Desulfonatronum thiodismutans sp. nov., a novel alkaliphilic, sulfate-reducing bacterium capable of lithoautotrophic growth

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A novel alkaliphilic, sulfate-reducing bacterium, strain MLF1T, was isolated from sediments of soda Mono Lake, California. Gram-negative vibrio-shaped cells were observed, which were 0·6–0·7 × 1·2–2·7 μm in size, motile by a single polar flagellum and occurred singly, in pairs or as short spirilla. Growth was observed at 15–48 °C (optimum, 37 °C), >1–7 % NaCl, w/v (optimum, 3 %) and pH 8·0–10·0 (optimum, 9·5). The novel isolate is strictly alkaliphilic, requires a high concentration of carbonate in the growth medium and is obligately anaerobic and catalase-negative. As electron donors, strain MLF1T uses hydrogen, formate and ethanol. Sulfate, sulfite and thiosulfate (but not sulfur or nitrate) can be used as electron acceptors. The novel isolate is a lithoheterotroph and a facultative lithoautotroph that is able to grow on hydrogen without an organic source of carbon. Strain MLF1T is resistant to kanamycin and gentamicin, but sensitive to chloramphenicol and tetracycline. The DNA G+C content is 63·0 mol% (HPLC). DNA–DNA hybridization with the most closely related species, Desulfonatronum lacustre Z-7951T, exhibited 51 % homology. Also, the genome size (1·6 × 10⁶ Da) and Tm value of the genomic DNA (71 ± 2 °C) for strain MLF1T were significantly different from the genome size (2·1 × 10⁶ Da) and Tm value (63 ± 2 °C) for Desulfonatronum lacustre Z-7951T. On the basis of physiological and molecular properties, the isolate was considered to be a novel species of the genus Desulfonatronum, for which the name Desulfonatronum thiodismutans sp. nov. is proposed (the type strain is MLF1T = ATCC BAA-395T = DSM 14708T).

The sulfate-reducing bacteria present a large spectrum of extremophiles and include psychrophilic, thermophilic, halophilic and alkaliphilic Archaea and Bacteria (Widdel & Hansen, 1992; Castro et al., 2000; Pikuta & Hoover, 2001). Among this group, there are two genera that contain obligately alkaliphilic species. The first alkaliphilic sulfate-reducer, Desulfonatronovibrio hydrogenovorans, was isolated from soda Lake Magadi in equatorial Africa (Zhilina et al., 1997). Later, the distribution of this species was extended to Tuva’s soda lakes in Siberia, central Asia (Pikuta et al., 1997) and a novel alkaliphilic species, Desulfonatronum lacustre, was described (Pikuta et al., 1998). Both genera include Gram-negative, non-spore-forming, mesophilic, obligately carbonate-dependent alkaliphiles that are incapable of growth below pH 8·0. The moderately thermophilic and alkaliphilic, spore-forming sulfate-reducer Desulfotomaculum alkaliphilum was isolated from manure with neutral pH (Pikuta et al., 2000), indicating that the adaptation of microorganisms to alkalic environments is not connected with deep genetic changes and that local micro-ecosystems with high pH and temperature could be created in composite substrates, such as soil or manure, by these micro-organisms. All previously described alkaliphilic sulfate-reducers had a lithoheterotrophic metabolism.

In this article we describe a novel alkaliphilic, mesophilic, sulfate-reducing bacterium with the capacity for lithoautotrophic growth.
Isolation, cultivation and morphology

