Thermodesulfatator atlanticus sp. nov., a thermophilic, chemolithoautotrophic, sulfate-reducing bacterium isolated from a Mid-Atlantic Ridge hydrothermal vent

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A novel, strictly anaerobic, thermophilic, sulfate-reducing bacterium, designated strain AT1325^T, was isolated from a deep-sea hydrothermal vent at the Rainbow site on the Mid-Atlantic Ridge. This strain was subjected to a polyphasic taxonomic analysis. Cells were Gram-negative motile rods (approximately 2.4×0.6 µm) with a single polar flagellum. Strain AT1325^T grew at 55–75 °C (optimum, 65–70 °C), at pH 5.5–8.0 (optimum, 6.5–7.5) and in the presence of 1.5–4.5 % (w/v) NaCl (optimum, 2.5 %). Cells grew chemolithoautotrophically with H₂ as an energy source and SO₄²⁻ as an electron acceptor. Alternatively, the novel isolate was able to use methylamine, peptone or yeast extract as carbon sources. The dominant fatty acids (>5 % of the total) were C_{16:0}, C_{18:1ω7c}, C_{18:0} and C_{19:0} cyclo ω8c. The G + C content of the genomic DNA of strain AT1325^T was 45.6 mol%. Phylogenetic analyses based on 16S rRNA gene sequences placed strain AT1325^T within the family *Thermodesulfobacteriaceae*, in the bacterial domain. Comparative 16S rRNA gene sequence analysis indicated that strain AT1325^T belonged to the genus *Thermodesulfatator*, sharing 97.8 % similarity with the type strain of *Thermodesulfatator indicus*, the unique representative species of this genus. On the basis of the data presented, it is suggested that strain AT1325^T represents a novel species of the genus *Thermodesulfatator*, for which the name *Thermodesulfatator atlanticus* sp. nov. is proposed. The type strain is AT1325^T (=DSM 21156^T=JCM 15391^T).

Over the past decades, microbiological investigations of a range of high-temperature marine and terrestrial environments have revealed the presence of a phylogenetically, metabolically and physiologically diverse community of thermophilic prokaryotes endemic to these particular habitats. Among the ubiquitous thermophilic taxa, members of the class *Thermodesulfobacteria* are commonly retrieved in hot biotopes, regardless of the geographical provenance of the samples (Skirnisdottir *et al.*, 2000; Nakagawa & Fukui, 2003; Nakagawa *et al.*, 2005).

At the time of writing, the class *Thermodesulfobacteria* comprises only the family *Thermodesulfobacteriaceae*. Representatives of this family have been isolated from terrestrial geothermal hot springs, petroleum reservoirs and

deep-sea hydrothermal vents located worldwide (Zeikus *et al.*, 1983; Jeanthon *et al.*, 2002; Kashefi *et al.*, 2002; Moussard *et al.*, 2004). The family *Thermodesulfobacteriaceae* (Hatchikian *et al.*, 2001) comprises two recognized genera, *Thermodesulfobacterium* (Zeikus *et al.*, 1983) and *Thermodesulfatator* (Moussard *et al.*, 2004). These genera comprise exclusively thermophilic, anaerobic, chemo-organotrophic or chemolithoautotrophic sulfate-reducing organisms. In addition, this family encompasses the informally described species '*Geothermobacterium ferrireducens*', which is unable to reduce sulfate (Kashefi *et al.*, 2002).

At the time of writing, the genus *Thermodesulfatator* comprises one recognized species, *Thermodesulfatator indicus*, a strict chemolithoautotrophic sulfate-reducer that was isolated from a deep-sea hydrothermal vent of the Kairei vent field on the Central Indian Ridge (Moussard *et al.*, 2004). In the present study, a novel hydrothermal bacterium belonging to the genus *Thermodesulfatator* is described.

In June 2001, during the ATOS oceanographic cruise, fragments of active hydrothermal chimney rocks were

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain AT1325^T is EU435435.

