Shewanella surugensis sp. nov., *Shewanella kaireitica* sp. nov. and *Shewanella abyssi* sp. nov., isolated from deep-sea sediments of Suruga Bay, Japan

Masayuki Miyazaki,¹ Yuichi Nogi,¹ Ron Usami² and Koki Horikoshi¹

Correspondence

Yuichi Nogi

nogi@jamstec.go.jp

¹Extremobiosphere Research Center, Japan Agency for Marine–Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka 237-0061, Japan

²Faculty of Engineering, Toyo University, 2100 Kuzirai, Kawagoe 350-8585, Japan

Six strains representing three novel species were isolated from deep-sea sediment in Suruga Bay, Japan, at a depth of 2406–2409 m. On the basis of 16S rRNA gene sequence analysis, the isolated strains, c931^T, c941^T, d943, c952, d954 and c959^T, are closely affiliated with members of the genus *Shewanella*. The hybridization values for DNA–DNA relatedness between these strains and *Shewanella* reference strains were significantly lower than that which is accepted as the phylogenetic definition of a species. On the basis of their distinct taxonomic characteristics, the isolated strains represent three novel *Shewanella* species, for which the names *Shewanella kaireitica* sp. nov. (three strains, type strain c931^T=JCM 11836^T=DSM 17170^T), *Shewanella abyssi* sp. nov. (two strains, type strain c941^T=JCM 13041^T=DSM 17171^T) and *Shewanella surugensis* sp. nov. (type strain c959^T=JCM 11835^T=DSM 17177^T) are proposed.

The genus *Shewanella* comprises Gram-negative, facultatively anaerobic gammaproteobacteria (MacDonell & Colwell, 1985) and is typical of deep-sea bacterial genera (DeLong *et al.*, 1997). The genus includes psychrophilic and mesophilic species that are widely distributed in nature, especially in aquatic environments such as freshwater and the ocean (Semple & Westlake, 1987; Myers & Nealson, 1988; Simidu *et al.*, 1990; Gauthier *et al.*, 1995; Bowman *et al.*, 1997; Makemson *et al.*, 1997; Nogi *et al.*, 1998; Venkateswaran *et al.*, 1999; Ivanova *et al.*, 2001, 2004; Satomi *et al.*, 2003; Hirota *et al.*, 2005). To date, at least 31 *Shewanella* species have been recognized. The genus *Shewanella* is divided into two subgenera on the basis of phylogenetic structure, growth properties in relation to pressure and polyunsaturated fatty acid production (Kato & Nogi, 2001). In this paper, we describe the results of taxonomic studies on six strains isolated from Suruga Bay, Japan. Several lines of evidence indicate that these isolates represent three novel species within the genus *Shewanella*.

Strains c931^T, c941^T, d943, c952, d954 and c959^T were isolated at a depth of 2406–2409 m from a deep-sea sediment, using sterilized mud samplers on the unmanned submersible *Kaiko* positioned off Matsuzaki in Suruga Bay (34°

36·55' N 138° 34·77' E). The following reference strains were used. *Shewanella benthica* ATCC 43992^T and *Shewanella pealeana* ATCC 700345^T were obtained from the American Type Culture Collection (Manassas, VA, USA), *Shewanella marinintestina* JCM 11558^T, *Shewanella sairae* JCM 11563^T and *Shewanella schlegeliana* JCM 11561^T were obtained from the Japan Collection of Microorganisms (Wako, Japan) and *Shewanella gelidimarina* ACAM 456^T was obtained from the Australian Collection of Antarctic Micro-organisms (Hobart, Tasmania, Australia). *Shewanella pneumatophori* SCRC-2738^T was obtained from Dr Kikue Hirota (Research Institute of Genome-based Biofactory, National Institute of Advanced Industrial Science and Technology, Sapporo, Japan). *Shewanella violacea* DSS12^T was from our laboratory stock. These bacteria were incubated on marine agar 2216 (Difco). Agar plates were incubated aerobically for 2–3 days at the optimum temperature. Unless indicated otherwise, physiological tests were performed with a slight modification (use of artificial seawater; 1 × artificial seawater consists of 3 % NaCl, 0·07 % KCl, 1·08 % MgCl₂·6H₂O, 0·54 % MgSO₄·7H₂O, 0·1 % CaCl₂·2H₂O) of the general procedures described by Barrow & Feltham (1993) and Baumann *et al.* (1972). Optimal temperatures for growth were determined on the basis of optical density in marine broth 2216 (Difco). Acid production from sugars was assessed using modified OF medium (Hugh & Leifson 1953) containing 0·5 × artificial seawater, 0·05 % (NH₄)₂SO₄, 0·01 % yeast extract (Difco), 0·05 % Tris base, 0·5 % agar, 0·003 %

