Deferrisoma palaeochoriense sp. nov., a thermophilic, iron(III)-reducing bacterium from a shallow-water hydrothermal vent in the Mediterranean Sea

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A novel thermophilic, anaerobic, mixotrophic bacterium, designated strain MAG-PB1T, was isolated from a shallow-water hydrothermal vent system in Palaeochori Bay off the coast of the island of Milos, Greece. The cells were Gram-negative, rugose, short rods, approximately 1.0 μm long and 0.5 μm wide. Strain MAG-PB1T grew at 30–70 °C (optimum 60 °C), 0–50 g NaCl l⁻¹ (optimum 15–20 g l⁻¹) and pH 5.5–8.0 (optimum pH 6.0). Generation time under optimal conditions was 2.5 h. Optimal growth occurred under chemolithoautotrophic conditions with H₂ as the energy source and CO₂ as the carbon source. Fe(III), Mn(IV), arsenate and selenate were used as electron acceptors. Peptone, tryptone, Casamino acids, sucrose, yeast extract, D-fructose, α-D-glucose and (−)-d-arabinose also served as electron donors. No growth occurred in the presence of lactate or formate. The G+C content of the genomic DNA was 66.7 mol%. Phylogenetic analysis of the 16S rRNA gene sequence indicated that this organism is closely related to Deferrisoma camini, the first species of a recently described genus in the Deltaproteobacteria. Based on the 16S rRNA gene phylogenetic analysis and on physiological, biochemical and structural characteristics, the strain was found to represent a novel species, for which the name Deferrisoma palaeochoriense sp. nov. is proposed. The type strain is MAG-PB1T (=JCM 30394T=DSM 29363T).

Iron, the most abundant redox-active metal in today’s Earth’s crust, is thought to have served as one of the earliest electron acceptors for life’s respiratory processes (Liu et al., 1997; Richter et al., 2012). This is, in part, supported by the widespread existence of bacteria and archaea capable of dissimilatory Fe(III) reduction in a variety of modern environments (Vargas et al., 1998; Slobodkin, 2005). Given their metal-rich nature, hydrothermal environments such as deep-sea, terrestrial and shallow-water hydrothermal vents are particularly significant for dissimilatory Fe(III) reduction activities (Liu et al., 1997; Vargas et al., 1998; Slobodkin et al., 2001; Holden & Adams, 2003; Flynn et al., 2014). Within the Bacteria, a variety of Fe(III) reducers have been isolated and described from these globally widespread hydrothermal systems. For example, at deep-sea hydrothermal vents, members of the classes Deltaproteobacteria (Kashefi et al., 2003; Slobodkin et al., 2012b) and Gammaproteobacteria (Gao et al., 2006) of the phylum Proteobacteria, as well as members of the phylum Deferrribacteres (species of the genus Deferrribacter) have been described (Miroshnichenko et al., 2003; Slobodkina et al., 2009a). In terrestrial hydrothermal vents and springs, members of the phyla Aquificae (Aguir et al., 2004), Acidobacteria (Losey et al., 2013) and Actinobacteria (Itoh et al., 2011) have been described; however, the majority of the Fe(III)-reducing species in culture belong to the phylum Firmicutes (Slobodkin et al., 1997, 1999, 2006; Zavarzina et al., 2002; Gorlenko et al., 2004; Sokolova et al., 2004; Haouari et al., 2008; Slobodkina et al., 2012a; Yoneda

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Abbreviations: CFA, cellular fatty acid.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain MAG-PB1T is KM386664.

Two supplementary figures and a supplementary table are available with the online Supplementary Material.
et al., 2012). In shallow-water hydrothermal vent environments, the only Fe(III)-reducing bacterium described to date is *Ardenticatenia maritima*, belonging to the phylum Chloroflexi (Kawaiuchi et al., 2013).

Documented chemical and microbiological evidence from hydrothermal vent systems shows a variety of yet unknown bacterial lineages with potential links to Fe(III) reduction (Sievert et al., 1999; Slobodkin et al., 2001; Slobodkin, 2005; Hirayama et al., 2007; Meyer-Dombard & Amend, 2014). Therefore, the full extent of the history and role of Fe(III)-reducing micro-organisms in these environments remains unknown. Here, we report the isolation and characterization of a thermophilic, strictly anaerobic, mixotrophic, dissimilatory metal-reducing deltaproteobacterium isolated from a shallow-water hydrothermal vent in the Mediterranean Sea.

