Desulfopila aestuarii gen. nov., sp. nov., a Gram-negative, rod-like, sulfate-reducing bacterium isolated from an estuarine sediment in Japan

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A strictly anaerobic, mesophilic, sulfate-reducing bacterial strain (MSL86^T) isolated from an estuarine sediment in the Sea of Japan (around the Japanese islands) was characterized phenotypically and phylogenetically. The cells were found to be Gram-negative, motile, non-spore-forming rods. Catalase was not detected. The optimum NaCl concentration for growth was 1.0 % (w/v) and the optimum temperature was 35 °C. Strain MSL86^T was slightly alkaliphilic, with optimum growth at pH 7.5–7.6. Organic electron donors were incompletely oxidized to (mainly) acetate. Strain MSL86^T utilized formate, pyruvate, lactate, fumarate, ethanol, propanol, butanol and glycerol as electron donors for sulfate reduction and did not use acetate, propionate, butyrate, succinate, malate, methanol, glycine, alanine, serine, aspartate, glutamate or H₂. Sulfite, thiosulfate and fumarate were used as electron acceptors with lactate as an electron donor. Without electron acceptors, the strain fermented pyruvate and fumarate. The genomic DNA G + C content was 54.4 mol%. Menaquinone MK-8(H₄) was the major respiratory quinone. The major cellular fatty acids were C_{16:0}, C_{16:1ω7}, C_{16:1ω5} and C_{17:1ω6}. A phylogenetic analysis based on the 16S rRNA gene sequence placed the strain in the class *Deltaproteobacteria*. The recognized bacterium most closely related to strain MSL86^T was [*Desulfobacterium*] *catecholicum* DSM 3882^T (sequence similarity 94.4 %), and the next most closely related recognized species were *Desulfotalea psychrophila* (94.2 % sequence similarity with the type strain) and *Desulfotalea arctica* (93.7 %). As the physiological and chemotaxonomic characteristics of MSL86^T were distinctly different from those of any related species, a novel genus and species *Desulfopila aestuarii* gen. nov., sp. nov. are proposed to accommodate the strain. The type strain of *Desulfopila aestuarii* is MSL86^T (=JCM 14042^T=DSM 18488^T).

Sulfate-reducing bacteria (SRB) include phylogenetically diverse anaerobic bacterial species (Castro *et al.*, 2000; Kuever *et al.*, 2005). As sulfate levels are sufficient in marine environments, it has been reported that SRBs are responsible for up to 50 % of the organic carbon mineralization in marine sediments (Jørgensen, 1982). Various novel species of SRB have been isolated recently from a wide range of marine sediments (Jéanthon *et al.*, 2002; Sass *et al.*, 2002; Audiffren *et al.*, 2003; Cravo-Laureau *et al.*, 2004; Moussard *et al.*, 2004; Kuever *et al.*, 2005). In addition, many studies on the diversity of SRB in natural environments have been performed using cultivation-independent molecular

techniques based on PCR amplification of the 16S rRNA gene or the dissimilatory sulfite reductase gene (Devereux & Mundfrom, 1994; Voordouw *et al.*, 1996; Wagner *et al.*, 1998; Joulain *et al.*, 2001; Klein *et al.*, 2001; Purdy *et al.*, 2002; Dhillon *et al.*, 2003; Leloup *et al.*, 2006), and these studies have revealed that phylogenetically diverse lineages of uncultivated SRB are still present in natural ecosystems.

In the course of an investigation on SRB in an estuarine sediment from a Japanese island, we isolated various sulfite-reducing strains. The phylogenetic, physiological and chemotaxonomic characteristics of one of the strains, MSL86^T, supported the proposal of a novel genus and species in the class *Deltaproteobacteria*. Because strain MSL86^T was isolated from estuarine sediment by the dilution colony-counting method using a sample diluted to 10⁻⁴, it was thought that the SRB group relating to the strain should be present in the sediment at rather high population levels.