The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA and *gyrB* gene sequences determined in this study are AB094597, AB094598, AB201475 and AB201780–AB201788, as detailed in Fig. 1.

bromothymol blue and 1 % test sugar (pH was adjusted to 7.1 at 20 °C), with incubation at the optimum temperature. Salt-tolerance tests were performed using medium containing 0.5 % Pepton (Difco), 0.5 % yeast extract, 0.32 % $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ and 0.1 % K_2HPO_4 , with NaCl concentrations of 0–15 % (w/v).

Cellular fatty acids were extracted and analysed as described by Komagata & Suzuki (1987). Isolated strains were cultured in marine broth 2216 medium at optimal temperatures. Cells were washed twice with 0.7 % NaCl at 4 °C; this was followed by centrifugation at 8000 g and freeze-drying. Dried cells (20 mg) were placed in Teflon-lined, screw-capped tubes containing 2 ml anhydrous methanolic HCl and heated to 100 °C for 3 h. After cooling, 1 ml water was added and the fatty acid methyl esters were extracted with n-hexane. Samples were analysed using a Shimadzu model GCMS-QP5050A gas-liquid chromatograph/mass spectrometer with a DB-5MS column (J&W Scientific). Isoprenoid quinones were extracted with chloroform/methanol (2:1) from dried cells (200 mg) and purified using TLC. The purified isoprenoid quinones were analysed using reversed-phase HPLC (Komagata & Suzuki, 1987).

Chromosomal DNA was purified by using a standard method (Saito & Miura, 1963). The DNA G+C content was determined using reversed-phase HPLC (Tamaoka & Komagata, 1984). For analysis of relatedness, DNA–DNA hybridization was carried out at 40 °C for 4 h and measured fluorometrically using the method of Ezaki *et al.* (1989).

16S rRNA and *gyrB* gene sequences were obtained by direct sequencing of PCR-amplified DNA as described previously (Kato *et al.*, 1998; Yamamoto & Harayama, 1995). Nucleotide substitution rates (K_{nuc}) (Kimura, 1980) were determined and a distance matrix tree was constructed with the neighbour-joining method (Saitou & Nei, 1987), using the CLUSTAL X program (Thompson *et al.*, 1997). Alignment gaps and unidentified base positions were not taken into consideration in the calculations. The topology of the phylogenetic tree was evaluated by performing bootstrap analysis with 1000 replicates. The GenBank/DBJ/EMBL accession numbers for the 16S rRNA and *gyrB* gene sequences of the isolates are shown in Fig. 1; reference sequences were obtained from the GenBank database.

Morphological, cultural, physiological and biochemical characteristics of the isolates are shown in Table 1 or given in the species descriptions below. The cells of the novel deep-sea strains were Gram-negative rods that were motile by means of single, unsheathed, polar flagella. These strains were facultatively anaerobic chemo-organotrophs, displaying both respiratory and fermentative types of metabolism. All of the isolates were able to grow in 1–5 % NaCl but not in the absence of NaCl, and the optimal concentration for growth was 2–3 % NaCl.

Phenotypic analysis segregated the strains into three groups, (i) strains c931^T, c952 and c954, (ii) strains c941^T and d943

and (iii) strain c959^T, with the following properties. (i) Strains c931^T, c952 and c954 grew at 2–28 °C, with an optimum at 24–25 °C. Strains c931^T and c952 (but not strain c954) were able to grow in 7 % NaCl. Tween 80 and chitin were hydrolysed. Acid, but not gas, was produced from cellobiose, D-fructose, D-galactose, D-glucose, maltose and D-sorbitol. The G+C content of the DNA was 43.0–44.3 mol%. The major isoprenoid quinones were Q-7 (70–80 %) and Q-8 (20–30 %). (ii) Strain c941^T exhibited growth at 2–18 °C, with an optimum at 10 °C, and strain d943 grew at 2–24 °C, with an optimum at 14 °C. Strains c941^T and d943 did not hydrolyse Tween 80 and strain c941^T utilized cellobiose. The G+C content of the DNA was 43.5–43.6 mol%. The major isoprenoid quinones were Q-7 (65–70 %) and Q-8 (30–35 %). (iii) Strain c959^T exhibited growth at 2–21 °C, with an optimum at 13 °C. No growth occurred at temperatures above 25 °C. Tests for cytochrome oxidase, H_2S production and reduction of nitrite to nitrogen were negative. Acid, but not gas, was produced from D-fructose, D-glucose, glycerol, D-mannose and sucrose. The G+C content of the DNA was 40.0 mol%. The major isoprenoid quinones were Q-7 (5 %) and Q-8 (95 %).