Black mud sediments (pH 9.9 ± 0.02) with a strong smell of sulfide were collected anaerobically from under shallow water (temperature, 21.6 ± 0.1°C; salinity, 7%) near the south shore of Mono Lake in California on 15 August 2000. Mud samples were hermetically sealed in sterile glass vessels with screw caps, maintained at 4°C during transportation and stored at 2°C in the Astrobiology Laboratory of the NASA Marshall Space Flight Center. For cultivation of the novel isolate, modified medium was used (Pikuta et al., 1998), which contained (1 M): Na₂SO₄, 3 g; NaCl, 30 g; Na₂CO₃, 2.76 g; NaHCO₃, 24.0 g; KCl, 0.2 g; K₂HPO₄, 0.2 g; MgCl₂·6H₂O, 0.1 g; NH₄Cl, 1.0 g; Na₂S·9H₂O, 0.4 g; resazurin, 0.001 g; yeast extract, 0.2 g; Na-formate, 5.0 g; 2 ml vitamin solution (Wolin et al., 1963); and 1 ml trace mineral solution (Whitman et al., 1982). The final pH was adjusted to 9.5. High-purity nitrogen was used as the gas phase, except in the case of cultivation with hydrogen as the electron donor, for which the gas phase was filled by pure hydrogen. To obtain enrichment cultures, 0.5 g wet sediment material (pH 10.0) was injected into standard Hungate tubes that contained medium and incubated at 35°C for 10–14 days. Pure cultures were obtained by the dilutions method on sulfate-containing medium with hydrogen as the electron donor. Growth of colonies was checked by the ‘roll-tube’ method on 3% (w/v) agar medium, where carbonates were added separately after autoclaving. Colonies were white-yellowish, lens-shaped in medium, where carbonates were added separately after autoclaving. Colonies were white-yellowish, lens-shaped in deep agar and 0.5–2.0 mm in diameter with irregular, smooth edges. One colony was chosen for further characterization and designated strain MLF₁ᵀ (= ATCC BAA-395ᵀ = DSM 14708ᵀ). Purity of the culture during this study was indicated by the absence of growth on glucose–peptone sulfate-free medium that contained excessive quantities of yeast extract and by microscopic control.

Transmission electron microscopy was carried out by using a JEOL TEM 100 CX II. Negative staining was performed with uranyl acetate. Cells of strain MLF₁ᵀ were highly motile and vibrio-shaped, 0.6–0.7 μm in diameter and 1.2–2.7 μm long and had a single polar flagellum (Fig. 1). Cells occurred singly, in pairs or as short spirilla. Multiplication occurred by binary fission. Gram-stained cells of strain MLF₁ᵀ exhibited the red colour typical for the reaction with Gram-negative cell walls. Spores were not observed.

Growth characteristics and metabolic properties

Bacterial growth was measured by direct cell count under a phase-contrast microscope (Fischer Micromaster), by measuring sulfide in the growth medium (Trüper & Schlegel, 1964) or by estimating an increase in OD₅₁₀ (Genius 5; Spectronic Instruments). All experiments were performed at 35°C. Obligate dependence on the CO₃²⁻ ion was detected by using a medium that was described previously (Pikuta et al., 2000). Dependence on Na⁺ ions was detected by substitution of Na-containing salts by K-containing salts. Dependence on Cl⁻ ions was checked by substitution of Cl⁻-containing salts by sulfates. The novel isolate grew only under strictly anaerobic conditions and was catalase-negative (Gerhardt et al., 1981). The isolate was mesophilic and grew at 15–45°C, with optimum growth at 37°C; growth was absent at 10 and 53°C. The novel isolate grew at pH 8–0–10; no growth was detected at pH values of 7.8 or 10.5. Strain MLF₁ᵀ required Na⁺ ions (from NaCl) for growth; it did not grow at 0% (w/v) NaCl. The optimum NaCl concentration was 3% (w/v), the range for growth was 1–7% (w/v) and growth was absent at 10% (w/v) NaCl. The generation time at optimal conditions [37°C, 3% (w/v) NaCl and pH 9.5] was 20 h. The novel isolate was obligately dependent on Na⁺ ions, as it did not grow on medium with potassium salts instead of sodium salts. The absence of growth on serine-buffered medium demonstrated obligate dependence on CO₃²⁻ ions. Strain MLF₁ᵀ was not dependent on Cl⁻ ions, but cell motility was significantly decreased on medium without Cl-containing salts. The novel isolate required sulfates for respiration. End-products of sulfate respiration in the liquid phase were determined by HPLC. Sodium salts (formate, acetate, lactate, pyruvate, propionate and isovalerate) were used as standards. Separation was done on an Aminex HPX-87H column (Bio-Rad), with 5 mM H₂SO₄ as the mobile phase. Gases (hydrogen, carbon dioxide, carbon monoxide and methane) were measured by using a model 3700 gas chromatograph (Varian) equipped with a Porapak Q column and a thermal conductivity detector. Nitrogen was used as the gas carrier. During sulfate respiration with formate, strain MLF₁ᵀ excreted only hydrogen sulfide (more than 30 mM) and no organic end-products were detected. CO₂ measurement at high pH was not feasible because of the high carbonate content of the medium.