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Abbreviations: CFA, whole-cell fatty acid; SRB, sulfate-reducing bacteria.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain MSL86^T is AB110542.

Sediment cores were collected to a depth of 10 cm using a core sampler (5 cm in diameter) from sediment at a water depth of 2 m in the Niida River estuary in Sakata harbour, Japan (i.e. from the Sea of Japan around the Japanese islands; 38° 54.5' N 139° 50.6' E), on 12 November 2000. The sediment sample was subjected to consecutive 10-fold dilutions with seawater bubbled with O₂-free N₂ gas. The diluted samples (0.2 ml) were inoculated into seawater agar medium (10 ml) containing 20 mM sodium lactate, and viable colony counts for SRB were determined by using the anaerobic roll-tube method (Hungate, 1966). Several strains of SRB were obtained by picking up black colonies of SRB that appeared on the roll-tube agar after incubation for about a month. Strain MSL86^T was finally obtained after several purification procedures through colony isolation by the anaerobic roll-tube method.

Two basal media (seawater medium and defined medium) were used in this study. The seawater medium contained the following (l⁻¹ seawater): 0.5 g KH₂PO₄, 0.3 g NH₄Cl, 0.1 g yeast extract, 1 mg sodium resazurin, 10 ml trace element solution (l⁻¹: 10 ml 25% (v/v) HCl, 1.5 g FeCl₂·4H₂O, 0.19 g CoCl₂·6H₂O, 0.1 g MnCl₂·4H₂O, 0.07 g ZnCl₂, 0.062 g H₃BO₃, 0.036 g Na₂MoO₄·2H₂O, 0.024 g NiCl₂·6H₂O and 0.017 g CuCl₂·2H₂O) and 0.5 g L-cysteine hydrochloride monohydrate, as well as an appropriate electron donor. The pH was adjusted to 7.2–7.4 with 1 M NaOH. Agar (Difco) (1.5%, w/v) was added to the medium and used for the anaerobic roll-tube method for isolation and in slant cultures (with lactate as an electron donor). A medium designated as the 'defined medium' (distinguishing it from seawater medium) was used for general physiological characterization of the strain, and contained the following (l⁻¹): 0.5 g KH₂PO₄, 1.0 g NH₄Cl, 1.0 g Na₂SO₄, 2.0 g MgSO₄·7H₂O, 0.1 g CaCl₂·2H₂O, 0.5 g yeast extract, 1 mg sodium resazurin, 10 ml trace element solution, 15 g NaCl and 0.5 g L-cysteine hydrochloride monohydrate (Nakamoto *et al.*, 1996; Ueki *et al.*, 1980; Widdel & Bak, 1992). The pH was adjusted to 7.2–7.4 with 1 M NaOH. Cultivation and transfer of the strain were performed under an O₂-free N₂ (100%) atmosphere. The strain was cultivated at 30 °C, unless indicated otherwise. The strain was maintained in slant cultures of the seawater medium or the defined medium with lactate as an electron donor. The pH of both media after autoclaving was around pH 6.3. Each electron donor was added at a final concentration of 20 mM.

The Gram reaction and cellular morphology were confirmed by light microscopy. The motility of the cells was examined by phase-contrast microscopy, and flagella staining was carried out according to Blenden & Goldberg (1965). Growth of the strain under aerobic conditions was examined in the presence of sodium lactate as an electron donor, using the defined medium without L-cysteine and sodium resazurin. The catalase and oxidase activities of the cells were tested as described by Akasaka *et al.* (2003a). The effects of NaCl concentration and pH on growth of the strain were examined in the presence of sodium lactate as an

electron donor, using the defined medium. The effects of temperature on growth were examined using the seawater medium, with sodium lactate as an electron donor. Growth of the strain was monitored by measuring the OD₆₆₀ with a spectrophotometer (U-1000; Hitachi).

