**Petrotoga mobilis** sp. nov., from a North Sea oil-production well

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INTRODUCTION

In recent years, several new members of the order *Thermotogales* have been isolated from volcanically and non-volcanically heated geothermal environments (Andrews & Patel, 1996; Fardeau et al., 1997; Jeanthon et al., 1995; Koch et al., 1997). *Thermotogales* currently comprises five genera, *Thermotoga* (Huber et al., 1986), *Thermosiphon* (Huber et al., 1989), *Fervidobacterium* (Huber et al., 1990), *Geotoga* and *Petrotoga* (Davey et al., 1993). All members of the *Thermotogales* group have a characteristic outer sheath-like structure ('toga'); they are thermophilic and hyperthermophilic prokaryotes representing an early divergence within the (eu)bacterial line of descent (Winkler & Woese, 1991).

The North Sea oil reservoirs constitute a hot subterranean biosphere 1-2-60 km below the sea floor. Environmental parameters (temperature, pressure, pH, salinity, concentration of heavy metals, petroleum composition) vary widely from reservoir to reservoir. For instance, the temperature is 60–200 °C with an increase of 1 °C per 24–30 m increase in depth and the *in situ* pressure is 150–800 bar (15–80 MPa). Various physiological types of thermophilic prokaryotes have been isolated from petroleum reservoirs, e.g. sulfidogens (Beeder et al., 1994, 1995; Nilsen et al., 1996; Rees et al., 1995; Rosnes et al., 1991a), methanogens (Nilsen & Torsvik, 1996), and *Thermotogales* genera (Andrews & Patel, 1996; Davey et al., 1993; Fardeau et al., 1997; Jeanthon et al., 1995; Stetter et al., 1993).

The only *Petrotoga* sp. described so far is *Petrotoga mithotera*, which was isolated from petroleum reservoirs in Oklahoma and Texas, USA (Davey et al., 1993). It is moderately thermophilic with an optimum growth temperature of 55 °C, non-motile, rod-shaped with a toga, obligately anaerobic, fermentative and

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**Keywords:** *Petrotoga mobilis* sp. nov., thermophile, oilfield water

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capable of reducing elemental sulfur to hydrogen sulfide. *Petrotoga* differs from the other *Thermotogales* genera by its higher salt tolerance and 16S rRNA sequence, which shows it to be a distinct lineage within this order.

Organisms with a sheath-like outer structure have been isolated from North Sea oil wells. In this paper, the general characteristics and phylogenetic position of one of the isolates, strain SJ95\(^T\), are described. Although it is phylogenetically closely related to *P. mithoferma*, strain SJ95\(^T\) differs in terms of its genotypic, phenotypic and immunological properties. Therefore, strain SJ95\(^T\) is proposed as a new species, *Petrotoga mobilis* sp. nov.

**METHODS**

**Organisms and source of inoculum.** Strain SJ95\(^T\) was enriched from anoxic samples of production water taken from the water separator tanks on off-shore oil platforms. The pressure in the separators was 1–80 bar (0.1–8 MPa), the temperature was 70 °C and the pH was 7.8, measured after pressure release. *P. mithoferma* (ATCC 51224\(^T\)) was obtained from the American Type Culture Collection (Rockville, MD, USA).

**Enrichment, isolation and cultivation.** Enrichment and routine cultivation were done in a medium containing the following components (l-1): NaCl, 30.0 g; MgSO\(_4\), 7H\(_2\)O, 7.0 g; KCl, 0.34 g; NH\(_4\)Cl, 0.25 g; CaCl\(_2\), 2H\(_2\)O, 0.14 g; KH\(_2\)PO\(_4\), 0.14 g; yeast extract (Difco), 0.2 g; 1 ml trace element solution SL-10 (Widdel et al., 1983); and 0.5 ml resazurin (0.02%). After autoclaving in a dispenser (Lien & Beeder, 1997), the hot medium was reduced with 4 ml 0.5 M Na\(_2\)S, 9H\(_2\)O under argon gas. The pH was adjusted to 6.5 with 6 M HCl and 10 ml vitamin solution (Balch et al., 1979) was added. The medium was dispensed into 50 or 200 ml serum bottles and Bellco tubes no. 2047 (Vineland) sealed with butyl rubber stoppers and aluminium crimp seals and a gas phase of argon (200 kPa). Before inoculation with 10% inoculum, the substrates were added separately by syringe from anoxic stock solutions. The incubation temperature was 60 °C. Pure cultures were isolated by dilution series using the shake tube culture method (Widdel & Pfennig, 1984) with anoxic Gelrite gellan gum (final concentration 0.3%, w/v); Kelco Division of Merck) as the gelling agent and starch (final concentration 0.5%, w/v) as the substrate.