The results of the phylogenetic analyses using 16S rRNA and *gyrB* gene sequences are shown in Fig. 1. These results support the conclusions described below and further clarify the taxonomic and phylogenetic positions of the novel isolates among members of the genus *Shewanella* and related genera. Strains c931^T, d954 and c952 were most closely related to *S. schlegeliana* (98.6–98.8 % similarity for 16S rRNA, 86.0–86.5 % similarity for *gyrB*), strains c941^T and d943 were most closely related to *S. gelidimarina* (97.7–98.0 % similarity for 16S rRNA, 86.8–87.4 % similarity for *gyrB*) and strain c959^T was most closely related to *S. gelidimarina* (97.1 % similarity for 16S rRNA), but showed less than 80 % *gyrB* gene sequence similarity to *Shewanella* species. The generally recommended and accepted criteria for delineating bacterial species state that strains with 16S rRNA gene sequence dissimilarity greater than 3 % are considered to belong to separate species (Stackebrandt & Goebel, 1994; Stackebrandt *et al.*, 2002); within the genus *Shewanella*, strains with *gyrB* gene sequence dissimilarity greater than 10 % are considered to belong to separate species (Venkateswaran *et al.*, 1999). However, bacterial strains with *gyrB* gene sequences that differ by less than 10 % cannot be allocated to the same species without support from DNA–DNA relatedness studies. The generally recognized criteria for delineating bacterial species state that strains with a DNA–DNA relatedness of less than 70 %, as measured by hybridization, represent separate species (Wayne *et al.*, 1987).

The results of DNA–DNA hybridization analysis indicated that the novel isolates fell into three groups (Table 2), the same grouping revealed by phenotypic characteristics and phylogenetic analyses. There was more than 70 % DNA relatedness among the strains in each group, and each group was clearly separate, representing distinct species

Fig. 1. Phylogenetic trees, constructed using the neighbour-joining method and based on 16S rRNA (a) and *gyrB* (b) gene sequences, showing the relationships of isolated strains c931^T, c941^T, d943, c952, d954 and c959^T within the genus *Shewanella*. Bootstrap values were calculated from multiple resamplings of the sequence data-set, which are the basis for multiple tree topologies. Bars, 0.01 (a) and 0.02 (b) nucleotide substitutions per site.

(i.e. showing significantly less than 70 % relatedness) according to the recommendations of Wayne *et al.* (1987). This, together with the other results shown in Table 1 and Fig. 1, suggests that the isolated strains represent three novel species of the genus *Shewanella*.

The whole-cell fatty acid compositions of strains c931^T, c941^T and c959^T and the reference strains are shown in Table 3. The major fatty acids were as follows: strain c931^T, iso-C_{15:0} (isopentadecanoic acid), C_{16:0} (hexadecanoic acid) and C_{16:1} (hexadecenoic acid); strain c941^T, iso-C_{13:0} (isotridecanoic acid) and C_{16:1}; strain c959^T, iso-C_{15:0} and C_{16:1}. For each of the strains, the fatty acid profile showed low levels of similarity to those of the reference

strains. For example, strain c931^T contained relatively large amounts of iso-C_{15:0} and C_{16:0} and small amounts of C_{20:5} (eicosapentaenoic acid), strain c941^T contained large amounts of iso-C_{13:0} and C_{15:0} (pentadecanoic acid) and small amounts of C_{16:0} and strain c959^T contained large amounts of C_{16:1} and did not contain C_{20:5}.