Electron micrographs of cells of strain AT1325^T and a graph showing the effects of temperature on the maximum growth rate of strain AT1325^T are available as supplementary material with the online version of this paper.

collected at a depth of 2275 m at the Rainbow vent field, on the Mid-Atlantic Ridge (36° 13' N 33° 54' W). Sample collection, subsampling and storage procedures were as described by Postec *et al.* (2005). All subsamples were pooled and used to inoculate a 2-litre gas-lift bioreactor (inoculum 2%, v/v). Continuous enrichment was performed in this bioreactor for 41 days, at 60 °C and pH 6.5, on a complex medium (modified SME medium) containing seawater salts (including sulfate), minerals, carbohydrates, peptides, organic acids (acetate and pyruvate) and colloidal sulfur (Postec *et al.*, 2007). This continuous enrichment was performed at a dilution rate of 0.04 h⁻¹ (80 ml h⁻¹), and under a stream of nitrogen gas (0.1 min⁻¹ v/v) to maintain anaerobic conditions and to drain possible inhibitors. A culture sample from day 28 was used as an initial inoculum on TYA medium [60 °C, pH 6.0, 9.3 mM sulfate, atmosphere of H₂/CO₂ 80:20 (v/v) at 200 kPa], as described by Postec *et al.* (2007). One strain was purified by both isolation on solid medium [TYA medium solidified with 1.5% Phytigel incubated in anaerobic jars under H₂/CO₂ 80:20 (v/v) at 200 kPa] and then repeated dilutions-to-extinction series. This strain was designated AT1325^T.

The purity of strain AT1325^T was confirmed routinely by microscopic examination and by repeated partial sequencing of the 16S rRNA gene by using several primers. Stock cultures were stored at -80 °C in TYA medium supplemented with 5% (v/v) DMSO.

The 16S rRNA gene (1491 bp) of the novel isolate was sequenced as described by Alain *et al.* (2002). This sequence was first compared with those in available databases by use of the BLAST program (Altschul *et al.*, 1990). It was then aligned with its nearest neighbours by using the CLUSTAL X program (Thompson *et al.*, 1997). The alignment was refined manually by using the SEAVIEW program (Galtier *et al.*, 1996) based on an alignment generated in parallel with the RDP II sequence aligner (http://rdp8.cme.msu.edu/cgis/seq_align.cgi). In total, 1395 nt corresponding to homologous regions could be unambiguously aligned by the RDP II Sequence Align

program and were used for subsequent calculations of similarity percentages (similarity matrix). Phylogenetic reconstructions were made via PHYLIP version 3.67 software (<http://evolution.genetics.washington.edu/phylip/getme.html>) on the basis of evolutionary distance (neighbour-joining method with Jukes and Cantor corrections) (Saitou & Nei, 1987) and maximum-likelihood (Felsenstein, 1981). The robustness of the inferred topologies was assessed by bootstrap analyses (1000 bootstrap resamplings with neighbour-joining and 100 replications with maximum-likelihood) (Felsenstein, 1985). Comparison of the 16S rRNA gene sequence of strain AT1325^T with sequences of *Bacteria* revealed a phylogenetic relationship with deeply branching bacterial lineages. Phylogenetic reconstructions indicated that the novel isolate belonged to the class 'Thermodesulfobacteria' (Garrity & Holt, 2001) and more particularly to the family Thermodesulfobacteriaceae, order Thermodesulfobacteriales (Hatchikian *et al.*, 2001). Within this lineage, the novel isolate clustered robustly with the type strain of *Thermodesulfatator indicus* (Moussard *et al.*, 2004), another deep-sea hydrothermal vent isolate (Fig. 1). The two isolates shared 97.8% 16S rRNA gene sequence similarity. Strain AT1325^T was more distantly related to members of the genera *Thermodesulfobacterium* and 'Geothermobacterium', sharing 87.7–88.7% 16S rRNA gene sequence similarity with representatives of these genera. Based on the above analyses, the novel isolate could be assigned to the genus *Thermodesulfatator*. The level of 16S rRNA gene sequence similarity with the type strain of *Thermodesulfatator indicus* also showed that strain AT1325^T displayed sufficient molecular differences for delineation at the species level (Stackebrandt & Ebers, 2006). The level of 16S rRNA gene sequence similarity between strain AT1325^T and the type strain of *Thermodesulfatator indicus* was well below the threshold value (98.7–99%) currently recommended as indicating the need for DNA–DNA hybridization to test for the genomic uniqueness of a novel isolate (Stackebrandt & Ebers, 2006).