**Microscopy.** Cells were observed with a Labophot (Nikon) and a Vanox (Olympus) phase microscope to determine purity, morphology and Gram reaction, and to make photomicrographs (Pfennig & Wagner, 1986). Cells for electron microscopy were fixed in the medium with 1.5% (w/v) glutaraldehyde for 30 min on ice. After washing with Tris/EDTA buffer (20 mM Tris, 1 mM EDTA, pH 6.8), a piece of carbon support film, about 10 nm thick, was floated on the surface of the sample. After attachment of the bacteria, the carbon film was washed with Tris/EDTA buffer and distilled water, picked up with 300 mesh copper grids and immediately blotted dry on filter paper. The grids were mounted on carbon conductivity tabs on stubs and, without further sputtering, observed in a Zeiss DSM982 Gemini at 1 kV, 10 μm aperture and 3 mm working distance using the in-lens detector.

**Serology.** Polyclonal antiserum was produced against strain SJ95\(^T\) as described previously (Christensen et al., 1992). Antigens were characterized by Western immunoblotting of SDS-soluble whole-cell extracts. SDS-PAGE of the whole-cell extracts was carried out as described by Laemmli (1970) with 12.5 and 4.5% (w/v) polyacrylamide in the separation and stacking gels, respectively. The electrophoresis and subsequent immunoblotting were run as described previously (Christensen et al., 1992).

**Growth and metabolism.** Growth (in Bellco tubes) was determined as an increase in OD\(_{600}\). Hydrogen and carbon dioxide gases were determined with a Varian model 3300 GC equipped with a thermal conductivity detector and a Chrompack 45/60 molecular sieve 10x 1/8” (3.0 m by 3.2 mm) stainless steel column. The oven, injector and detector temperatures were 60, 125 and 125 °C, respectively, and the carrier gases for determination of hydrogen and carbon dioxide were argon and helium, respectively.

Short-chain fatty acids and alcohols were determined by HPLC using an Aminex HPX-87 column (300 x 7.5 mm; Bio-Rad; eluent, 40 mM H\(_2\)SO\(_4\); column temperature, 65 °C; flow rate 0.6 ml min\(^{-1}\)) and a Refractive Index Detector 156 (Altek) at 35 °C. The injection volume was 100 μl.

Xylanase activity was determined photometrically by measuring the increase in reducing sugars released from birch wood xylan (Roth) using p-hydroxybenzoic acid hydrazide (PAHBH) reagent (Lever, 1972). The standard incubation mixture contained: 1 ml 1% birch wood xylan suspended in 50 mM potassium phosphate buffer, pH 6.5, and 0.2 ml enzyme solution. Standard incubation conditions were 5 h at 60 °C, after which the reaction was stopped by the addition of 3 ml PAHBH reagent. After colour development for 5 min at 90–100 °C, A\(_{410}\) was determined. In the enzyme blank, the enzyme was added after the addition of the PAHBH reagent. Potassium phosphate buffer (50 mM) was used for the determination of the effect of pH (at 60 °C) and temperature (at pH 6.5) on enzyme activity. Xylanase activity was measured in a cell-free extract, intact cells and a culture filtrate of cells grown on xylan. These different fractions were obtained as follows. Samples of 20 ml culture were centrifuged at 10000 g for 10 min, and the supernatant was used as the culture filtrate. A suspension of intact cells (examined by microscopy) was made by suspending the pellet in 1 ml growth medium without a substrate. The cell-free extract was prepared from 0.5 ml cell suspension using ultrasonic disintegration followed by 10 min centrifugation at 10000 g. The activity of glucose isomerase was assayed as described by Lee et al. (1990).