Strain MLF₁ᵀ had a lithoautotrophic type of metabolism. Growth was observed during three consequent inoculations.
on hydrogen medium with no organic carbon source. Growth on media without an organic carbon source was slow (10–14 days) with lower optical density (0.08–0.1) and the number of cells was approximately $10^8$ ml$^{-1}$. During lithoautotrophic growth ($H_2$ + CO$_2$), high sulfidogenesis (10–15 mM H$_2$S) was registered. Strain MLF1$^T$ also grew on H$_2$ media with yeast extract or acetate (2 mM). Organic carbon sources stimulated growth, with more rapid growth occurring on media with yeast extract than with acetate (optical density of growth on acetate was 0.2–0.25, and on yeast extract it was 0.3–0.5). Strain MLF1$^T$ does not have a fermentative type of metabolism for organic substrates and has a very restricted spectrum of electron donors; only hydrogen, formate and ethanol were utilized. Growth did not occur on acetate, propionate, butyrate, pyruvate, lactate, methanol, glycerol, glycine, cysteine, cystine, serine, alanine, glutamate, aspartate, Casamino acids, yeast extract, peptone, bacitracin, betaine, trimethylamine, glucose, fructose, mannose, starch or citrate. Sulfate, sulfite and thiosulfate were utilized as electron acceptors and elemental sulfur inhibited growth. Nitrate did not support growth. The novel isolate was capable of performing dismutation (inorganic fermentation); good growth, with optical density 0.2–0.25, was observed on sulfite (5 mM) or thiosulfate (10 mM) with 2 mM acetate. Sulfidogenesis was registered at thiosulfate dismutation (8 mM H$_2$S) and at sulfite dismutation (3–4 mM H$_2$S). Sulfate production was measured nephelometrically with BaCl$_2$. Sulfate concentration was 8 mM during thiosulfate dismutation and 3–8 mM during sulfite dismutation; this stoichiometry is close to the dismutation data for Desulfovibrio sulfodismutans ThAc01$^T$ (Bak & Pfennig, 1987). Growth was inhibited by 5 mM molybdate, which blocks ATP sulfurylase in sulfate-reducing bacteria. Strain MLF1$^T$ was resistant to kanamycin and gentamicin (250 µg ml$^{-1}$), as growth without morphological changes was observed, and sensitive to tetracycline (250 µg ml$^{-1}$) and chloramphenicol (125 µg ml$^{-1}$).

**Fatty acids**

Fatty acid methyl esters were extracted from fresh biomass grown for 5 days and identified by using the Microbial Identification system (MIDI) Moore Library of anaerobic bacteria. The major fatty acid methyl esters were (%): C$\text{14.0}$ (16–08); C$\text{16.1}$ (21–23); C$\text{18.0}$ (17–91); and a mixture of C$\text{18}$ unsaturated fatty acids in cis- and trans-configurations (19–80). In lower amounts were (%): C$\text{16.0}$ (11–54); C$\text{18.1}$ (10–61); and C$\text{18.2}$ (2–84).

**DNA analysis**

The G+C content of the genomic DNA of strain MLF1$^T$ was measured by the HPLC method as described previously (Mesbah et al., 1989). An Alltima C$\text{18}$ column [250 × 4·6 mm, 5 µm particle size (Alltech)] and 8 % (v/v) methanol were used in this study. The results reported are the mean of three determinations for each of two degradations of the DNA. The G+C content of the genomic DNA of strain MLF1$^T$ was 63·0 ± 0·1 mol% (mean ± standard deviation, $n = 6$).