Sediment samples were collected by scuba diving from a shallow-water hydrothermal vent (10 m depth) in Palaeochori Bay off the coast of the island of Milos, Greece, in May 2012. The sediment core sample was collected at 200 cm lateral distance from a venting site (with venting fluids at 80 °C), and the strain was isolated from a depth of 10–15 cm in the sediment at *in-situ* temperatures of 22.8–26 °C and pH 7.3. Upon arrival at the field laboratory, samples were processed and stored at 4 °C under a N₂ (100 %, v/v; 200 kPa) atmosphere. Primary enrichment cultures were initiated at the Geophysical Laboratory by adding about 1 ml inoculum (prepared by resuspending sediment material in 1 ml culturing medium) anaerobically to 10 ml of a modified version of the basal medium described by Slobodkina et al. (2009b). The basal medium contained (l⁻¹ distilled water): KH₂PO₄ (0.33 g), (NH₄)₂SO₄ (0.5 g), KCl (0.33 g), MgCl₂-6H₂O (4.0 g), CaCl₂-2H₂O (0.33 g), NaHCO₃ (0.8 g), NaCl (18.0 g), 1 ml trace-element solution SL-10 (Sleat et al., 1984), 1 ml selenite-tungstate solution (Tschech & Schink, 1985) and 1 ml vitamin solution (Wolin et al., 1963). The pH of the medium was not adjusted and no reducing agent was added. Fe(III) was provided in the form of amorphous Fe(III) oxide (88 mmol l⁻¹), synthesized by titrating a solution of FeCl₃·6 H₂O with NaOH (10 %, w/v) to pH 8.5. The medium was reduced under a H₂/CO₂ atmosphere (80 : 20, v/v; 200 kPa). The final pH of the medium was 6.3–6.5. The pure culture, which was isolated by 10 consecutive series of dilutions at 50 °C, was designated strain MAG-PB1T. The pure culture was confirmed both by cell morphology observations and by sequencing 30 16S rRNA gene clones obtained from a PCR amplification of genomic DNA, as described previously (Vetriani et al., 2004). The clones were obtained by using the TOPO TA Cloning kit (Invitrogen). Long-term stocks of the new isolate, stored at −80 °C, were prepared by adding 50 μl DMSO (Fisher Scientific) to 1 ml culture.

Cells were routinely stained with acridine orange (0.1 %, w/v) and visualized with an Olympus BX 61 microscope with an oil-immersion objective (UPlanFL 100/1.3) (Vetriani et al., 2004). All growth experiments were carried out in duplicate. For scanning electron micrographs, cells were grown on silicon wafer surfaces and fixed overnight in 4 % paraformaldehyde in PBS, rinsed twice with 0.05 M phosphate buffer and then dehydrated in a graded ethanol series (as a modified procedure from the one described by Vetriani et al., 2004). Scanning electron micrographs were taken using a model JSM-6500F field-emission scanning electron microscope (JEOL) after sputter coating with 0.5 nm iridium. The beam was operated at 1 nA and 15 kV.

Cells of MAG-PB1T were rugose, short rods, approximately 1.0 μm long and 0.5 μm wide, and displayed flagella (Fig. 1). Replicated growth assays on silicon wafers, together with *Caminibacter mediatlanticus* DSM 16658T (Voordeckers et al., 2005) as a positive control, were performed in order to confirm the rugose qualities of MAG-PB1T. Cells stained Gram-negative and the presence of endospores was not observed. The chemolithoautotrophic (under H₂/CO₂, 80 : 20, v/v; 200 kPa) Fe(III)-reducing capabilities of MAG-PB1T were tested with both soluble...
(ferric citrate; 10 mM) and insoluble [amorphous Fe(III) oxide] Fe(III). The highest cell density \((1.9 \times 10^7 \text{ cells ml}^{-1} \text{ after 24 h})\) was observed when ferric citrate was used as electron acceptor, in comparison with amorphous Fe(III) oxide \((1.1 \times 10^7 \text{ cells ml}^{-1} \text{ after 65 h})\). The doubling time was 6.9 h with ferric citrate and 8.9 h with amorphous Fe(III) oxide. Strain MAG-PB1\textsuperscript{T} reduced amorphous Fe(III) oxide to a black magnetic precipitate. No changes in colour or amount of precipitate were observed in uninoculated controls with ferrihydrite or ferric citrate during the incubation period of these assays at 50 °C, pH 6.3–6.5 and 18 g NaCl l\textsuperscript{-1}.

