not contain magnetosomes. Cells grown microaerobically produced slightly fewer magnetosomes than cells grown on N₂O, but more than on nitrate, a mean of about 8 per cell when the major source of iron was included in the growth medium (Bazylinski, 1991).

Nitrogenase activity of whole cells was determined by acetylene (C₂H₂) reduction to ethylene (C₂H₄) in [O₂]-gradient cultures as described by Bazylinski et al. (2000), using *Magnetospirillum magnetotacticum* MS-1T as a positive control (Bazylinski & Blakemore, 1983a; Bazylinski et al., 2000). Cells of strain MV-1T showed relatively high nitrogenase activity (Table S2) as measured by C₂H₂ reduction to C₂H₄ in semi-solid [O₂] gradient cultures with succinate and acetate as electron donors. C₂H₂ reduction was inhibited by the addition of the fixed nitrogen sources NH₄Cl and NaNO₃ (both at 4 mM). The fact that nitrate inhibited C₂H₂ reduction suggests that strain MV-1T is capable of assimilatory nitrate reduction.

Cells of strain MV-1T for chemical analyses were grown to late-exponential phase, harvested by centrifugation and freeze-dried. These cells were analysed for relative amounts of carbon, hydrogen and nitrogen as described by Bazylinski & Blakemore (1983b) and protein (Lowry et al., 1951) using BSA as the standard; and for relative amounts of iron and magnetite (see below). Measurements were performed in triplicate. Whole freeze-dried cells of strain MV-1T from late-exponential anaerobic growth cultures consisted of (on a dry weight basis) 42.9 ± 0.5 % C, 10.5 ± 0.4 % N, 5.7 ± 0.2 % H and 51.4 ± 1.0 % protein. These values are generally comparable to those for another magnetotactic bacterium, *Magnetospirillum magnetotacticum* MS-1T (Bazylinski & Blakemore, 1983b).

In the case of iron and magnetite, two separate batches of cells grown with and without the major source of iron (ferric quinate) were analysed. All glassware for the determination of total iron in cells was soaked overnight in 10 % HCl and then rinsed five times with Nanopure water (Millipore). All acids used for iron determinations were trace-metal grade (Mallinckrodt Baf Inc.). Approximately 15 mg freeze-dried cells was acid-digested as described by Dubbels et al. (2004). Samples of growth medium were acidified and diluted directly with concentrated HCl to a final concentration of 1 %. Total iron was determined using the ferrozine reagent (Stokey, 1970) and/or atomic absorption spectroscopy (Dubbels et al., 2004). The percentage of magnetite was determined from the saturation magnetization (Ms) obtained from room temperature hysteresis loops measured with a vibrating sample magnetometer using an electromagnet to produce fields up to 1.5 T (Jackson & Solheid, 2010). Saturation magnetization was determined after the loops were corrected for high-field slopes to remove the effects of diamagnetic or paramagnetic contributions to the magnetization. The percentage magnetite by weight in samples consisting of a known mass of whole freeze-dried cells (~10–30 mg) was determined from the measured Ms values and the known value for pure magnetite (Ms=92 Am² kg⁻¹) as follows: wt% magnetite=100 % × Ms/(92 Am² kg⁻¹).

Percentages of total iron and magnetite of whole freeze-dried cells are shown in Table S3. The percentage of total iron in cells grown with the major iron source appeared to vary from culture to culture, and we obtained values of about 1.9 and 1.3 % in two separate cultures grown in the same way. Cells from cultures grown without the major source of iron appeared to have a more consistent iron content, containing about 0.5 % total iron. Values for the percentage of magnetite by weight were similar. The presence of magnetite in cells grown with low iron is consistent with the previously discussed magnetosome results, in which these cells produced a significant number of magnetosomes under low-iron conditions. It is noteworthy that the amount of total iron calculated from the percentage of magnetite was less, in all cases, than the measured total iron, showing that there is a significant amount of iron associated with cells that is not in the form of magnetite.

Cells for lipid analyses were grown anaerobically with N₂O and were harvested at the mid- to late-exponential phase of growth by centrifugation at 4 °C. Membrane lipids from cells of strain MV-1T were extracted at room temperature in test tubes containing a monophasic mixture of methanol/dichloromethane/phosphate buffer (50 mM, pH 7.4) (2 : 1 : 0.8 by vol.) (Fang & Findlay, 1996). The extraction mixture was allowed to stand overnight in the dark at 4 °C. Crude lipids were collected after phase partitioning by adding dichloromethane and deionized water to a final ratio of methanol/dichloromethane/water of 1 : 1 : 0.9 (by vol.). Total lipids were fractionated into different lipid classes using miniature columns (Supelco, Inc.) containing 100 mg silicic acid. Neutral lipids, glycolipids and phospholipids were obtained by sequential elution with 5 ml aliquots of chloroform, acetone and methanol, respectively.

