***Shewanella denitrificans* sp. nov., a vigorously denitrifying bacterium isolated from the oxic–anoxic interface of the Gotland Deep in the central Baltic Sea**

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Three strains of denitrifying estuarine bacteria, OS217^T, OS220 and OS226, were characterized for their physiological and biochemical features, fatty acid profiles and their phylogenetic position based on 16S rDNA sequences. The strains were isolated from the oxic–anoxic interface of an anoxic basin of the central Baltic Sea. Phylogenetic analyses of the 16S rDNA sequences revealed a clear affiliation with members of the genus *Shewanella* of the γ -*Proteobacteria*. The closest sequence similarity was seen with *Shewanella baltica*, *Shewanella putrefaciens* and *Shewanella frigidimarina* (95–96%). The dominant fatty acids were 16:1 ω 7c, 15:0 iso, 16:0 and 13:0 iso. The G+C content of the DNA ranged from 46.8 to 48.1 mol%. The strains were unpigmented, polarly flagellated, mesophilic, facultatively anaerobic and able to use nitrate, nitrite and sulphite as electron acceptors. Growth was observed at salinities from 0 to 6‰, with an optimum between 1 and 3‰. According to their morphology, physiology, fatty acid composition and 16S rRNA sequences, the described bacteria fitted well into the genus *Shewanella*, but could be easily distinguished from the *Shewanella* species described to date. Because of their capacity for vigorous denitrification, the name *Shewanella denitrificans* sp. nov. is suggested for the Baltic isolates, for which the type strain is OS217^T (= DSM 15013^T = LMG 21692^T).

Keywords: marine, estuarine bacteria, Baltic Sea, denitrifier, *Shewanella*

INTRODUCTION

The genus *Shewanella* (MacDonell & Colwell, 1985) comprises 13 species of facultatively anaerobic γ -*Proteobacteria* at the time of writing, with a major fraction isolated from aquatic habitats, including the most recently described species, *Shewanella japonica* (Ivanova *et al.*, 2001). A comprehensive study on the phylogenetic relationships and the taxonomy of the genus *Shewanella* was provided by Venkateswaran *et al.* (1999). A notable feature of members of the genus *Shewanella* is their ability to use a variety of different electron acceptors that can be of special relevance for

survival and competition in aquatic ecosystems with oxic–anoxic interfaces (Brettar & Höfle, 1993).

In this study, we describe three denitrifying strains of the genus *Shewanella* that were isolated from the oxic–anoxic interface of the Gotland Deep, a basin with anoxic deep water in the central Baltic. The strains were recognized by their unique low-molecular-weight (LMW) RNA fingerprints (Höfle & Brettar, 1996). Investigations on *in situ* denitrification in the water column of the Gotland Deep provided strong evidence that the oxic–anoxic interface was the layer in which most of the denitrification occurred in anoxic basins of the central Baltic (Brettar & Rheinheimer, 1991, 1992). The three novel strains are vigorous denitrifiers present in the denitrifying layer of the interface, and thus could have contributed to nitrogen elimination by denitrification in the central Baltic (Brettar & Höfle, 1993; Brettar *et al.*, 2001). In addition

Detailed fatty acid composition data for the novel isolates are available as supplementary material in IJSEM Online (<http://ijs.sgmjournals.org>).

The GenBank/EMBL/DBJ accession numbers for the 16S rDNA sequences of *S. denitrificans* sp. nov. strains OS217^T, OS220 and OS226 are respectively AJ311964, AJ457093 and AJ457092.

to the three novel strains, a larger set of *Shewanella* strains were isolated from the same samples of the interface and were described earlier as another novel *Shewanella* species, *Shewanella baltica* (Ziemke *et al.*, 1998). Phylogenetic analyses of the 16S rDNA sequences showed that the three novel strains were included in the robust cluster formed by the genus *Shewanella* and suggest, concomitantly with the physiological features, fatty acid composition and LMW RNA fingerprints, that the strains represent a novel species of the genus *Shewanella*.