Once the higher growth efficiency during chemolithoautotrophy using ferric citrate was established, the heterotrophic (with yeast extract; 0.02 %, w/v) Fe(III)-reducing capabilities of strain MAG-PB1\textsuperscript{T} were tested. The calculated doubling time with yeast extract (under a 100 % N\textsubscript{2} gas phase; 200 kPa) and ferric citrate was 8.8 h. No growth of strain MAG-PB1\textsuperscript{T} was observed under strictly fermentative conditions with yeast extract (under 100 % N\textsubscript{2}, 200 kPa, in the absence of ferric citrate). The ability of MAG-PB1\textsuperscript{T} to grow with H\textsubscript{2} as an electron donor was also tested by adding nitrate (20 mM), sulfate (15 mM), elemental sulfur \((S^\text{0} \text{; } 30 \text{ g l}^{-1})\), Mn(IV) \((\text{MnO}_2 \text{; } 30 \text{ g l}^{-1})\), selenate \((20 \text{ mM})\), arsenate \((20 \text{ mM})\) or oxygen \((0.5 \% \text{, v/v})\) in the absence of ferric citrate. Strain MAG-PB1\textsuperscript{T} grew when arsenate, Mn(IV) or selenate were offered as electron acceptors. Doubling times under these conditions were 7.0 ± 0.7, 16.2 ± 5.2 and 35.7 ± 1.8 h, respectively. However, growth with Mn(IV) and selenite did not exceed \(3 \times 10^6\) cells ml\textsuperscript{-1}. No growth of strain MAG-PB1\textsuperscript{T} was observed when oxygen, nitrate, sulfate or sulfur were offered as electron acceptors. All of the remaining physiological assays were performed in duplicate, in 10 ml basal medium supplemented with 10 mM ferric citrate under a H\textsubscript{2}/CO\textsubscript{2} (80 : 20, v/v; 200 kPa) atmosphere unless stated otherwise.

The optimal growth temperature for strain MAG-PB1\textsuperscript{T} was determined by incubating cultures at temperatures between 25 and 75 °C (at 5 °C intervals). Strain MAG-PB1\textsuperscript{T} grew at 30–70 °C, with optimal growth at 60 °C (Fig. S1a, available in the online Supplementary Material). The optimal salt requirement was determined by varying the concentration of NaCl between 0 and 50 g l\textsuperscript{-1}, at 5 g l\textsuperscript{-1} intervals (no growth was detected at 55 g l\textsuperscript{-1}; Fig. S1b). Optimal growth was observed at 15–20 g NaCl l\textsuperscript{-1}. The optimal pH requirement was determined by varying the pH between 5.0 and 8.5 using the following buffers as described previously (Voordecker et al., 2005): acetate buffer for pH 5.0, MES for pH 5.5 and 6.0, PIPES for pH 6.5 and 7.0, HEPES for pH 7.5 and Tris for pH 8.0 and 8.5. Growth of strain MAG-PB1\textsuperscript{T} occurred between pH 5.5 and 8.0, with an optimum at pH 6.0 (Fig. S1c). No changes in colour or amount of precipitate were observed in uninoculated controls with ferric citrate during these experiments, with the exception of initial and immediate precipitated material (very distinguishable from biogenic precipitation) during pH adjustments at pH 8.0 and 8.5. However, pH adjustments by organic buffers, especially for higher pH, is not recommended. Under the optimal conditions of temperature (60 °C), salinity (1.5 g NaCl l\textsuperscript{-1}) and pH (6.0), the generation time of isolate MAG-PB1\textsuperscript{T} was 2.5 h \((4.1 \times 10^7 \text{ cells ml}^{-1} \text{ after 32 h of growth})\). No organic buffers were added for the remainder of the growth assays under optimal growth conditions at pH 6.0.