The utilization of electron donors by strain MSL86^T was determined by using the defined medium containing each compound at a final concentration of 20 mM. H₂ utilization was determined in the presence of acetate (5 mM) and with H₂ in the atmosphere. Utilization of electron acceptors was determined with a sulfate-free medium that contained chloride at the same concentration as that of sulfate in the defined medium; sodium lactate (20 mM) served as an electron donor. Sodium sulfite (3 mM), sodium thiosulfate (15 mM) or disodium fumarate (20 mM) was added to the sulfate-free medium as a possible electron acceptor. The utilization of pyruvate, lactate, fumarate or malate (20 mM each) in the absence of electron acceptors in the medium was also determined by using the sulfate-free medium. Fatty acids and amino acids were used in the form of sodium salts and added to the medium from sterilized stock solutions. Utilization of each electron donor or acceptor was determined by comparing growth in the presence and absence of each compound, as well as by measuring the concentration in the medium after cultivation.

Volatile fatty acids and alcohols were analysed by GC (G-5000 or 263-30; Hitachi), as described by Ueki *et al.* (1986). Non-volatile fatty acids and formate were analysed by HPLC (LC-10AD; Shimadzu), as described by Akasaka *et al.* (2003a). Sulfate, sulfite and thiosulfate were analysed with an ion chromatograph (Dionex 2000i), as described by Nakamoto *et al.* (1996). Genomic DNA was extracted according to the method described by Kamagata & Mikami (1991). Extracted DNA was digested with P1 nuclease by using a YAMASA GC kit (Yamasa shoyu) and its G+C content was measured by HPLC with Hitachi L-7400 apparatus equipped with a μ Bondpack C18 column (3.9 × 300 mm; Waters). Isoprenoid quinones were extracted as described by Komagata & Suzuki (1987) and analysed by using a mass spectrometer (JMS-SX102A; JEOL). Whole-cell fatty acids (CFAs) were converted to methyl esters by saponification, methylation and extraction according to the method of Miller (1982). Methyl esters of the CFAs were analysed with a gas chromatograph (Hewlett Packard Hp6890 or Hitachi G-3000) equipped with an HP Ultra2 column. CFAs were identified by means of equivalent chain-lengths (Miyagawa *et al.*, 1979; Ueki & Suto, 1979) according to the protocol of TechnoSuruga, based on the MIDI Microbial Identification System (Microbial ID) of Moore *et al.* (1994).

The 16S rRNA gene of strain MSL86^T was extracted according to the method described by Akasaka *et al.* (2003a, b) and amplified by PCR using a primer set comprising 27f and 1492r. The PCR-amplified 16S rRNA gene was sequenced by using a Thermo Sequenase primer cycle sequencing kit (Amersham Biosciences) and a DNA

sequencer (model 4000L; Li-COR). Multiple alignments of the sequence with reference sequences in GenBank were performed with the BLAST program (Altschul *et al.*, 1997). A phylogenetic tree was constructed with the neighbour-joining method (Saitou & Nei, 1987) by using the CLUSTAL W program (Thompson *et al.*, 1994) as well as the maximum-likelihood program (DNAML) of the PHYLIP 3.66 package (Felsenstein, 2006). All gaps and unidentified base positions in the alignments were excluded before assembly.

The cells of strain MSL86^T were Gram-negative rods, 0.7–1.2 µm wide and 1.9–3.8 µm long with rounded ends; they usually occurred singly or in pairs (Fig. 1). The cells were motile by means of single polar flagella. The strain produced thin, greyish colonies on agar slants of the defined medium as well as the seawater medium. Cells of strain MSL86^T aggregated during growth in the liquid medium and were deposited at the bottom of the test tubes. Spore formation was not observed.