Lowering of temperature has a physical effect on the fluidity of membrane lipids. As the growth temperature is lowered, biological membranes undergo a reversible change from a fluid, disordered state to a non-fluid, ordered state (Hazel & Williams, 1990). The most common adaptive change observed among deep-sea bacteria involves the incorporation of increased proportions of unsaturated fatty acids into

Table 1. Differential characteristics of *Shewanella* species

Taxa: 1, *Shewanella kaireitica* sp. nov. (strains c931^T, c952 and d954); 2, *Shewanella abyssi* sp. nov. (strains c941^T and d943); 3, *Shewanella surugensis* sp. nov. (strain c959^T); 4, *S. marinintestina*; 5, *S. schlegeliana*; 6, *S. sairae*; 7, *S. pealeana*; 8, *S. gelidimarina*; 9, *Shewanella fidelis*; 10, *S. violacea*; 11, *S. benthica*. Cells of all species are Gram-negative rods that are motile by means of single polar flagella. The following tests were positive for all species: catalase activity, hydrolysis of gelatin and reduction of nitrate to nitrite. The following tests were negative for all species: hydrolysis of starch, production of indole and utilization of D-lactose. v, Variable depending on strain; ND, no data available. Data for reference species are from Satomi *et al.* (2003), Leonardo *et al.* (1999), Bowman *et al.* (1997), Ivanova *et al.* (2003) and Nogi *et al.* (1998), except where indicated otherwise.

Characteristic	1	2	3	4	5	6	7	8	9	10	11
Optimum growth temperature (°C)	24–25	10–14	13	20–25	20–25	20–25	25	15–17	20–25	8	4
Growth at/in:											
30 °C	–	–	–	+	+	–	+	–	+	–	–
0% NaCl	–	–	–	–	+	–	–	–	–	–	–
7% NaCl	v	–	–	–	–	–	+	+	+	–	–
Ubiquinone (%)†											
Q-7	70–80	65–70	5	Major	Major	Major	70	75	ND	30	70
Q-8	20–30	35–30	95	Major	Major	Major	30	25	ND	70	30
Oxidase	+	+	–	+	+	+	+	+	+	+	+
Lipase (tri-n-butylin)	+	+	+	ND	ND	ND	+	+	ND	+	–
Chitinase	+	–	–	–	–	–	–	+	–	ND	+
Urease	–	–	–	–	+	–	–	–	ND	ND	ND
DNase	+	+	+	+	+	+	–	+	+	ND	ND
Tween 80 hydrolysis	+	–	+	+	–	+	–	+	v	ND	ND
ONPG test	+	+	–	+	+	–	+	+	ND	+	+
Production of H ₂ S	+	+	–	+	+	+	+	+	+	–	+
Nitrite reduced	+	+	–	+	+	+	+	+	ND	+	+
Acid from:											
Cellobiose	+	v	–	–	–	–	–	–	–	+	+
D-Fructose	+	–	+	–	–	–	–	–	–	–	–
D-Galactose	+	–	–	–	–	–	+	–	–	+	–
D-Glucose	+	–	+	–	–	–	+	–	+	+	+
Glycerol	–	–	+	–	–	–	–	–	–	–	–
Maltose	+	–	–	–	–	–	+	–	ND	–	–
D-Mannitol	–	–	–	–	–	–	–	–	ND	–	–
D-Mannose	–	–	+	–	–	–	–	–	–	–	–
L-Rhamnose	–	–	–	–	–	–	–	–	ND	–	–
D-Sorbitol	+	–	–	–	–	–	–	–	ND	–	–
Sucrose	–	–	+	–	–	–	+	–	–	–	–

*Data from this study.

†Proportions not given for *S. marinintestina*, *S. schlegeliana* or *S. sairae*; Q-7 and Q-8 are listed as major components.

membrane phospholipids (Allen *et al.*, 1999). The largely psychrophilic or piezophilic *Shewanella* strains produce eicosapentaenoic acid (Margesin & Nogi, 2004). However, strain c959^T, adapted to a deep-sea environment, contained large amounts of C_{16:1}.

On the basis of the phenotypic, genotypic and phylogenetic data, it is logical to conclude that the deep-sea isolates we studied are members of the genus *Shewanella* and that they represent three novel species within this genus. We propose the names *Shewanella kaireitica* sp. nov. (type strain c931^T), *Shewanella abyssi* sp. nov. (type strain c941^T) and *Shewanella surugensis* sp. nov. (type strain c959^T).

Description of *Shewanella kaireitica* sp. nov.

Shewanella kaireitica (kai.rei'tic.a. N.L. n. *Kairei* a research vessel; L. fem. suff. *-tica* adjectival suffix meaning 'belonging to'; N.L. fem. adj. *kaireitica* belonging to the research vessel *Kairei*).