**16S rRNA gene sequence analysis**

Isolation of genomic DNA, amplification of the 16S rRNA gene and sequence determination were performed as described previously (Hoover et al., 2003). The quality of the consensus sequence was confirmed with data from eight different clones. The sequence of strain MLF1$^T$ was aligned with closely related sequences found in GenBank after a BLAST search (Altschul et al., 1990) by using the TreeView program from the GCG Wisconsin package. Pairwise distances were computed with MEGA version 2.0 (Kumar et al., 2001) by using the Jukes–Cantor (1969) model. An unrooted phylogenetic tree was constructed with the MEGA program by using the neighbour-joining method (Saitou & Nei, 1987). A sequence that covered 1481 nt of the 16S rRNA gene of strain MLF1$^T$ was obtained, corresponding to positions 28–1515 of the Escherichia coli 16S rRNA gene sequence. The G+C content of this sequence was 56·58 mol%. The sequence was compared with all sequences presently available in GenBank and appeared to be highly homologous to sequences from sulfate-reducing bacteria that belong to the δ-branch of the Proteobacteria. The phylogenetic tree, based on 1258 common nucleotide positions, shows that the closest relationship of strain MLF1$^T$ is to the genus Desulfonatronum, which is located between two large clusters that represent the genera Desulfovibrio and Desulfo microbium (Fig. 2). The highest degree of relatedness of strain MLF1$^T$ was observed with Desulfonatronum lacustre Z-7951$^T$. Pairwise comparison of the complete 16S rRNA gene sequences of strain MLF1$^T$ and Desulfonatronum lacustre Z-7951$^T$ showed only 97·6 % similarity over an alignment of 1359 nt.

**DNA melting temperatures**

Melting temperatures ($T_m$) of total genomic DNA from strain MLF1$^T$ and Desulfonatronum lacustre Z-7951$^T$ were determined by procedures described previously (De Ley et al., 1970; Gillis et al., 1970). Purified genomic DNA (200 µg) from strain MLF1$^T$ and Desulfonatronum lacustre Z-7951$^T$ was sonicated to generate DNA fragments of 500–700 bp. Any residual RNA and single-stranded DNA was removed by treatment with RNase A and S1 nuclease, respectively (Ausubel et al., 1987). Concentration and purity of the DNA were determined from $A_{260}$ readings and the ratio between $A_{260}$ and $A_{280}$ readings, by using a Shimadzu UV-160 spectrophotometer. DNA (80 µg) from each of these micro-organisms was then denatured in 1 × SSC buffer (pH 7·0) by increasing the temperature of the sample from 26 to 100°C (at a rate of 1°C min$^{-1}$) and $A_{260}$ was recorded. The experiment was conducted in triplicate. The melting temperature ($T_m$) was determined by calculating the temperature at which the hyperchromicity reached half of the value obtained after complete melting. The $T_m$ value of the genomic DNA of strain MLF1$^T$ was 71 ± 2°C (mean ±
standard deviation, \( n=3 \), whereas it was 63 ± 2 °C for *Desulfonatronum lacustre* Z-7951\(^T\).

**DNA–DNA hybridization**

To determine the homology of genomic DNA between strain MLF1\(^T\) and *Desulfonatronum lacustre* Z-7951\(^T\), DNA–DNA hybridization was performed by DNA reassociation kinetics as described previously (De Ley et al., 1970; Johnson, 1985). Purified, sonicated genomic DNA (80 \( \mu \)g) from each of these micro-organisms was added to 4 \( \times \) SSC buffer (pH 7-0) and 25 % deionized formamide. DNA was denatured by raising the temperature to 100 °C and then cooled to 5 °C above their respective melting temperatures. Then the temperature was rapidly lowered (1-5 min) to the reassociation temperature and \( A_{260} \) was recorded at 5 s intervals for a total of 20 min. The initial reassociation kinetics were determined by linear regression analysis. The experiment was conducted in triplicate. The homology of the DNA from these two micro-organisms was calculated by using the equation described by De Ley et al. (1970). All statistical analyses were performed using Microsoft Excel software. DNA–DNA hybridization established 51 % homology between the genomes of strain MLF1\(^T\) and *Desulfonatronum lacustre* Z-7951\(^T\).

**Genome size**

The genome sizes of strain MLF1\(^T\) and *Desulfonatronum lacustre* Z-7951\(^T\) were determined by using DNA reassociation kinetics, following the equation described by Gillis et al. (1970). The genome size for strain MLF1\(^T\) was 1.6 \( \times \) 10\(^9\) Da, whereas that for *Desulfonatronum lacustre* Z-7951\(^T\) was 2.1 \( \times \) 10\(^9\) Da.