Strain MSL86^T reduced sulfate, with lactate as an electron donor, and produced acetate at a molar ratio of about 2 : 1 : 2 (lactate/sulfate/acetate) in the defined medium. Thus, the strain showed an incomplete type of oxidation of electron donors. Neither catalase activity nor oxidase activity was detected. The strain could not grow in air in the defined liquid medium. The strain grew in the presence of NaCl at concentrations up to 5.0 % (w/v), and the optimum NaCl concentration for growth was 1.0 % (w/v). The strain grew in the defined medium even in the absence of added NaCl. The temperature range for growth was 10–40 °C, with an optimum at 35 °C. The strain was slightly alkaliphilic and had a pH optimum at 7.5–7.6; the pH range for growth was 6.3–8.5. It could not grow at an initial pH of 5.6.

Fig. 1. Phase-contrast photomicrograph of cells of strain MSL86^T grown anaerobically on an agar slant comprising seawater medium. Bar, 10 µm.

Strain MSL86^T grew even in the absence of added electron donors, and reduced sulfate with the concomitant production of acetate, suggesting that yeast extract or L-cysteine added to the medium was used as an electron donor. The strain utilized formate, pyruvate, fumarate, ethanol, propanol, butanol and glycerol, as well as lactate, as electron donors for sulfate reduction. Although all organic electron donors were usually oxidized to (mainly) acetate, succinate (2.9 mM) was produced in addition to acetate (8.3 mM) when fumarate was used as the electron donor. Propanol and butanol were oxidized to their corresponding carboxylic acids. Strain MSL86^T did not utilize acetate, propionate, butyrate, malate, succinate, methanol, glycine, alanine, serine, aspartate, glutamate or H₂ as electron donors.

Strain MSL86^T utilized sulfite, thiosulfate and fumarate in addition to sulfate as electron acceptors with lactate as the electron donor. Growth rates in defined medium supplemented with 1.5 % (w/v) NaCl were assessed with fumarate, sulfate, sulfite or thiosulfate as the electron acceptor: the comparison showed that growth was slightly faster with fumarate ($\mu = 0.096 \text{ h}^{-1}$) than with sulfate ($\mu = 0.085 \text{ h}^{-1}$), sulfite ($\mu = 0.052 \text{ h}^{-1}$) and thiosulfate ($\mu = 0.038 \text{ h}^{-1}$). When fumarate was utilized as an electron acceptor, succinate (3.2 mM) and propionate (1.4 mM) were produced in addition to acetate (7.5 mM), in accordance with the oxidation of lactate (6.7 mM). In the absence of electron acceptors, strain MSL86^T oxidized pyruvate (10.4 mM) and produced acetate (7.8 mM) and propionate (2.3 mM). The strain also oxidized fumarate (13.0 mM) without any electron acceptors, and produced acetate (9.5 mM) and succinate (7.0 mM). The strain did not use lactate or malate in the absence of electron acceptors.

The G + C content of the genomic DNA of strain MSL86^T was 54.4 ± 0.2 mol%. The major respiratory quinone was MK-8(H₄). The predominant CFAs of strain MSL86^T were C_{16:0} (33.6 %), C_{16:1ω7} (6.0 %), C_{16:1ω5} (17.1 %) and C_{17:1ω6} (13.7 %). About 66 % of the total CFAs were even-numbered, straight-chain fatty acids. Smaller amounts of hydroxy fatty acids, iso-C_{11:0} 3-OH (1.1 %), C_{14:0} 3-OH (1.8 %) and C_{16:0} 3-OH (1.6 %), and branched C_{17:1} (4.6 %) were also detected.

On the basis of the almost-complete 16S rRNA gene sequence (1471 bp), strain MSL86^T is affiliated with the class *Deltaproteobacteria*. The closest relative (96.3 % sequence similarity) in the public databases was *Desulfotalea* sp. SFA4, which was isolated from an intertidal flat. The closest known named relative (94.4 % sequence similarity) of strain MSL86^T was the SRB [*Desulfobacterium*] *catecholicum* DSM 3882^T (Szewzyk & Pfennig, 1987). The next most closely related recognized species were *Desulfotalea psychrophila* (94.2 % similarity to the type strain) and *Desulfotalea arctica* (93.7 %) of the *Desulfobulbaceae* (Kuever *et al.*, 2005). Strain MSL86^T formed a distinct cluster with strain MSL53, which was isolated from the same sediment as that used to isolate strain MSL86^T (Fig. 2); the sequence similarity between these two strains was 98.6 %.