**DNA analyses.** Genomic DNA for determination of the G+C content and DNA-DNA hybridization was isolated from 0.4-1.0 g frozen and thawed bacterial pellets. RNase (10 μl ml\(^{-1}\)) was added, and the mixture was incubated for 60 min at 65 °C. Thereafter, 0.5 ml 10% (w/v) SDS and 50 μl (20 mg ml\(^{-1}\)) proteinase K were added followed by incubation at 37 °C for 1 h. After mixing the solution with 1.8 ml 5 M NaCl, 1.5 ml hexadeoxytrimethyl ammonium bromide (Murray & Thompson, 1980) was added and the mixture was incubated at 65 °C for 20 min. An equal volume of chloroform:isoamylalcohol (24:1) was then added, and the mixture was centrifuged at 6000 g for 10 min. The water phase was transferred to another tube and 0.6 vol. 2-propanol was added. After 15 min, the DNA was collected and transferred to 1 ml 70% ethanol and centrifuged for 5 min at 10000 g. The pellet was washed in 70% ethanol and
finally dissolved in 1 ml 20 mM Tris/HCl buffer containing 1.0 mM EDTA. The G+C content of the DNA was measured by both the thermal denaturation method (De Ley, 1970), with *Escherichia coli* B type VIII DNA (no. D-2001; Sigma) as a reference, and the chemical method using HPLC to separate and quantify nucleosides (Mesbah et al., 1989). For DNA–DNA hybridization studies, DNA was first subjected to hydroxyapatite chromatography (Cashion et al., 1977); hybridization was carried out according to De Ley et al. (1970) with modifications using a Gilford System 2600 spectrophotometer equipped with a Gilford 2527-R thermoprogrammer and plotter. The DNA–DNA hybridization was carried out by M. Steffen at the DSMZ.

16S rDNA sequence determination and analysis. Genomic DNA extraction, PCR-mediated amplification of the 16S rDNA, and purification of PCR products were carried out using procedures described previously (Rainey et al., 1996; Rainey & Stackebrandt, 1993). Purified PCR products were sequenced using the *Taq* DyeDeoxy Terminator Cycle Sequencing kit (Applied Biosystems) as directed in the manufacturer’s protocol. The Applied Biosystems 373A DNA Sequencer was used for electrophoresis of the sequence reaction products. The 16S rDNA sequence was manually aligned against *P. miotherma*, *Geotoga* and other Thermotogales representatives. Pairwise evolutionary distances were computed using the correction of Jukes & Cantor (1969). The least-squares distance method of De Soete (1983) was used in the construction of the phylogenetic dendrogram from distance matrices.

Nucleotide sequence accession numbers. The accession numbers of the reference strains used in the sequence comparison are as follows: *Aquifex pyrophilus*, M83548; *Fervidobacterium islandicum*, M59176; *Fervidobacterium nodosum*, M59177; *Geotoga petraea*, L10658; *Geotoga subterranea*, L10659; *Petrotoga miotherma*, L10657; *Thermosiphon africanus*, M24022; *Thermotoga maritima*, M21774; and *Thermotoga therarmarum*, ARB8587.

RESULTS

Enrichment and isolation

Bacteria with an outer sheath (toga) were first observed in enrichment cultures of a thermophilic spore-forming *Desulfotomaculum* sp. This binary culture grown at 60 °C converted mono- and disaccharides to hydrogen sulfide, acetate, hydrogen and ethanol (Rosnes et al., 1991b). Efforts were made to isolate the different members of the culture; *Desulfotomaculum* sp. was isolated by autoclaving the culture at 121 °C for 20 min, which killed the sheathed bacteria, but not the sporulators with extremely heat-resistant spores (Rosnes et al., 1991a). Several dilution series were carried out in a glucose-containing medium without sulfate, but the spore-forming sulfate reducers ultimately appeared in all of the dilution tubes. However, successful enrichment of the sheathed bacteria was obtained by growing the binary culture in a mineral salt medium with starch and without sulfate, but the spore-forming sulfate reducers ultimately appeared in all of the dilution tubes. However, successful enrichment of the sheathed bacteria was obtained by growing the binary culture in a mineral salt medium with starch and without sulfate. The enrichment was subcultured in this medium and during three subsequent transfers, the population developed into a culture dominated by rod-shaped bacteria with a sheath-like outer structure (toga). Several of these bacteria were isolated in pure cultures. One of the isolates, strain SJ95T, forming circular and whitish colonies, is described in this paper.