**DISCUSSION**

The presence of alkaliphilic sulfatereducers in continental athalassic soda lakes on the African, Eurasian and American continents demonstrates the wide geographical distribution of these related organisms. The ancient nature of alkaline soda lakes could provide insights into the origin of bacterial diversity and distribution on planet Earth (Zavarzin et al., 1999). In previous work, a study of anaerobic bacterial communities was performed on samples of equatorial soda Magadi Lake (Kenya) and central Asian Khadyn alkaline lake (Siberia). Our investigation dealt with the unique ecosystem of an ancient soda lake in California, which also has an athalassic nature. The novel isolate MLF1\(^T\) is a typical secondary anaerobe, the main function of which in the bacterial anaerobic community is the consumption of hydrogen and low-molecular-mass end-products of primary anaerobes. Two novel primary anaerobes, AspG1\(^T\) and APO\(^T\), were also isolated from the same sample. Detailed study of these new isolates showed that they belonged to novel species: *Spirochaeta americana* sp. nov. (Hoover et al., 2003) and *Tindallia californiensis* sp. nov. (Pikuta et al., 2003), respectively. In both cases, the closest relationships (with <1 % difference) were with the species *Spirochaeta alkalica* and *Tindallia magadiensis*, respectively, isolated from the alkaline anaerobic community of soda Lake Magadi (Zhilina et al., 1996; Kevbrin et al., 1998, 1999). It is interesting to note that the sulfate-reducer *Desulfonatronovibrio hydrogenovorans* Z-7935\(^T\), which was also isolated from Lake Magadi in Kenya (Zhila et al., 1997), exhibited 10 % difference in 16S rDNA sequence from strain MLF1\(^T\). The most closely related species to strain MLF1\(^T\) was *Desulfonatronum lacustre* Z-7951\(^T\), a sulfate-reducer from the alkaline anaerobic bacterial community of Khadyn Lake, central Asia. Notwithstanding the fact that strains MLF1\(^T\) and Z-7951\(^T\) have the same morphology and catabolism (an identical list of electron donors and electron acceptors), these strains have different physiologies and anabolisms: American strain MLF1\(^T\) is an alkaliphile with dependence on NaCl and an autotrophic type of anabolism, but Asian strain Z-7951\(^T\) is a lithoheterotroph that does not need NaCl in the growth medium. Also, analyses of DNA G+C content showed a significant difference between strain MLF1\(^T\) and Z-7951\(^T\) (>6 mol%). DNA–DNA hybridization of genomic DNA between strain MLF1\(^T\) and *Desulfonatronum lacustre* Z-7951\(^T\) exhibited 51 % homology. The melting temperature \( (T_m) \) of the genomic DNA of strain MLF1\(^T\) was 8 °C higher than that of *Desulfonatronum lacustre* Z-7951\(^T\). Finally, there was a significant difference in the genome size between strain MLF1\(^T\) and the closely related species *Desulfonatronum lacustre* Z-7951\(^T\). Comparison of these DNA data of strain MLF1\(^T\) with those of the most closely related species, *Desulfonatronum lacustre* Z-7951\(^T\), indicates that there are sufficient differences for strain MLF1\(^T\) to be considered as a separate species. In Table 1, comparative characteristics for all known alkaliphilic sulfatereducers are provided.

On the basis of phenotypic and genotypic characteristics
Table 1. Characteristics that distinguish Desulfonatronum thiodismutans MLF1<sup>T</sup> from other alkalophilic sulfate-reducing bacteria