Cells are rod-shaped; cell width ranges from 0.8 to 1.0 µm and cell length ranges from 2.5 to 3.0 µm. Cells are Gram-negative and motile by means of single, unsheathed, polar flagella. Colonies on marine agar 2216 are entire, smooth, semitranslucent and salmon-coloured; 2–4 mm in diameter after 1–2 days incubation at 20 °C. The bacterium is

Table 2. DNA–DNA reassociation between the isolated strains and closely related *Shewanella* species

Strain	DNA–DNA reassociation (%) with labelled DNA from:									
	1	2	3	4	6	9	10	11	12	13
1. Strain c959 ^T	100	31	23	–						
2. <i>S. violacea</i> DSS12 ^T		100	–	–						
3. <i>S. gelidimarina</i> ACAM 456 ^T		29	100	–						
4. Strain c941 ^T			35	100						
5. Strain d943			29	74						
6. Strain c931 ^T					100	35	22	21	19	17
7. Strain c952					93	41	26	–	–	–
8. Strain d954					89	33	23	–	–	–
9. <i>S. pealeana</i> ATCC 700345 ^T						100	–	–	–	–
10. <i>S. pneumatophori</i> SCRC-2738 ^T							100	–	–	–
11. <i>S. marinintestina</i> JCM 11558 ^T								100	–	–
12. <i>S. schlegeliana</i> JCM 11561 ^T									100	–
13. <i>S. sairae</i> JCM 11563 ^T										100

Table 3. Fatty acid compositions of the novel isolates and authentic *Shewanella* species

Taxa: 1, strain c931^T; 2, strain c941^T; 3, strain c959^T; 4, *S. marinintestina* JCM 11558^T; 5, *S. schlegeliana* JCM 11561^T; 6, *S. sairae* JCM 11563^T; 7, *S. pealeana* ATCC 700345^T; 8, *S. gelidimarina* ACAM 456^T; 9, *S. fidelis* KMM 3582^T; 10, *S. violacea* DSS12^T; 11, *S. benthica* ATCC 43992^T. Values are percentages of total fatty acids. –, Not detected; tr, trace (<1%). Data for reference species are from Satomi *et al.* (2003), Leonardo *et al.* (1999), Bowman *et al.* (1997), Ivanova *et al.* (2003) and Kato & Nogi (2001).

Fatty acid	1	2	3	4	5	6	7	8	9	10	11
C _{11:0}	–	–	–	–	–	–	–	–	–	3	tr
C _{12:0}	2.7	2.5	1.4	0.3	1.1	0.5	4	1	1.2	4	2
C _{12:0} 3-OH	–	–	–	–	–	–	3	–	–	1	1
iso-C _{13:0}	10.3	23.1	15.3	2.8	2.8	3.4	8	16	10.7	7	5
iso-C _{13:0} 3-OH	2.1	4.1	3.5	–	–	–	5	–	–	8	5
C _{13:0}	–	1.4	–	–	–	1.9	tr	1	1.5	tr	–
iso-C _{14:0}	–	–	–	–	–	–	tr	1	0.4	–	tr
C _{14:0}	3.4	3.9	1.1	4.4	4.2	5.0	4	4	2.3	5	14
C _{14:0} 3-OH	–	–	–	–	–	–	1	–	–	–	–
C _{14:1}	–	–	–	–	–	–	–	1	0.2	1	–
iso-C _{15:0}	21.1	9.5	18.1	9.2	6.4	14.0	12	8	22.3	13	11
anteiso-C _{15:0}	tr	tr	1.9	0.1	0.7	0.2	–	–	0.4	–	–
C _{15:0}	1.4	11.2	–	0.6	0.1	0.3	1	7	8.7	6	–
C _{15:1}	–	–	–	–	–	–	3	1.7	–	–	–
C _{16:0}	21.8	10.5	8.0	22.1	22.7	18.1	20	6	12.9	14	14
C _{16:1}	26.4	19.6	48.5	26.1	26.1	28.1	19	27	20.0	16	31
iso-C _{17:0}	–	–	–	–	–	–	2	tr	0.6	–	–
iso-C _{17:1}	–	–	–	–	–	–	–	–	0.3	–	–
C _{17:0}	–	1.4	–	0.6	–	0.1	2	1	1.5	1	tr
C _{17:1}	tr	2.5	–	1.0	0.5	0.8	1	5	8.2	2	tr
C _{18:0}	–	–	–	3.1	1.2	1.0	2	tr	0.3	–	–
C _{18:1}	8.9	1.2	2.2	9.0	9.8	9.8	6	1	6.0	4	2
C _{20:5} ω3	1.9	9.1	–	17.5	18.6	15.2	11	16	–	14	16