Microbial reduction of Fe(III) was quantified by redox titration of aqueous Fe(II) produced during the growth of strain MAG-PB1\textsuperscript{T} under optimal growth conditions in duplicated 250 ml batches, using a potassium dichromate \((K_2\text{Cr}_2\text{O}_7)\) solution as the titrant (Mettler Toledo application method M459-2010). Fifteen-millilitre aliquots of filtered, anaerobic samples were taken at different time points during growth into prepared anaerobic tubes (under 100 % N\textsubscript{2}; 200 kPa) using a 0.2 µm filter membrane. Each sample was diluted to 25 ml with 10 ml 2 M HCl before titration. The titrant was a 3.41 mM potassium dichromate solution. The volume of titrant solution consumed at the equivalence point was used to calculate the concentration of Fe(II) in each sample using the following equation:

\[
[\text{Fe(II)}] = 6 \times (V_{\text{pd}} \times 3.41 \text{ mM})/15\text{ml}
\]

where \([\text{Fe(II)}]\) is the concentration of Fe(II) at a given time point and \(V_{\text{pd}}\) is the volume of titrant consumed. Titrations were performed using the Mettler Toledo T50 titrator and the Mettler Toledo DM140-SC combined platinum ring redox electrode. Fe(II) concentrations increased from \(~1\) to 7 mM over the course of 32 h during the exponential growth phase of strain MAG-PB1\textsuperscript{T} (Fig. S2).

The effects of organic substrates on the growth of strain MAG-PB1\textsuperscript{T} were investigated by adding the following substrates to the medium under a H\textsubscript{2}/CO\textsubscript{2} gas phase (80 : 20, v/v; 200 kPa): acetate (23 mM), formate (44 mM), lactate, peptone, tryptone, Casamino acids, sucrose (all at 0.2 %, w/v), citrate (10 mM) and yeast extract, D-fructose, Z,D-glucose and \((-)\)-D-arabinose (all at 0.02 %, w/v). These substrates were also tested as possible energy and/or carbon sources by using the following gas phases (all at 200 kPa): N\textsubscript{2}/CO\textsubscript{2} (80 : 20, v/v), N\textsubscript{2} (100 %, v/v) or H\textsubscript{2} (100 %, v/v). Citrate, present in every trial in the form of ferric citrate (10 mM), was shown to support growth (delayed; \(~2\) days) of MAG-PB1\textsuperscript{T} as a carbon source (under H\textsubscript{2}) but not as an electron donor (under N\textsubscript{2} or N\textsubscript{2}/CO\textsubscript{2}). No growth of strain MAG-PB1\textsuperscript{T} occurred in the presence of formate (44 mM) or lactate (0.2 %, w/v) under all gas phases. Peptone (0.2 %, w/v) and yeast extract (0.02 %, w/v) did not affect the growth of strain MAG-PB1\textsuperscript{T} under any gas phase, indicating that these organic substrates can be used as electron donors and carbon sources. Tryptone (0.2 %, w/v), Casamino acids (0.2 %, w/v), Z,D-glucose (0.2 and 0.02 %, w/v) and D-fructose (0.02 %, w/v) did not affect growth of strain MAG-PB1\textsuperscript{T} under H\textsubscript{2}/CO\textsubscript{2}. These sugars were also used as electron donors (under N\textsubscript{2}/CO\textsubscript{2}), carbon sources...
(under $H_2$) and simultaneously as electron donor and carbon sources (under $N_2$), but with much slower growth in some cases (Table S1). This effect was especially evident with growth using glucose, which ranged from 2 days under $N_2/CO_2$ to 25 days of observable growth under $N_2$ and $H_2$ (Table S1). Delayed growth (7 days) was also observed in the presence of acetate (23 mM) under $H_2$ and $H_2/CO_2$. However, no growth was observed in samples containing acetate (23 mM) under $N_2$ or $N_2/CO_2$, showing that acetate is not utilized as an energy source. Growth of strain MAG-PB1$^T$ was observed with sucrose (0.2 %, w/v) and (−)-D-arabinose (0.02 %, w/v), except under pure $N_2$, where no growth was observed, indicating that these organic substrates cannot function simultaneously as an electron donor and carbon source. Strain MAG-PB1$^T$ was shown to be a mixotroph, capable of growing both autotrophically and heterotrophically.

Antibiotic resistance was tested in the presence of ampicillin, vancomycin and tetracycline (all at 100 µg ml$^{-1}$). Antibiotics were added aseptically before incubation at 60 °C. Strain MAG-PB1$^T$ was resistant to ampicillin and tetracycline, and inhibited by vancomycin. Strain MAG-PB1$^T$ exhibited catalase activity, detected by the formation of gas bubbles after concentrated cells were resuspended in 70 µl of a solution of $H_2O_2$ (3 %, v/v) at room temperature.