It has been proposed that [*Desulfobacterium*] *catecholicum* should not remain within the genus *Desulfobacterium*; 16S rRNA gene sequence analysis performed after the original description revealed the need for reclassification of the species as a member of a novel genus within the *Desulfobulbaceae* (Kuever *et al.*, 2005). The cells of [*Desulfobacterium*] *catecholicum* are non-motile and oval to lemon-shaped, whereas strain MSL86^T has motile cells that are typically rod-shaped. Furthermore, [*Desulfobacterium*] *catecholicum* belongs to the type of SRB that performs complete oxidation (Szewzyk & Pfennig, 1987), whereas strain MSL86^T is of the type that performs incomplete oxidation. As other important physiological characteristics of strain MSL86^T (including utilization of propionate and butyrate as electron donors for sulfate reduction) also differ from those of [*Desulfobacterium*] *catecholicum* (Table 1), strain MSL86^T should not be affiliated with the novel genus that is needed to accommodate [*Desulfobacterium*] *catecholicum*.

Some physiological and chemotaxonomic characteristics of strain MSL86^T and the two most closely related *Desulfotalea* species are compared in Table 1. Both of the *Desulfotalea* species (isolated from permanently cold, Arctic, marine sediments) are psychrophilic SRBs and the optimum growth temperatures of *Desulfotalea psychrophila* and *Desulfotalea arctica* are 10 and 18 °C, respectively (Knoblauch *et al.*, 1999), whereas strain MSL86^T is mesophilic and has an optimum growth temperature of 35 °C. Both of these *Desulfotalea* species are also SRBs that oxidize incompletely, but the range of electron donors used by strain MSL86^T differs from those of these species. Strain MSL86^T utilizes glycerol but not malate, whereas *Desulfotalea psychrophila* utilizes malate but not glycerol. Strain MSL86^T utilizes fumarate, propanol and butanol as electron donors, whereas *Desulfotalea arctica* does not. Strain MSL86^T does not use amino acids or H₂ (with acetate as a carbon source), unlike both of the *Desulfotalea* species. The range of electron

acceptors used by strain MSL86^T is similar to that of *Desulfotalea psychrophila* but differs from that of *Desulfotalea arctica*. *Desulfotalea arctica* does not utilize sulfite or thiosulfate, whereas strain MSL86^T utilizes both. In the absence of electron acceptors, strain MSL86^T and *Desulfotalea psychrophila* utilize fumarate, unlike *Desulfotalea arctica*. Strain MSL86^T produced a small amount of propionate, together with acetate, from pyruvate in the absence of electron acceptors. Furthermore, propionate was also produced when fumarate served as an electron acceptor, with lactate as an electron donor. Although some SRBs such as *Desulfobulbus* and *Desulfosarcina* species also produce propionate from the fermentation of lactate or pyruvate, these species utilize propionate as an electron donor for sulfate reduction (Kuever *et al.*, 2005). As MSL86^T does not utilize propionate as an electron donor, propionate production appears to constitute one of the distinctive physiological characteristics of this strain.