Ester-linked phospholipid fatty acids were subjected to a mild alkaline transmethylation procedure to produce fatty acid methyl esters (Fang & Findlay, 1996). The fatty acid methyl esters were analysed on an Agilent 6890 GC interfaced with an Agilent 5973N mass selective detector. Analytical separation of the compounds was accomplished using a 30 m × 0.25 mm i.d. DB-5 MS fused-silica capillary column (J&W Scientific). The column temperature was programmed from 50 to 140 °C at 20 °C min⁻¹ and then to 300 °C at 5 °C min⁻¹, and then held at 300 °C for 15 min. Individual compounds were identified from their mass spectra. Response factors were obtained for each
compound by using duplicate injections of quantitative standards at five different concentrations. Concentrations of individual compounds were obtained based on the GC/MS response relative to that of an internal standard (C18:0 fatty acid ethyl ester). Method blanks were extracted with samples and were assumed to be free of contamination if chromatograms of the blanks contained no peaks. A standard containing known concentrations of 26 fatty acids was analysed daily on the GC/MS to check analytical accuracy (>90%). Replicate analyses of samples were done to ensure reproducibility (variation ≤10%). The following fatty acid profile was obtained for strain MV-1\textsuperscript{T}: C18:1\textasciitilde\textasciitilde\textasciitilde (49.6 mol%), C16:1\textasciitilde\textasciitilde\textasciitilde (30.6 mol%), C16:0 (13.7 mol%), C16:1\textasciitilde\textasciitilde\textasciitilde (4.1 mol%), C14:0 (0.8 mol%), C18:0 (0.3 mol%), C18:1\textasciitilde\textasciitilde\textasciitilde (0.4 mol%) and C16:1\textasciitilde\textasciitilde\textasciitilde (0.4 mol%). Analysis of cellular fatty acids and polar lipids was also carried out by the Identification Service of the DSMZ, Braunschweig, Germany. The total fatty acid profile from the DSMZ was similar to the profile described above. Major polar lipids were phosphatidylethanolamine and phosphatidylglycerol, as well as an unknown phospholipid and two aminophospholipids (Fig. S3).

The genome of strain MV-1\textsuperscript{T} consists of a single, circular chromosome, about 3.7 Mb in size; extrachromosomal elements (e.g. plasmids) were not detected (Dean & Bazylnski, 1999). The G+C content of the genomic DNA of strain MV-1\textsuperscript{T} was determined by HPLC by the DSMZ, according to the method of Mesbah et al. (1989) and by the thermal denaturation technique (Herdman et al., 1979) after purification of genomic DNA using the method described by Kimble et al. (1995). The G+C content of the genome as determined by HPLC was 52.9 ± 0.1 mol% (three measurements); that determined by thermal denaturation was 53.5 ± 0.1 mol% (three measurements).

Phylogenetic analysis based on a partial 16S rRNA gene sequence (GenBank accession no. L06455; 1128 of 1361 nt), obtained as described by Delong et al. (1993), shows strain MV-1\textsuperscript{T} as a member of the Rhodospirillaceae within the Alphaproteobacteria (Fig. 2). Strain MV-1\textsuperscript{T} does not share a close relationship with Magnetospirillum or with Magnetococcus (Bazylnski et al., 2013). Strain MV-1\textsuperscript{T} is most closely related to Magnetospira thiophila MMS-1\textsuperscript{T} (89.2% 16S rRNA gene sequence identity; Williams et al., 2012) and strain QH-2 (89.2%; Zhu et al., 2010) among magnetotactic bacteria, and to the non-magnetotactic species Terasakiella pusilla (87.6% sequence identity to the type strain; Satomi et al., 2002) and Thalassospira lucentensis (85.9%; López-López et al., 2002) and an undescribed marine bacterium, ‘Candidatus Koprioniomas byunsanensis’ (88.1%). This cluster may constitute a novel clade within the Rhodospirillaceae, although the node currently has weak bootstrap support (Fig. 2). Within this cluster, strain MV-1\textsuperscript{T} shares magnetotactic abilities with Magnetospira thiophila and strain QH-2. Strain MV-1\textsuperscript{T} is capable of anaerobic growth using several nitrogen species as terminal electron acceptors (N₂O, nitrate, nitrite). The type strains of Terasakiella pusilla, Thalassospira lucentensis and Magnetospira thiophila all require oxygen as the terminal electron acceptor (Satomi et al., 2002; López-López et al., 2002; Williams et al., 2012), although other Thalassospira species are facultative anaerobes that are
capable of growth on nitrate (Liu et al., 2007; Kodama et al., 2008; Zhao et al., 2010). Characterized species of Terasakiella and Thalassospira are obligate chemo-organoheterotrophs, unlike strain MV−1 T and Magnetospira thiophila, both of which are capable of chemolithoautotrophic growth using the CBB cycle (Williams et al., 2012).

Among characterized magnetotactic members of the Alphaproteobacteria, strain MV−1 T shows the greatest metabolic versatility in the compounds that can be used as potential electron donors and carbon sources for growth during microaerobic and anaerobic growth (Table 1). This is in contrast to its closest characterized relative, Magnetospira thiophila MMS−1 T, which is an obligate microaerophile that can use only a relatively small number of organic acids as carbon and energy sources (Table 1). Chemo-organoheterotrophic growth of strain MV−1 T is supported by a large number of organic acids (including formate for methylotrophic growth) and certain amino acids (Table S1). Unique among characterized magnetotactic bacteria, strain MV−1 T is also capable of using N2O for respiration. N2O is available in the marine environment as an alternative terminal electron acceptor.