METHODS

Bacterial strains, isolation and growth conditions. During a cruise aboard the RV *Poseidon* in August 1986, three strains, OS217^T, OS220 and OS226, were isolated from the water column of a basin with anoxic, sulphide-containing deep water in the central Baltic Sea (Gotland Deep: BY 15, 57°19'20" N, 20°03'02" E). The strains were isolated from the oxic-anoxic interface (120–130 m depth) of the Gotland Deep. The medium for isolation was nutrient broth (Difco) plus nitrate (2 g KNO₃ l⁻¹). The strains were isolated from liquid cultures inoculated with 1 and 10 ml sea water, i.e. the abundance of the novel strains according to the viable counts was estimated to be as low as one cell per ml (in comparison, *S. baltica* showed viable counts, from the same samples, that were three orders of magnitude higher; Brettar *et al.*, 2001). All details of the environmental conditions, sampling and isolation procedures have been given elsewhere (Brettar & Rheinheimer, 1992; Brettar & Höfle, 1993; Höfle & Brettar, 1995, 1996). Strains grew well on ZoBell agar (Oppenheimer & ZoBell, 1952) and half-strength as well as full-strength marine broth or agar (Difco).

Physiological and biochemical tests and morphology. The isolates were tested for a number of key characteristics by using standard procedures (Gerhardt *et al.*, 1994), such as the Gram reaction (Gram staining, Gram string test), cell size and morphology (phase-contrast microscopy and electron microscopy after negative staining with 1% uranyl acetate) and tests for cytochrome oxidase and catalase (3% H₂O₂). Furthermore, production of hydrogen sulphide (Dye, 1968), haemolysis (bovine-blood agar), acid production from glucose, ribose and arabinose and hydrolysis of starch, gelatin, Tween 80 and lecithin were tested. Strains were additionally characterized by the whole test spectrum of the identification systems API 50CH, API 20NE and API ZYM (bioMérieux) at 20 °C. Growth at different temperatures was tested at 4, 10, 20, 25, 30 and 37 °C. Growth at different salinities was tested at 0, 1, 3, 6 and 10% (w/v) salinity. For these tests, we used half-strength marine broth (Difco), except for the salinity test, for which half-strength Caso medium (DSMZ, catalogue no. 220) was supplemented with the appropriate amount of NaCl.

For testing anaerobic respiration, strains were inoculated in marine broth (Difco) plus the electron acceptors [KNO₃, KNO₂, Na₂S₂O₃, Na₂SO₃, iron(III) citrate, trimethylamine-oxide] at a final concentration of 10 mmol l⁻¹. Incubation was done anaerobically in the dark for up to 18 days at 20 °C. No growth was observed in marine broth in an anoxic environment without the addition of electron acceptors. Growth under anoxic conditions in the presence of the added electron acceptors was considered as an indicator of electron acceptor utilization. Additionally, growth on triple-sugar-iron agar (Difco) was observed. In addition, denitrifi-

cation was studied in nutrient broth (Difco) (plus nitrate at 20 mmol l⁻¹ and sea salt at 8%, w/v) as described in more detail by Brettar & Höfle (1993). As a positive control, *S. baltica* OS155, a strain isolated concomitantly with the novel strains from the central Baltic (Ziemke *et al.*, 1998), was used for a comparison. *S. baltica* OS155 was able to use the electron acceptors provided.

Phylogenetic analysis based on 16S rRNA gene sequence comparison. Genomic DNAs were prepared from individual colonies as described by Moore *et al.* (1996). 16S rRNA genes were amplified by PCR (Mullis & Faloona, 1987) and the PCR products were sequenced directly as described previously (Moore *et al.*, 1999).