The G + C content of the genomic DNA of strain MSL86^T (54.4 mol%) is significantly different from those of *Desulfotalea psychrophila* (46.8 mol%) and *Desulfotalea arctica* (41.8 mol%) (Knoblauch *et al.*, 1999). The respiratory quinones of *Desulfotalea* species are MK-6(H₂) or MK-6 (Knoblauch *et al.*, 1999), whereas strain MSL86^T possesses MK-8(H₄). Many of the SRBs in the class *Deltaproteobacteria* (including *Desulfovibrio* species) contain menaquinone MK-6 or MK-6(H₂), and some species in the *Desulfobacteraceae* possess MK-7 or MK-7(H₂) (Kuever *et al.*, 2005). Although it is known that *Desulfofaba gelida* in the *Desulfobacteraceae*, a psychrophilic SRB, and sulfur-reducing *Desulfuromonas* species in the *Desulfuromonaceae* possess MK-8, this is a relatively rare menaquinone in SRBs and related organisms (Kuever *et al.*, 2005). The CFA profiles of strain MSL86^T and related *Desulfotalea* species are compared in Table 2. Even-numbered, unsaturated fatty acids (C_{16:1}ω7 and C_{16:1}ω5) are the main CFAs found in

Fig. 2. Neighbour-joining phylogenetic tree, based on 16S rRNA gene sequences, showing the relationships of strain MSL86^T and related species in the class *Deltaproteobacteria*. Bootstrap values shown are based on analysis of 1000 replicates. *Escherichia coli* ATCC 11775^T was used as the outgroup. The tree topology obtained using the maximum-likelihood method was almost the same as that obtained with the neighbour-joining method. Bar, estimated difference of 2% in nucleotide sequence positions.

Table 1. Characteristics useful for differentiating strain MSL86^T from related species

Strains: 1, MSL86^T; 2, *Desulfotalea psychrophila* LSv54^T (data from Knoblauch *et al.*, 1999); 3, *Desulfotalea arctica* LSv514^T (Knoblauch *et al.*, 1999); 4, [*Desulfobacterium*] *catecholicum* NZva20^T (Szewzyk & Pfennig, 1987). ND, No data available.

Characteristic	1	2	3	4
Isolation source	Estuarine sediment	Arctic marine sediment	Arctic marine sediment	Anoxic mud from a bay
Cell shape	Rod	Rod	Rod	Oval to lemon-shaped
Motility	+	+	—	—
Optimum growth conditions				
NaCl (% w/v)	1.0	1.0	1.9–2.5	0.1*
Temperature (°C)	35	10	18	28
pH	7.5–7.6	7.3–7.6	7.2–7.9	6.9–7.1
Utilization of electron donors				
Acetate	—	—	—	+
Propionate	—	—	—	+
Butyrate	—	—	—	+
Fumarate	+	+	—	+
Malate	—	+	—	+
Methanol	—	—	—	+
Propanol	+	+	—	+
Butanol	+	+	—	+
Glycerol	+	—	+	ND
Glycine	—	+	—	ND
Alanine	—	+	—	ND
Serine	—	+	+	ND
Glutamate	—	ND	ND	+
H ₂	—	+	+	+
Utilization of electron acceptors				
Sulfite	+	+	—	+
Thiosulfate	+	+	—	+
Fumarate utilization in the absence of electron acceptor	+	+	—	+
DNA G + C content (mol%)	54.4	46.8	41.8	52.4
Isoprenoid quinone	MK-8(H ₄)	MK-6(H ₂)	MK-6	ND

*Strain NZva20^T grows best in freshwater medium containing 0.1 % (w/v) NaCl and does not grow in medium with NaCl concentrations exceeding 85 mmol l⁻¹ (approximately 0.5 %, w/v).

Desulfotalea species. The high percentages of unsaturated fatty acids (about 90 %) in CFAs of *Desulfotalea* species probably represent an adaptation to low temperatures (Knoblauch *et al.*, 1999). Strain MSL86^T contains much larger amounts of saturated CFAs than do related *Desulfotalea* species, and the strain contains an odd-numbered, unsaturated fatty acid (C_{17:1}) as one of the main CFAs (this being absent, or present as only a minor CFA, in *Desulfotalea* species). Thus, strain MSL86^T has chemotaxonomic characteristics that are distinct from those of the closely related *Desulfotalea* species.