Morphological characteristics of cells of strain AT1325^T were determined by using light microscopy (Olympus

Fig. 1. Phylogenetic relationships of strain AT1325^T and its closest relatives within the class *Thermodesulfobacteria*. 16S rRNA gene sequence data of reference strains were obtained from the GenBank/EMBL/DBJ databases. Accession numbers are given in parentheses. The topology shown corresponds to an unrooted tree obtained by the maximum-likelihood algorithm, established by using the PHYLIP package. Bootstrap percentages (based on 100 replicates) are given at branch points. The positioning of the novel isolate was confirmed by using the neighbour-joining method. Bar, 1 substitution per 100 nt.

CX40), transmission electron microscopy (JEOL JEM 100 CX II) and scanning electron microscopy (FEI Quanta 200). Cells were straight rods, 1.0–6.1 µm in length (mean ± SD 2.4 ± 1.5 µm, $n=10$) and 0.3–0.8 µm in width (0.6 ± 0.1 µm, $n=10$) in the mid-exponential phase of growth (see Supplementary Fig. S1 in IJSEM Online). Cells stained Gram-negative. Cells occurred mainly singly and divided by constriction (Supplementary Fig. S1a). They possessed a single polar flagellum (Supplementary Fig. S1b) and were highly motile. Formation of spores was not observed.

Physiological characterization of the novel isolate was carried out in a basal medium referenced as 'SO4PNsalts' and containing (per litre): 0.33 g NH₄Cl, 0.5 g KCl, 0.5 g CaCl₂ · 2H₂O, 3 g MgCl₂ · 6H₂O, 22 g NaCl, 3.0 g Na₂SO₄, 5 g PIPES buffer (Sigma) and 1 mg resazurin (Sigma). The pH was adjusted to 6.7. Once prepared, this medium was autoclaved and cooled to room temperature under an oxygen-free nitrogen gas flow. Then, 1 ml vitamin mixture [solution from Widdel & Bak (1992) supplemented with 4 mg folic acid and 1.5 mg lipoic acid], 1 ml thiamine solution, 1 ml selenite-tungstate solution and 1 ml non-chelated trace element mixture (all as per Widdel & Bak, 1992) were added to the basal medium from concentrated anaerobic filter-sterilized solutions. Finally, KH₂PO₄ was injected from sterile stock to a final concentration of 40 mM. Medium (10 ml) was then dispensed anaerobically in 50-ml vials sealed with butyl-rubber stoppers and reduced with 0.1 ml of a 10 % (w/v) Na₂S · 9H₂O sterile solution, just before inoculation. Unless stated otherwise, experiments were carried out anaerobically, under a gas phase of H₂/CO₂ (80:20 v/v, 200 kPa), and incubation was performed in the dark at 65 °C.