![Morphology of strain SJ95T](image_url)
Table 1. Comparison of characteristics of strain SJ95<sup>T</sup> and <i>P. miotherma</i>

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>&lt;i&gt;Petrotoga mobilis&lt;/i&gt; SJ95&lt;sup&gt;T&lt;/sup&gt;</th>
<th>&lt;i&gt;Petrotoga miotherma&lt;/i&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell shape</td>
<td>Rod-shaped with toga</td>
<td>Rod-shaped with toga</td>
</tr>
<tr>
<td>Cell size (μm):</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Width</td>
<td>0.5-1.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Length</td>
<td>1.0-50.0</td>
<td>2.0-7.5</td>
</tr>
<tr>
<td>No. of cells per sheath</td>
<td>1-24</td>
<td>1-5</td>
</tr>
<tr>
<td>Motility and flagellation</td>
<td>Motile, subpolar</td>
<td>Non-motile</td>
</tr>
<tr>
<td>Formation of spherical bodies</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Optimum temperature (°C)</td>
<td>58-60</td>
<td>55</td>
</tr>
<tr>
<td>Optimum NaCl requirement (g l&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>30-40</td>
<td>20</td>
</tr>
<tr>
<td>Growth factors requirements:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vitamins</td>
<td>+</td>
<td>ND</td>
</tr>
<tr>
<td>Yeast extract</td>
<td>(+)</td>
<td>+</td>
</tr>
<tr>
<td>Reduction of S&lt;sup&gt;2&lt;/sup&gt; to H&lt;sub&gt;2&lt;/sub&gt;S</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>DNA G+C content (mol %)</td>
<td>31, 34*</td>
<td>32, 34-25, 40†</td>
</tr>
<tr>
<td>Substrates utilized:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xylan</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Cellulose</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ribose</td>
<td>+</td>
<td>ND</td>
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<tr>
<td>Maltodextrin, glucose, lactose,</td>
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<td>+</td>
</tr>
<tr>
<td>sucrose</td>
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<tr>
<td>Galactose, maltose, xylose,</td>
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<td>+</td>
</tr>
<tr>
<td>cellobiose, fructose</td>
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<td></td>
</tr>
<tr>
<td>Arabinose</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

* Values obtained by the thermal denaturation and HPLC methods, respectively.
† Values obtained by the thermal denaturation and HPLC methods and the HPLC value reported by Davey et al. (1993), respectively.
ND, Not determined.

**Morphology**

Cells of strain ST95<sup>T</sup> are rod-shaped and vary widely in size from small ones of only about 1 μm in length to those with a length of 40-50 μm. The width of the cells also varied (Fig. 1a; Table 1). A surrounding sheath was clearly visible under phase microscopy. The cells frequently appeared singly, in pairs or in chains within the sheath, sometimes with more than twenty small cells per sheath or with a single small cell within a long sheath which otherwise seemed to be empty. In contrast to <i>P. miotherma</i>, strain SJ95<sup>T</sup> did not form enlarged spherical bodies in the stationary phase (Davey et al., 1993). Gram staining was negative and no endospores were observed. However, motile cells were frequently observed and electron microscopy revealed some very long flagella (15-16 μm) and subpolar flagellation (Fig. 1b). The smaller single rods moved more rapidly than the longer single cells and pairs of rods which showed a slow flexing, fish-swimming motion. No twiddles, but a reversion of their swimming direction was observed.