On the basis of the phylogenetic, physiological and chemotaxonomic characteristics described above, strain MSL86^T represents the type species of a novel genus and species in the class *Deltaproteobacteria*, for which we propose the name *Desulfopila aestuarii* gen. nov., sp. nov.

Description of *Desulfopila* gen. nov.

Desulfopila (De.sul.fo.pi'la. L. pref. *de* from; L. n. *sulfur* sulfur; L. fem. n. *pila* pillar; N.L. fem. n. *Desulfopila* a sulfate-reducing pillar).

Mesophilic. Strictly anaerobic. Cells are Gram-negative, non-spore-forming rods. Sulfate, other inorganic sulfur compounds and fumarate serve as electron acceptors. Organic electron donors are oxidized incompletely to (mainly) acetate. The type species is *Desulfopila aestuarii*.

Description of *Desulfopila aestuarii* sp. nov.

Desulfopila aestuarii (ae.stu.a'ri.i. L. gen. n. *aestuarii* of an estuary).

Has the following characteristics in addition to those described for the genus. Cells are rod-shaped with rounded

Table 2. Cellular fatty acid compositions (%) of strain MSL86^T and related species

Strains: 1, MSL86^T; 2, *Desulfotalea psychrophila* LSV54^T (data from Knoblauch *et al.*, 1999); 3, *Desulfotalea arctica* LSV514^T (Knoblauch *et al.*, 1999). —, Not detected.

Fatty acid	1	2	3
Saturated straight-chain			
C _{14:0}	1.4	1.4	—
C _{15:0}	—	0.4	—
C _{16:0}	33.6	6.5	8.3
C _{17:0}	3.4	—	—
C _{18:0}	2.5	—	—
Unsaturated straight-chain			
C _{14:1} ω5	—	1.1	1.5
C _{15:1} ω6	1.1	1.7	—
C _{16:1} ω9	—	1.5	3.6
C _{16:1} ω7	6.0	55.0	53.9
C _{16:1} ω5	17.1	25.5	29.4
C _{17:1} ω6	13.7	2.4	—
C _{18:1} ω9	1.3	—	—
C _{18:1} ω7	1.7	1.5	1.5
C _{18:1} ω5	2.7	0.7	1.0
Hydroxy acids			
iso-C _{11:0} 3-OH	1.1	—	—
C _{14:0} 3-OH	1.8	—	—
C _{16:0} 3-OH	1.6	—	—
Unsaturated branched-chain			
Branched C _{17:1}	4.6	—	—

ends, 0.7–1.2 µm wide and 1.9–3.8 µm long. Motile by a single polar flagellum. Catalase- and oxidase-negative. Colonies are greyish and thin and spread on slant media. The NaCl concentration range for growth is 0–5.0 % (w/v), with an optimum at 1.0 % (w/v). The temperature range for growth is 10–40 °C, with an optimum at 35 °C. Slightly alkaliphilic; the pH range for growth is 6.3–8.5, with optimum growth at pH 7.5–7.6. Utilizes formate, pyruvate, lactate, fumarate, ethanol, propanol, butanol and glycerol as electron donors for sulfate reduction. Does not use acetate, propionate, butyrate, succinate, malate, methanol, glycine, alanine, serine, aspartate, glutamate or H₂. Sulfate, sulfite, thiosulfate and fumarate serve as electron acceptors. With fumarate as an electron acceptor and lactate as an electron donor, propionate is produced together with succinate. Pyruvate and fumarate are fermented in the absence of electron acceptors. The genomic DNA G+C content is 54.4 mol%. The major CFAs are C_{16:0}, C_{16:1}ω7, C_{16:1}ω5 and C_{17:1}ω6. The major respiratory quinone is MK-8(H₄).

The type strain, MSL86^T (=JCM 14042^T=DSM 18488^T), was isolated from an estuarine sediment located in the Sea of Japan around the Japanese islands.

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