Growth was routinely monitored by direct cell counting by using a modified Thoma chamber (depth 10 µm), or by counting after fixation with 1 % (v/v) glutaraldehyde and storage at –20 °C. Growth rates were calculated by using linear regression analysis of five to nine points along the linear portions of the growth curves (exponentially transformed). Determination of the temperature range for growth was tested at 50, 55, 60, 65, 70, 75, 80 and 85 °C. No growth was observed at 50 °C or above 80 °C. The novel isolate was able to grow at 55–75 °C, with an optimum growth rate at 65–70 °C (see Supplementary Fig. S2 in IJSEM Online). The pH range for growth was tested at an initial pH of 4.0–9.0 (at 65 °C), in basal medium buffered and adjusted to the required pH (initial pH at 20 °C) as described by Alain *et al.* (2002). Growth was observed at pH 5.5–8.0, the optimum being around pH 6.5–7.5. No growth was observed at pH 5.0 and below or at pH 8.5 and above. Salt tolerance was tested at 65 °C in 'SO4PNsalts' medium prepared with various concentrations of NaCl (0, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, 6.0, 8.0 and 10 %, w/v). Growth was observed at 1.5–4.5 % (w/v) NaCl, the optimum salinity being around 2.5 %. No growth was observed at 1 or 5 % (w/v) NaCl. Under optimal growth conditions, the generation time of strain AT1325^T was around 3 h and 20 min.

Determination of the whole-cell fatty acid composition was performed on cultures grown at 70 °C on 'SO4PNsalts' medium, under a gas phase of H₂/CO₂ (80:20 v/v, 200 kPa). Biomass was prepared in media both with and without yeast extract (0.1 g l^{–1}). In both cases, cells were harvested at the end of the exponential phase of growth. In parallel, *Thermodesulfator indicus* CIR29812^T was grown under the same conditions and in the same culture medium. Fatty acid analyses were carried out at the Deutsche Sammlung von Mikroorganismen und Zellkulturen according to the standard protocol of the Microbial Identification System (MIDI Inc.). Extracts were analysed by using a Hewlett Packard model HP6890A gas chromatograph equipped with a flame-ionization detector as described by Kämpfer & Kroppenstedt (1996). Results are detailed in Table 1. Similar to the results for *Thermodesulfator indicus*, the profile of strain AT1325^T comprised hydroxylated fatty acids, cyclic fatty acids, and saturated and unsaturated straight-chain fatty acids; the dominant components were C_{16:0}, C_{18:0} and C_{18:1ω7c}. However, when *Thermodesulfator indicus* CIR29812^T and strain AT1325^T were grown under identical conditions, some minor differences were observed (Table 1).

Strain AT1325^T was a strictly anaerobic, chemolithoautotrophic bacterium that used hydrogen and sulfate as primary electron donor and acceptor, respectively. Its ability to use alternative electron acceptors was tested by adding elemental sulfur (12 g l^{–1}), L-cystine (12 g l^{–1}), sulfite (1 mM), thiosulfate (20 mM), nitrate (10 mM), nitrite (1 mM) or oxygen (1 %, v/v) to sulfate-depleted media, under an H₂/CO₂ atmosphere (80:20 v/v, 200 kPa). Quantitative determination of hydrogen sulfide production was determined as described by Cord-Ruwisch (1985). The novel isolate was able to reduce sulfate to H₂S, but was unable to utilize sulfur, L-cystine, sulfite, thiosulfate, nitrate, nitrite or oxygen as electron acceptors. As a sulfate-reducer, the inability of strain AT1325^T to use sulfite as sole terminal electron acceptor is surprising but not unique (Itoh *et al.*, 1999; Jeanthon *et al.*, 2002; Moussard *et al.*, 2004). To examine possible carbon sources other than CO₂, a variety of organic carbon sources were tested in the presence of sulfate, under an atmosphere of 100 % H₂ (200 kPa). Formate (10 mM), acetate (20 mM), propionate (20 mM), methanol (0.5 %, v/v), pyruvate (10 mM), glucose (20 mM), monomethylamine (10 mM), peptone (0.2 g l^{–1}) and yeast extract (0.2 g l^{–1}) were tested as potential substrates. Significant growth coupled with hydrogen sulfide production was still observed after three transfers on the same medium (inoculation to 1:200 in all cases) when monomethylamine, peptone or yeast extract were provided as the sole carbon source and when H₂ and sulfate were the respective electron donor and acceptor. Under the conditions tested, formate, acetate, propionate, methanol, pyruvate and glucose were not utilized as sole carbon source. In order to compare the carbon source utilization abilities of the novel isolate with those of *Thermodesulfator indicus*