The 16S rDNA sequences of strains OS217^T, OS220 and OS226 were aligned automatically and then manually by reference to a database of 37 000 already-aligned bacterial 16S rDNA sequences. The same sequences were then submitted to a BLAST search against the current content of the EMBL database (*Bacteria* division) to check for the presence of newly submitted, related sequences. Phylogenetic trees were constructed using three different methods (bioNJ, maximum-likelihood and maximum-parsimony). For the neighbour-joining (NJ) analysis, a matrix distance was calculated according to Kimura's two-parameter correction. Bootstraps were done using 500 replications, bioNJ and Kimura's two-parameter correction; bioNJ was used according to Gascuel (1997) and the maximum-likelihood and maximum-parsimony programs were from PHYLIP version 3.573c (distributed by J. Felsenstein, Department of Genetics, University of Washington, Seattle). The phylogenetic trees were drawn using NJPLOT (Perrière & Gouy, 1996) and CLARIS DRAW software for Apple Macintosh. The domains used to construct phylogenetic trees were regions of the small-subunit rDNA sequences available for all sequences and excluding positions likely to show homoplasy.

For the tree shown in Fig. 2, the retention of only sequences of related genera, mostly from type strains (26 sequences), allowed the inclusion in the analysis of almost the entire 16S rDNA sequences, corresponding to positions 1–1194 of the OS217^T sequence. The topology shown is that of the bootstrap analysis, as it has been demonstrated that this topology is often better than that of a simple NJ analysis (Berry & Gascuel, 1996). As a result, there is no distance bar in this tree; note, also, that one should consider the distance bar with caution in a simple tree, as the distance bar represents the distances calculated after corrections (Kimura's two-parameter; Jukes & Cantor, 1969), and that the lengths of the branches do not simply represent the real numbers of differences between the sequences themselves.

DNA isolation and spectroscopic DNA–DNA hybridization. DNA was isolated by chromatography on hydroxyapatite (Cashion *et al.*, 1977). DNA–DNA hybridization was carried out as described by De Ley *et al.* (1970) with modifications as described by Huß *et al.*, (1983) and Escara & Hutton (1980), using a Gifford System model 2600 spectrometer. Renaturation rates were calculated with the program TRANSFER.BAS (Jahnke, 1992).

Determination of the G + C content. The DNA G + C content of the strains was determined using HPLC analysis of hydrolysed DNA, according to Tamaoka & Komagata (1984) and Mesbah *et al.* (1989).

Cellular fatty acid profiles. The strains were grown on half-strength marine broth (Difco) for 24 h at 28 °C. The fatty acid methyl esters were obtained from washed cells by

Fig. 1. Cells of strain OS217^T as visualized by electron microscopy after negative staining with 1% uranyl acetate. The two cells shown were at exponential growth in half-strength marine broth. Bar, 2 µm.

saponification, methylation and extraction. Analysis by GC was controlled by the MIS software (Microbial ID) and peaks were integrated and identified automatically by the Microbial Identification software package (Sasser, 1990).

RESULTS AND DISCUSSION

Physiological, morphological and biochemical characteristics

The novel strains are Gram-negative, polarly flagellated rods. Light and electron microscopy revealed a rod-shaped bacterium, 0.5–0.8 µm wide and 2.0–3.0 µm long, with two polar flagella per cell (Fig. 1). Colonies are circular, transparent and unpigmented to slightly yellow or brownish on ZoBell or marine agar.

In terms of physiological features (Table 1), the three strains analysed showed a rather homogeneous pattern. The strains were catalase-, cytochrome oxidase- and aminopeptidase-positive. Growth was observed at temperatures from 4 to 30 °C, with an optimum around 20–25 °C. Growth was observed at salinities from 0 to 6%, with an optimum between 1 and 3%. All strains were able to grow in marine broth under oxic conditions. Growth occurred under anoxic conditions in the presence of sulphite, nitrate and nitrite. The novel strains were not able to use trimethylamineoxide, thiosulphate or ferric iron as an electron acceptor. Under the same conditions, *S. baltica* OS155

Table 1. Differential characteristics of strains OS217^T, OS220 and OS226 in comparison with related *Shewanella* species

Taxa are identified as: 1–3, *S. denitrificans* sp. nov. strains OS217^T (1), OS220 (2) and OS226 (3); 4, *S. baltica* (data from Ziemke *et al.*, 1998; plus new data for strain OS155); 5, *S. putrefaciens*; 6, *S. frigidimarina*; 7, *S. oneidensis* (data for taxa 5–7 from Venkateswaran *et al.*, 1999); 8, *S. japonica* (Ivanova *et al.*, 2001). Reaction: +, good; (+), weak; –, no reaction; numbers indicate percentages of strains testing positive. NA, No data available. Cells of all taxa are rods. All taxa grew in the absence of NaCl.