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell shape</td>
<td>Vibrioid</td>
<td>Vibrioid</td>
<td>Vibrioid</td>
<td>Curved rod</td>
</tr>
<tr>
<td>Flagella</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
</tr>
<tr>
<td>Spores</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Size (µm)</td>
<td>0–6–0.7 × 1–2–2.7</td>
<td>0–7–0.9 × 2–5–3.0</td>
<td>0–4–0.5 × 1–5–2.0</td>
<td>0–6–0.7 × 3–0–3.5</td>
</tr>
<tr>
<td>pH range (optimum)</td>
<td>8–0–10–0 (9–5)</td>
<td>8–0–10–1 (9–3–9.5)</td>
<td>8–0–10–2 (9–5–9.7)</td>
<td>7–8–9–2 (8–7)</td>
</tr>
<tr>
<td>NaCl range (%) (optimum)</td>
<td>&gt; 1–7 (3)</td>
<td>0–10 (0)</td>
<td>1–0–12–0 (3)</td>
<td>0–5–0 (0–1)</td>
</tr>
<tr>
<td>Temperature range (°C) (optimum)</td>
<td>15–48 (37)</td>
<td>22–45 (40)</td>
<td>22–45 (37)</td>
<td>37–58 (53)</td>
</tr>
<tr>
<td>DNA G+C content (mol%)</td>
<td>63–1</td>
<td>57–3</td>
<td>48–6</td>
<td>40–9</td>
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<tr>
<td>Electron donors (with SO&lt;sub&gt;4&lt;/sub&gt;&lt;sup&gt;2-&lt;/sup&gt;):</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>H&lt;sub&gt;2&lt;/sub&gt; + CO&lt;sub&gt;2&lt;/sub&gt;</td>
<td>(+)</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Lactate</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Pyruvate</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Ethanol</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Genome size (Da)</td>
<td>1·6 × 10&lt;sup&gt;9&lt;/sup&gt;</td>
<td>2·1 × 10&lt;sup&gt;9&lt;/sup&gt;</td>
<td>2·1 × 10&lt;sup&gt;9&lt;/sup&gt;</td>
<td>ND</td>
</tr>
<tr>
<td>Melting temperature (T&lt;sub&gt;mel&lt;/sub&gt;) (°C)</td>
<td>71 ± 2</td>
<td>63 ± 2</td>
<td>74 ± 5</td>
<td>ND</td>
</tr>
</tbody>
</table>

(Gram-negative cell wall, sulfate type of respiration, 16S rDNA sequence and DNA–DNA hybridization), strain MLF1<sup>T</sup> was identified as a novel species of the genus Desulfonatronum. The name Desulfonatronum thiodismutans sp. nov. is suggested for this organism, in accordance with the capability of this bacterium to perform dismutation.

**Description of Desulfonatronum thiodismutans sp. nov.**

Desulfonatronum thiodismutans (thi.o.dis'mu.tans. Gr. thio sulfur; N.L. part. adj. dismutans dismutating, splitting; N.L. part. adj. thiodismutans sulfur-dismutating, pertaining to the ability of the organism to dismute thiosulfate and sulfate).

Motile, vibrio-shaped cells with a single polar flagellum, 0–6–0–7 × 1–2–2.7 µm in size. Gram-negative. Non-spore-forming. Haloalkaliphilic; pH range for growth is 8–0–10–0, with optimum growth at pH 9–5. Growth is obligately dependent on Na<sup>+</sup> and CO<sub>3</sub><sup>2-</sup> ions. Range of NaCl for growth is > 1–7% (w/v); optimum growth occurs at 3% (w/v) NaCl. Mesophilic: temperature range for growth is 15–48°C; optimum growth occurs at 37°C. Cells can be stored frozen in liquid medium. Strictly anaerobic and catalase-negative. Does not grow without sulfate, which is used as an electron acceptor with H<sub>2</sub>S as the end product. Sulfite and thiosulfate are alternative electron acceptors, but sulfur and nitrate are not. Elemental sulfur and molybdate inhibit growth. Lithoheterotrophic, facultatively lithoautotrophic (slow growth on H<sub>2</sub> + CO<sub>2</sub>) and uses H<sub>2</sub>, formate and ethanol as electron donors. A supplement of vitamins is required and yeast extract stimulates growth. Capable of receiving energy by the dismutation of thiosulfate or sulfate (with 2 mM sodium acetate and carbonate as carbon sources). Resistant to kanamycin and gentamicin, but sensitive to tetracycline and chloramphenicol. Genomic DNA G + C content of the type strain is 63–0 mol% (HPLC). Major fatty acid methyl esters are C<sub>14:0</sub>, C<sub>16:1</sub>, C<sub>18:0</sub> and a mixture of C<sub>18</sub> unsaturated fatty acids.

The type strain is MLF1<sup>T</sup> (= DSM 14708<sup>T</sup> = ATCC BAA-395<sup>T</sup>). Isolated from mud sediments of alkaline, hypersaline, soda Mono Lake in California, North America.

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