Table 1. Whole-cell fatty acid profiles of strain AT1325^T and the type strain of *Thermodesulfatator indicus*

Strains: 1, AT1325^T; 2, *Thermodesulfatator indicus* CIR29812^T. Values are percentages of total fatty acids. The nomenclature is as follows: the first number indicates the number of carbon atoms in the molecule; prefixes 'anteiso', 'iso', 'OH' and 'cyclo' indicate anteiso- or iso-branched, hydroxy or cyclic fatty acids; the second number following the colon indicates the number of double bonds; the position of the double bond is indicated by the carbon atom position starting from the methyl (ω) end of the molecule; the suffix *c* indicates the *cis* isomer. Major fatty acids (>5%) are indicated in bold type. ND, Not detected. (a) Strain AT1325^T grown on 'SO4PNsalts' medium (under a gas phase of H₂/CO₂ and without yeast extract). (b) The two strains were grown under identical conditions on 'SO4PNsalts' medium, in the presence of yeast extract (0.1 g l⁻¹) and under an H₂/CO₂ atmosphere.

(a) Fatty acid	1
Saturated	
C _{16:0}	6.37
C _{17:0}	1.12
C _{18:0}	16.14
Monounsaturated	
C _{16:1} ω 5 <i>c</i>	0.82
C _{17:1} ω 6 <i>c</i>	2.23
C _{18:1} ω 9 <i>c</i>	1.16
C _{18:1} ω 7 <i>c</i>	59.43
C _{18:1} ω 5 <i>c</i>	2.07
C _{20:1} ω 7 <i>c</i>	1.23
Hydroxyl	
C _{16:0} 3-OH	1.90
Cyclic	
C _{19:0} cyclo ω 8 <i>c</i>	6.40
Summed feature 3*	1.13

(b) Fatty acid	1	2
Saturated		
C _{12:0}	0.56	0.40
C _{14:0}	1.26	0.76
C _{15:0}	ND	0.59
C _{16:0} N alcohol	ND	0.19
iso-C _{16:0}	0.49	0.39
C _{16:0}	21.79	19.61
anteiso-C _{17:0}	0.22	ND
C _{17:0}	2.27	10.04
iso-C _{18:0}	0.24	ND
C _{18:0}	33.87	29.82
C _{19:0}	0.27	1.16
C _{20:0}	0.81	0.35
Monounsaturated		
C _{16:1} ω 5 <i>c</i>	0.24	0.20
C _{17:1} ω 6 <i>c</i>	1.88	3.62
C _{17:1} ω 8 <i>c</i>	0.19	0.35
iso-C _{18:1} H	0.39	0.31
C _{18:1} ω 9 <i>c</i>	4.08	2.68
C _{18:1} ω 7 <i>c</i>	21.76	21.63
C _{18:1} ω 5 <i>c</i>	0.77	0.71
C _{18:3} ω 6 <i>c</i> (6, 9, 12)	0.30	0.28

Table 1. cont.

(b) Fatty acid	1	2
C _{20:1} ω 7 <i>c</i>	>max ar/ht‡	ND
Hydroxyl		
C _{16:0} 3-OH	1.08	0.42
C _{18:0} 3-OH	0.38	ND
Cyclic		
C _{19:0} cyclo ω 8 <i>c</i>	4.42	4.34
Summed feature 3*	1.29	1.16
Summed feature 5†	1.46	0.97

*Summed feature 3 comprises C_{16:1} ω 7*c* and/or iso-C_{15:0} 2-OH.

†Summed feature 5 comprises C_{18:2} ω 6,9*c* and/or anteiso-C_{18:0}.

‡ar/ht, Area/height of the peak in the chromatogram.