psychrotolerant. Exhibits optimal growth at NaCl concentrations of approximately 3–5 %; able to grow at 7 % NaCl (with the exception of strain d954). No growth occurs in the absence of NaCl. Optimal temperature for growth is 24–25 °C. No growth at temperatures above 30 °C. Facultatively anaerobic chemo-organotroph, having both respiratory and fermentative types of metabolism. Catalase and cytochrome oxidase tests are positive. H₂S is produced. Nitrate is reduced to N₂. Acid is formed oxidatively from cellobiose, D-fructose, D-galactose, D-glucose, maltose and D-sorbitol. No acid is produced from L-arabinose, glycerol, *myo*-inositol, D-lactose, D-mannitol, D-mannose, D-raffinose, L-rhamnose, sucrose, D-trehalose or xylose. The G+C content of the DNA is approximately 43.0 mol%. The major isoprenoid quinone is Q-7. The predominant cellular fatty acids are iso-C_{13:0}, iso-C_{15:0}, C_{16:0} and C_{16:1}.

The type strain, c931^T (=JCM 11836^T = DSM 17170^T), and strains c952 and d954 were isolated from deep-sea sediment in Suruga Bay, Japan.

Description of *Shewanella abyssi* sp. nov.

Shewanella abyssi (a.bys'si. N.L. gen. n. *abyssi* from the abyss).

Cells are rod-shaped; cell width ranges from 0.8 to 1.0 µm and cell length ranges from 2.0 to 2.5 µm. Cells are Gram-negative and motile by means of single, unsheathed, polar flagella. Colonies on marine agar 2216 are entire, smooth, semitranslucent and salmon-coloured; 2–4 mm in diameter after 2–3 days incubation at 10 °C. The bacterium is psychrotolerant. Optimal growth occurs at a NaCl concentrations of 3–5 %. No growth occurs in the absence of NaCl. The optimal temperature for growth is 10 °C. No growth occurs at temperatures above 25 °C. Facultatively anaerobic chemo-organotroph, having both respiratory and fermentative types of metabolism. Catalase and cytochrome

oxidase tests are positive. H₂S and indole are produced. Nitrate is reduced to nitrite; nitrite is reduced to N₂. Acid is formed oxidatively from cellobiose. No acid is produced from L-arabinose, D-fructose, D-galactose, D-glucose, glycerol, *myo*-inositol, D-lactose, maltose, D-mannitol, D-mannose, D-raffinose, L-rhamnose, D-sorbitol, sucrose, D-trehalose or xylose. The G+C content of the DNA is approximately 43.5 mol%. The major isoprenoid quinones are Q-7 and Q-8. The predominant cellular fatty acids are iso-C_{13:0}, iso-C_{15:0}, C_{16:0} and C_{16:1}.

The type strain, c941^T (=JCM 13041^T=DSM 17171^T), and strain d943 were isolated from deep-sea sediment in Suruga Bay, Japan.

Description of *Shewanella surugensis* sp. nov.

Shewanella surugensis (su.ru.gen'sis. N.L. fem. adj. *surugensis* pertaining to Suruga Bay, where the type strain was isolated).

Cells are rod-shaped; cell width ranges from 0.4 to 0.6 µm and cell length ranges from 3.2 to 4.0 µm. Cells are Gram-negative and motile by means of single, unsheathed, polar flagella. Colonies on marine agar 2216 are entire, smooth, semitranslucent and cream-coloured; 2–4 mm in diameter after 2–3 days incubation at 10 °C. The bacterium is psychrotolerant. Optimal growth occurs at an NaCl concentration of approximately 3 %. No growth occurs in the absence of NaCl. The optimal temperature for growth is 13 °C. No growth occurs at temperatures above 25 °C. Facultatively anaerobic chemo-organotroph, having both respiratory and fermentative types of metabolism. The catalase test is positive. The cytochrome oxidase test is negative. Does not produce H₂S. Nitrate is reduced to nitrite. Acid is formed oxidatively from D-fructose, D-glucose, glycerol, D-mannose and sucrose. No acid is produced from L-arabinose, cellobiose, D-galactose, *myo*-inositol, D-lactose, maltose, D-mannitol, D-raffinose, L-rhamnose, D-sorbitol, D-trehalose or xylose. The G+C content of the DNA is approximately 40.0 mol%. The major isoprenoid quinone is Q-8. The predominant cellular fatty acids are iso-C_{13:0}, iso-C_{15:0} and C_{16:1}.

The type strain, c959^T (=JCM 11835^T=DSM 17177^T), was isolated from deep-sea sediment in Suruga Bay, Japan.

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