Genomic DNA was extracted from cells of strain MAG-PB1$^T$ by using the UltraClean microbial DNA isolation kit (MoBio). A 1322 bp fragment of the 16S rRNA gene was amplified from the genomic DNA by PCR and sequenced as described previously (Vetriani et al., 2004).

An alignment between this fragment and other 16S rRNA gene sequences retrieved from GenBank was generated and refined using SSU-ALIGN, its dependents (Cannone et al., 2002; Nawrocki et al., 2009) and MEGA version 6.06 (Tamura et al., 2013). The resulting alignment was used to reconstruct a phylogenetic tree using the general time reversible (GTR) substitution model with gamma rate variation in the MrBayes plugin (Huelsenbeck & Ronquist, 2001) of Geneious R6 (Biomatters; http://www.geneious.

![Fig. 2. Phylogenetic position of strain MAG-PB1$^T$ based on 16S rRNA gene sequences as inferred from Bayesian analysis using the MrBayes plugin of Geneious R6. GenBank accession numbers are given in parentheses. Taxonomic orders are identified when known as follows: *, Bdellovibrionales; **, Desulfobacterales; ***, Desulfuromonadales; ****, Syntrophobacterales. Posterior probabilities above 0.80 are shown. Bar, 0.2 changes per nucleotide position.](http://ijs.microbiologyresearch.org)
com/). Phylogenetic analysis of the 16S rRNA gene sequence placed strain MAG-PB1T within the class Delta-proteobacteria, with its closest relatives being uncultured, unclassified Delta-proteobacteria. This is evidenced by the 16S rRNA gene sequence alignment with representatives of seven families from four orders within the Delta-proteobacteria and sequences from several uncultured deltaproteobacterial strains with >90% sequence identity to MAG-PB1T. The highest sequence identity (99%) to strain MAG-PB1T belonged to an uncultured microorganism reported from alkaline hydrothermal springs of Ambitle Island, Papua New Guinea (Meyer-Dombard & Amend, 2014). Its next closest relative is the cultured microorganism Deferrisoma camini S3R1T (97% sequence identity), isolated from a deep hydrothermal vent system in the Eastern Lau Spreading Center (Slobodkina et al., 2012b). Other members of the larger clade include organisms isolated from heavy-metal-contaminated soil, Yellow Sea sediment and sulfate reducers, as reported previously by Slobodkina et al. (2012b). Most internal clades in Fig. 2 are consistent with the phylogeny reconstructed by Slobodkina et al. (2012b).

The DNA G+C content and cellular fatty acid (CFA) composition of strain MAG-PB1T were determined by the Identification Service of the Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany. The DNA G+C content was determined by HPLC analysis of deoxyribonucleosides as described by Mesbah et al. (1989). Major CFAs were analysed as the methyl ester derivatives using the Sherlock Microbial Identification System (MIDI; Microbial ID) and an Agilent model 6890N gas chromatograph (Labrenz et al., 1998). The genomic DNA G+C content of MAG-PB1T was 66.7 mol%. The major CFAs found in strain MAG-PB1T, of 84% of total CFAs named, were C18:1ω9c (24.4%), C16:0 (23.9%), C18:0 (13.7%), iso-C17:0 (9.6%) and iso-C15:0 (6.1%). These were followed by a greater diversity (14 different types) of low-abundance CFAs.

Strain MAG-PB1T exhibited several divergent characteristics from its closest cultured relative, D. camini S3R1T (Table 1). The 16S rRNA gene-based phylogeny placed strain MAG-PB1T in a separate lineage from D. camini S3R1T at the species level (97% identity). In addition to genetic distinctions, strain MAG-PB1T also had slightly a higher DNA G+C content. While strain MAG-PB1T and D. camini S3R1T shared some common major CFAs, they differed in their relative abundances. In D. camini S3R1T, iso-C17:0, iso-C15:0 and C18:0 represented 34.0, 19.2 and 8.2% (Slobodkina et al., 2012b), whereas these represented 9.0, 6.1 and 13.7% of the major CFAs in strain MAG-PB1T. The rest of the major CFAs in D. camini S3R1T were not found in strain MAG-PB1T (Slobodkina et al., 2012b). The phenotypic characteristics of the new isolate also distinguish it based on its higher optimal growth temperature, overall broader growth ranges, its capacity for chemolithoautotrophy, Mn(IV) reduction and its inability to oxidize acetate or reduce S0. On the basis of the physiological and molecular properties of