CIR29812^T, carbon source tests were performed in parallel with *Thermodesulfatator indicus* under identical conditions. *Thermodesulfatator indicus* CIR29812^T did not grow when monomethylamine, peptone or yeast extract were provided as sole carbon source and when H₂ and sulfate were the respective electron donor and acceptor. To test for use of electron donors other than molecular hydrogen, strain AT1325^T was cultivated under a gas phase of N₂/CO₂ (80:20 v/v, 200 kPa) in the presence of formate (10 mM), acetate (20 mM), butyrate (10 mM), lactate (10 mM), methanol (0.5 %, v/v), yeast extract (0.2 g l⁻¹) or peptone (0.2 g l⁻¹) with sulfate as a terminal electron acceptor. No growth was observed with the alternative energy sources, indicating that strain AT1325^T was a strict hydrogen-oxidizer. Finally, nitrogen sources for growth were also examined in a nitrogen-depleted medium. The novel isolate was found to grow on organic and inorganic nitrogen sources. Significant growth was observed when NH₄Cl (20 mM), glutamate (10 mM), yeast extract (0.2 g l⁻¹), tryptone (0.2 g l⁻¹), gelatin (0.05 %, v/v) and urea (0.05 %, v/v) were provided as sole nitrogen source.

Antibiotic resistance was tested in the presence of a variety of compounds. Resistance to vancomycin, streptomycin, chloramphenicol, kanamycin, rifampicin, penicillin G, ampicillin and tetracycline was investigated at concentrations of 10, 50, 100 and 200 µg ml⁻¹. When the antibiotic was diluted in ethanol (chloramphenicol) or DMSO (rifampicin), the same volume of solvent was added to control cultures rather than water. All antibiotics were added aseptically before inoculation and the cultures were incubated at 65 °C for 1 week. Strain AT1325^T was sensitive to ampicillin and penicillin G at 10 µg ml⁻¹. It was resistant to vancomycin and tetracycline at 10 µg ml⁻¹, and rifampicin and chloramphenicol at 50 µg ml⁻¹, but was sensitive to higher concentrations of these four antibiotics. Strain AT1325^T was resistant to streptomycin and kanamycin at 200 µg ml⁻¹.

The G + C content of the genomic DNA of strain AT1325^T was determined from the melting point according to Marmur & Doty (1962), as described by Alain *et al.* (2002). A calibration curve was constructed by use of ultrapure

DNA from *Clostridium perfringens* (26.5 mol% G + C), calf thymus (42 mol%), *Escherichia coli* strain B (50 mol%) and *Micrococcus luteus* (72 mol%) as standards (Sigma). The DNA G + C content of strain AT1325^T was 45.6 mol%.

In summary, strain AT1325^T shared many physiological, chemotaxonomic and metabolic properties with its closest phylogenetic relative, *Thermodesulfatator indicus*. Its phenotypic and genotypic properties generally met the characteristics described for the genus *Thermodesulfatator* (Moussard *et al.*, 2004). Strain AT1325^T is a marine, thermophilic, strictly anaerobic bacterium growing chemolithoautotrophically from H₂ oxidation and using sulfate as sole electron acceptor. It robustly branches with the unique representative of the genus *Thermodesulfatator*, namely *Thermodesulfatator indicus*. Nevertheless, strain AT1325^T can be distinguished from *Thermodesulfatator indicus* and from other species of the family *Thermodesulfobacteriaceae* based on a number of genotypic and physiological characteristics (Table 2). It differs from *Thermodesulfatator indicus* by its clear phylogenetic distance and its broader pH range for growth. In addition, the novel isolate is able to use several organic compounds (methylamine, peptone and yeast extract). Based on the data presented, we suggest that strain AT1325^T represents a novel species of the genus *Thermodesulfatator*, for which the name *Thermodesulfatator atlanticus* sp. nov. is proposed.

Description of *Thermodesulfatator atlanticus* sp. nov.

Thermodesulfatator atlanticus (at.lan'ti.cus. L. masc. adj. *atlanticus* from the Atlantic Ocean, referring to the site of isolation of the type strain).