**Physiology**

Strain SJ95<sup>T</sup> is an obligate anaerobe that grows at temperatures between 40 and 65 °C (optimum at 58-60 °C). The pH range for growth was pH 5.5-8.5 (optimum at pH 6.5-7.0) (Table 1). The shortest doubling time was about 12 h. Growth was observed in 0.5-9.0% (w/v) NaCl and 0.1-0.8% (w/v) MgSO₄·7H₂O and was optimal at 3-4% NaCl and 0.7% MgSO₄·7H₂O. Several vitamins, e.g. folic acid, riboflavin, pantothenic acid, cobalamin, <i>p</i>-aminobenzoate and lipoic acid (200, 500, 500, 10, 500 and 500 μg l<sup>-1</sup>, respectively) were required. Yeast extract (0.02%, w/v) stimulated growth.

The growth studies were done in the presence of vitamins, 0.02% final concentration yeast extract, and 0.5% final concentration substrate. Growth was observed on: starch, xylan, maltodextrin, maltose, cellobiose, sucrose, lactose, glucose, galactose, fructose, arabinose, xylose, ribose and rhamnose as carbon and energy sources. Highest yield was obtained with ribose, maltose and dextrin. Xylanase activity, optimum at 60-65 °C and pH 5.5-6.0, was detected in intact cells, in cell-free extract but not in the culture filtrate of cells grown on xylan. This indicates that the xylanase activity is located inside the toga as reported for amylases and xylanases from <i>Thermotoga</i> spp. (Senna et al., 1997). Glucose isomerase was detected in cell-free extracts of cells grown on xylose.

The following substrates were tested, but not utilized: cellulose, mannose, raffinose, Casamino acids, man-
**Petrotoga mobilis** sp. nov.

Figrn 2. Protein pattern (a) and immunoblotting with anti-SJ95T (b) after SDS-PAGE of SDS-soluble whole-cell extracts of strain SJ95T (lane 1) and *P. miotherma* (lane 2). The positions of molecular mass standards (in kDa) are indicated on the left (standards in lane 5).

Nitritol, inositol, methanol, ethanol, propanol, butanol, formate, acetate, butyrate, valerate, caproate, malate, lactate, fumarate and pyruvate.

The fermentation products detected in cultures growing on glucose were hydrogen gas, carbon dioxide, acetate and ethanol. As observed with *P. miotherma* (Davey et al., 1993), no growth occurred with a headspace of 80% hydrogen and 20% carbon dioxide; this inhibition by hydrogen was eliminated by adding elemental sulfur or thiosulfate to the culture which caused production of hydrogen sulfide. Growth inhibition also occurred at low (0.1%, v/v) concentration of hydrogen in the headspace. Thiosulfate reduction increased cellular yields and growth rates of strain SJ95T and *P. miotherma* (Fig. 3) similarly to that described by Ravot et al. (1995, 1996) for other members of the order *Thermotogales*.

**Antibiotic sensitivity**

Growth was inhibited at 10 μg ml⁻¹ final concentration of penicillin, ampicillin, vancomycin, chloramphenicol, rifampicin and streptomycin. The inhibition was irreversible since no viable cells were obtained after washing and resuspension in the growth medium. In contrast to the results of Davey et al. (1993), streptomycin (100 μg ml⁻¹) inhibited the growth of *P. miotherma*.

**Whole-cell protein patterns and serology**

Although *P. miotherma* and strain SJ95T have proteins with the same electrophoretic behaviour in common, for example a protein with a molecular mass of about 97 kDa, strain SJ95T contained specific protein bands (e.g. at 60, 38 and 19 kDa) that differentiate it from *P. miotherma* (Fig. 2a). The immunoblotting (Fig. 2b) using antiserum to SJ95T demonstrated serological differences which discriminate strain SJ95T from *P. miotherma*.

**DNA base composition**

The G+C content of the DNA of strain SJ95T was 31.4 and 34.00 ± 0.10 mol% (n = 8), determined by the thermal denaturation and HPLC methods, respectively. The corresponding values found for DNA from *P. miotherma* were 32 and 34.25 ± 0.16 mol% (n = 7). In addition, it is noteworthy that neither DNA sample contained detectable 5-methylcytidine. The sensitivity of the chemical method for detecting this modified base in the DNA was >0.3% of the total DNA or 1.7% of the cytidine.