Table 1. Characteristics that differentiate strain MV−1 T from other magnetotactic strains within the Alphaproteobacteria

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>MV−1 T</th>
<th>1</th>
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<td>Cell morphology</td>
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<td>Amphitrichous</td>
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<td>Magnetotaxis</td>
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<td>Polar</td>
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<td>Magnetite shape</td>
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<td>Cuboctahedral</td>
<td>Cuboctahedral</td>
<td>Elongated pseudohexahedral</td>
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<td>Electron donor(s)</td>
<td>Thiosulfate, sulfide, organic C (=C sources)</td>
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<td>Organic C</td>
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<td>Thiosulfate, sulfide</td>
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<td>Heterotrophic*</td>
<td>Microaerobic: acetate, formate, fumarate, lactate, malate, maleate, 2−oxoglutarate, propionate, pyruvate, succinate, aspartate, glutamate, alanine, glutamine, serine. Anaerobic (N2O): malate, malonate, oxaloacetate, 2−oxoglutarate, succinate</td>
<td>Acetate, fumarate, malate, succinate</td>
<td>Acetate, lactate, malate, pyruvate, succinate</td>
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<td>55.8</td>
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</tbody>
</table>

*Defined carbon sources only.
acceptor to oxygen: under suboxic or anaerobic conditions, heterotrophic denitrifying bacteria produce N₂O as an intermediate, and ammonia-oxidizing archaea and bacteria generate N₂O by nitrite reduction (Santoro et al., 2011). Thus, we posit an important role for MV-1T in nitrogen cycling in its environment. In light of the characteristics of this magnetotactic strain, a new genus is warranted for the reception of strain MV-1T, within the family Rhodospirillaceae.

**Description of Magnetovibrio gen. nov.**

*Magnetovibrio* (Ma.gne.to.ví’bri.o. Gr. n. magnēs -ētos a magnet; N.L. pref. magneto- pertaining to a magnet; N.L. masc. n. vibrio a vibrio; N.L. masc. n. *Magnetovibrio* the magnetic vibrio, which references the vibrioid morphology and magnetotactic behaviour of this bacterium).

Cells are Gram-negative and vibrioid to helicoid in morphology, and motile by means of a single polar flagellum. Cells assimilate inorganic carbon (as CO₂) chemolithoautotrophically with thiosulfate and sulfide as the electron donors, using a form II RubisCO (CbbM) and the CBB cycle. Cells exhibit characteristics of both axial and polar magnetotaxis, and biomineralize a single chain of magnetosomes that contain magnetite crystals of truncated hexagonal habit, positioned along the long axis of the cell. Major polar lipids identified include phosphatidylethanolamine and phosphatidylglycerol. The genus belongs to the family Rhodospirillaceae within the class Alphaproteobacteria. The type species is *Magnetovibrio blakemorei*.

**Description of Magnetovibrio blakemorei sp. nov.**

*Magnetovibrio blakemorei* (blak.mo’re.i. N.L. gen. masc. n. blakemorei of Blakemore, named in honour of US microbiologist Richard P. Blakemore, who was the first to describe scientifically and publish on magnetotactic behaviour in bacteria).

Exhibits the following characteristics in addition to those for the genus. Cells are 1–3 µm long by 0.2–0.4 µm wide. Facultatively microaerophilic and anaerobic. Catalase-negative, oxidase-positive. Mesophilic, with a growth temperature range of 4–31 °C and optimal growth temperature of 26–28 °C. Cells produce internal sulfur-rich globules when grown on sulfide. Terminal electron acceptors include oxygen, N₂O, nitrate and nitrite. Capable of chemolithoautotrophic growth on thiosulfate and sulfide with oxygen as the terminal electron acceptor and on thiosulfate using N₂O as the terminal electron acceptor. Capable of chemooxygenautotrophic and methylothrophic growth on formate under microaerobic (but not anaerobic) conditions. Capable of chemo-organoheterotrophic growth under microaerobic conditions using certain organic acids (acetate, fumarate, lactate, malate, maleate, 2-oxoglutarate, propionate, pyruvate, succinate), amino acids (aspartate, glutamate, alanine, glutamine, serine), Casamino acids, peptone, yeast extract and tryptone. Capable of chemo-organoheterotrophic growth under anaerobic conditions (N₂O as the terminal electron acceptor) using certain organic acids (maleate, oxaloacetate, 2-oxoglutarate, succinate) and Casamino acids. Cellular fatty acids are dominated by C₁₈:₁₀₀₇, C₁₆:₁₀₀₇, C₁₆:₀ and C₁₆:₁₀₀₅. The genome consists of a single, circular chromosome with a size of 3.7 Mb and a G+C content of 52.9–53.5 mol%.

The type strain is MV-1T (=ATCC BAA-1436T =DSM 18854ᵀ), originally isolated from a salt marsh pool at the Neponset River estuary near Boston, MA, USA.

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**References**


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