Cells are Gram-negative motile rods (1.04–6.08 µm long by 0.30–0.75 µm wide) with a single polar flagellum. Optimal growth occurs at 65–70 °C (range, 55–75 °C), at pH 6.5–7.5 (range, 5.5–8.0) and in the presence of 2.5 % (w/v) NaCl (range, 1.5–4.5 %). Growth occurs under strictly anaerobic conditions with H₂ as an electron donor, sulfate as a terminal electron acceptor and CO₂ as a carbon source. Strict hydrogen-oxidizer. The following are not utilized as electron donors: formate, acetate, lactate, methanol, peptone and yeast extract. In the presence of H₂ and sulfate, monomethylamine, peptone or yeast extract can be used as sole carbon source. No growth is observed when formate, acetate, propionate, methanol, pyruvate and glucose are provided as sole carbon source. Does not ferment pyruvate or lactate. The following are not utilized as electron acceptors: elemental sulfur, L-cystine, thiosulfate, sulfite, nitrate, nitrite and oxygen. Is able to utilize a wide range of organic and inorganic nitrogen sources. Resistant to streptomycin and kanamycin (200 µg ml⁻¹), sensitive to ampicillin and penicillin G (10 µg ml⁻¹), sensitive to vancomycin and tetracycline (50 µg ml⁻¹).

Table 2. Differential characteristics between strain AT1325^T and representative members of the family *Thermodesulfobacteriaceae*

Taxa: 1, strain AT1325^T; 2, *Thermodesulfatator indicus* (data from Moussard *et al.*, 2004); 3, *Thermodesulfobacterium hydrogeniphilum* (Jeanthon *et al.*, 2002); 4, *Thermodesulfobacterium commune* (Zeikus *et al.*, 1983); 5, '*Geothermobacterium ferrireducens*' (Kashefi *et al.*, 2002). +, Positive; –, negative; ND, not determined.

Characteristic	1	2	3	4	5
Temperature range for growth (optimum) (°C)	55–75 (65–70)	55–80 (70)	50–80 (75)	45–82 (70)	65–100 (85–90)
pH range for growth (optimum)	5.5–8.0 (6.5–7.5)	6.0–6.7 (6.25)	6.3–6.8 (6.5)	6.0–8.0 (7.0)	ND (6.8–7.0)
NaCl concentration range for growth (optimum) (%)	1.5–4.5 (2.5)	1.0–3.5 (2.5)	0.5–5.5 (3.0)	0–2.0 (0)	0–0.75 (0–0.05)
Carbon sources					
CO ₂	+	+	+	–	+
Organic compounds	+	–	–	+	–
Electron donors					
H ₂	+	+	+	–	+
Pyruvate	–	–	–	+	–
Lactate	–	–	–	+	–
Electron acceptors					
Sulfate	+	+	+	+	–
Thiosulfate	–	–	–	+	–
Iron (III)	ND	ND	ND	ND	+
Fermentation	–	–	–	+	–
DNA G + C content (mol%)	45.6	46	28	34.4	ND
16S rRNA gene sequence similarity (%) [*]	100	97.8	88.7	87.7	88.7

^{*}Calculated with reference to the 16S rRNA gene sequence of strain AT1325^T.

and sensitive to rifampicin and chloramphenicol ($100 \mu\text{g ml}^{-1}$). Predominant fatty acids are $\text{C}_{16:0}$, $\text{C}_{18:1\omega7c}$, $\text{C}_{18:0}$ and $\text{C}_{19:0}$ cyclo $\omega8c$. The genomic DNA G+C content of the type strain is 45.6 mol%.

The type strain, AT1325^T (=DSM 21156^T=JCM 15391^T), was isolated from the walls of an active deep-sea hydrothermal vent chimney at the Rainbow vent field, on the Mid-Atlantic Ridge. It is also available under request at the 'Souchothèque de Bretagne' (catalogue LMBE) culture collection (<http://www.ifremer.fr/souchotheque/>).

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