**Phylogenetic analysis**

A 16S rDNA sequence comprising 1473 nt between positions 32 and 1534 (*E. coli* positions) was determined for strain SJ95T. A comparison of 1179 nt between positions 32 and 1357 (*E. coli* positions) of the 16S rDNA sequence of strain SJ95T was made with eight representatives of the order *Thermotogales* and *Aquifex pyrophilus*. The resulting phylogenetic dendro-
Fig. 4. Phylogenetic dendrogram based on 16S rDNA sequence comparison indicating the position of Petrotoga mobilis (strain SJ95T) within the radiation of the bacterial Thermotogales group. Bar, 10 nucleotide changes per 100 nucleotides.

Fig. 4 shows strain SJ95T to be closely related to the Geotoga/Petrotoga lineage within the Thermotogales. 16S rDNA similarity values between SJ95T and members of the Thermotogales are 77.9–97.9%.

The highest 16S rDNA sequence similarity in the comparison of the sequences of the strains shown in Fig. 4 is to P. miotherma at 97.9%. Direct pairwise comparison of the 16S rDNA sequences of strain SJ95T and P. miotherma showed a similarity of 97.7%.

DNA–DNA homology

The DNA–DNA homology of strain SJ95T and P. miotherma was examined; the hybridization value was 35.6%.

DISCUSSION

Strain SJ95T was tentatively identified as a member of the Thermotogales mainly because of its rod-shaped cells with an outer sheath-like structure and its thermophilicity. This relationship was confirmed by 16S rDNA sequence analysis which showed that strain SJ95T is most closely related to P. miotherma. Furthermore, strain SJ95T shares several phenotypic properties with this species, e.g. moderate thermophilicity, a high salt tolerance, capability of fermenting a broad spectrum of carbohydrates, and a variable cell size (Table 1).

However, strain SJ95T is significantly different from P. miotherma. Firstly, strain SJ95T is motile with subpolar flagellation. The cells are longer (40–50 μm) than those of P. miotherma (7.5 μm) and they do not form enlarged spherical bodies in the stationary phase. Secondly, strain SJ95T is able to grow on xylan with toga-associated xylanase activity. Thirdly, the protein profile and the antigen pattern of SDS-soluble whole-cell extracts are different in strain SJ95T and P. miotherma. Fourthly, the level of 16S rDNA sequence similarity of 97.7% is sufficiently low to establish a new species (Stackebrandt & Goebel, 1994). Fifthly, the DNA base composition is slightly different according to results obtained using two different and unreliable methods, but differs by 6% according to the reported values for P. miotherma (Davey et al., 1993).

Finally, the level of DNA–DNA hybridization of 35.6% between strain SJ95T and P. miotherma is too low for these organisms to be considered as members of the same species. On the basis of these data, strain SJ95T can be considered a new species of the genus Petrotoga, for which the name Petrotoga mobilis is proposed.

Description of Petrotoga mobilis sp. nov.

Petrotoga mobilis (mo'bi.lis. L. fem. adj. mobilis motile).

Rod-shaped cells with a sheath-like outer structure, Gram-negative, obligately anaerobic, heterotrophic, able to ferment a broad spectrum of carbohydrates including xylan. The cells vary in size (0.5–1.0 by 1.0–50 μm) and can be single, in pairs or in chains, sometimes with more than 20 cells within the sheath. Frequently motile with subpolar flagellation. Neither endospores nor enlarged spherical bodies in stationary phase are formed. Growth occurs at pH 5.5–8.5, 40–65°C and at NaCl concentrations of 0.5–9.0% NaCl (optimum at 3–4%). Several vitamins are required and yeast extract stimulates growth. The DNA G + C content is 31 and 34 mol%, as determined by thermal denaturation and HPLC methods, respectively. Isolated from hot oilfield water from an oil reservoir in the North Sea. The type strain is SJ95T (= DSM 10674T).

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