| Table 1. Differentiating features of strain MAG-PB1T and D. camini S3R1T |
|-------------------------------------------------|-----------------|-----------------|
| **Feature**                                      | MAG-PB1T         | D. camini S3R1T |
| Source of isolation (depth)                     | Palaeochori Bay, Greece (10 m) | Eastern Lau, EPR (2150 m) |
| Catalase                                        | +                | ND              |
| DNA G+C content (mol%)                          | 66.7             | 64.4            |
| Temperature for growth (°C)                     |                   |                 |
| Range                                           | 30–70            | 36–62           |
| Optimum                                         | 60               | 50              |
| NaCl concentration for growth (% w/v)           |                   |                 |
| Range                                           | 0–5.0            | 1.0–5.0         |
| Optimum                                         | 1.5–2.0          | 2.0–2.5         |
| pH for growth                                   |                   |                 |
| Range                                           | 5.5–8.0          | 5.5–7.5         |
| Optimum                                         | 6.0              | 6.5             |
| Terminal electron acceptors                     |                   |                 |
| Sulfur                                          | –                | +               |
| Mn(IV)                                          | +                | –               |
| Arsenate                                        | +                | ND              |
| Selenate                                        | +                | ND              |
| Autotrophic growth                              | +                | –               |
| Shortest generation time (h)                    | 2.5              | 2.6             |
strain MAG-PBI\textsuperscript{T}, we propose a novel species, *Deferrisoma palaeochoriense* sp. nov.

The occurrence of *D. palaeochoriense* in Palaeochori Bay as well as in Ambite Island (based on the 99 % 16S rRNA gene sequence similarity) coincides with shallow-water vent environments associated with high arsenic and sulfide contents (Akerman et al., 2011; Price et al., 2013; Yu¨cel et al., 2013). The characteristics of these vents provide a mechanism, either through reactions with arsenite generating arsenate-rich hydrous ferric oxide (Meyer-Dombard & Amend, 2014) or by FeS oxidation with O\textsubscript{2} (Yu¨cel et al., 2013), for consistent supply of Fe(III) and arsenate for the organism’s functions. The characterization of strain MAG-PBI\textsuperscript{T} as a bacterium capable of chemolithoautotrophy through several dissimilatory metal-reduction pathways sheds light on the functions of Deltaproteobacteria present in these environments.

**Description of *Deferrisoma palaeochoriense* sp. nov.**

*Deferrisoma palaeochoriense* (pa.lae.o.cho.ri.en’se N.L. neut. adj. palaeochoriense from Palaeochori Bay, referring to the place of isolation of the type strain).

Cells are motile, rugose, short rods (0.8–1.0 \( \mu \text{m} \) long and 0.5 \( \mu \text{m} \) wide). Obligate anaerobe. Gram-negative. Catalase-positive. Growth occurs at 30–70 °C, 0–55 g NaCl \textsuperscript{-1} \text{P} and pH 5.5–8.0. Optimal growth conditions are 60 °C, 15–20 g NaCl \textsuperscript{-1} \text{P} and pH 6.0 under strictly anaerobic, chemolithotrophic conditions in the presence of H\textsubscript{2} and CO\textsubscript{2} with Fe(III) as terminal electron acceptor (shortest generation time 2.5 h). The following are also utilized as electron acceptors: Mn(IV), selenate and arsenate.

No growth occurs in the presence of lactate or formate. Acetate drastically delays growth under a H\textsubscript{2}/CO\textsubscript{2} gas phase. Resistant to ampicillin and tetracycline; sensitive to vancomycin (each at 100 mg mL\textsuperscript{-1}).

The type strain is MAG-PBI\textsuperscript{T} (=JCM 30394\textsuperscript{T}=DSM 29363\textsuperscript{T}), isolated from sediments of an active shallow-water vent in Palaeochori Bay off the coast of the island of Milos, Greece. The genomic DNA G+C content of the type strain is 66.7 mol\%.  

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