Characteristic	1	2	3	4	5	6	7	8
Cell shape	Straight or curved	Straight or curved	Straight or curved	Straight	Straight	Straight or curved	Straight	Straight
DNA G+C content (mol %)	46.8	NA	48.1	46	43–47	40–43	45	43–44
Haemolysis	–	–	–	–	0	NA	0	+
Optimal growth temperature (°C)	20–25	20–25	20–25	20–25	25–35	20–22	25–35	20–25
Growth at/in:								
4 °C	+	+	+	+	+	+	20	–
37 °C	–	–	–	–	+	–	+	+
40 °C	–	–	–	–	–	–	60	–
6 % NaCl	+	+	+	+	100	+	40	–
10 % NaCl	–	–	–	–	0	–	0	–
Production of:								
Amylase	+	+	+	–	0	–	0	+
Gelatinase	+	+	+	+	0	+	100	+
Lipase	–	–	–	+	0	+	0	+
Chitinase	+	NA	NA	100*	NA	–	NA	–
Utilization of:								
D-Galactose	–	–	–	–	100	–	80	+
D-Fructose	–	–	–	–	0	–	0	+
Sucrose	–	–	–	100	40	+	0	–
Maltose	+	(+)	+	100	60	+	0	+
Lactose	–	–	–	–	30	–	0	–
Cellobiose	–	–	–	100	–	+	–	+
Succinate	–	(+)	(+)	–	60	+	100	+
Fumarate	–	(+)	(+)	–	60	+	80	–
Citrate	–	–	–	100	0	NA	0	–
D-Mannitol	–	–	–	–	0	+	0	–
DL-Malate	–	–	–	75	0	NA	0	–
Reduction of:								
NO ₃ [–] to NO ₂ [–]	+	+	+	100	100	+	80	NA
NO ₂ [–] to N ₂	+	+	+	+	0	NA	0	NA
Iron oxide	–	–	–	+	100	+	100	–
Trimethylamineoxide	–	–	–	+	+	+	+	NA
S ₂ O ₃ ^{2–}	–	–	–	+	+	+	+	NA
SO ₃ ^{2–}	+	+	+	+	NA	NA	+	NA

* Chitinase activity measured as described by Cottrell *et al.* (2000).

Fig. 2. Unrooted phylogenetic tree resulting from the analysis of nearly complete 16S rDNA sequences. The topology shown was obtained using an NJ algorithm and 500 bootstrap replications. Percentages of bootstrap support are indicated for branches that were also found using parsimony and maximum likelihood ($P < 0.1$), and therefore define robust clusters. The novel species *S. denitrificans* (OS217^T, OS220, OS226) appeared to be part of the robust cluster formed by the genus *Shewanella* within the γ -Proteobacteria.

was able to use all electron acceptors tested. Denitrification in nutrient broth plus nitrate could yield nitrous oxide or nitrogen as the final product, thereby converting up to 80 % of the 20 mmol nitrate l⁻¹ added to gaseous forms (N₂O, N₂).

All strains were able to grow in marine broth at pH 5.7 to 7.8 (a broader spectrum was not tested). The strains were able to produce hydrogen sulphide from cysteine (Dye, 1968). There was no haemolysis of blood. All strains hydrolysed starch, gelatin, Tween 80 and lecithin. There was no distinct production of acid observed from sugars such as D-glucose, D-ribose and D-arabinose. The strains were able to use a variety of substrates provided by API 50CH (Table 1). They utilized D-glucose, N-acetylglucosamine, aesculin, maltose, starch, glycogen and β -gentiobiose. In the API NE20 tests, the strains were able to assimilate glucose, N-acetylglucosamine and maltose. In terms of enzymic activity, the strains showed activities for β -glucosidase, protease (gelatinase), alkaline phosphatase and leucine arylamidase.

Genotypic relationships among the tested strains and analysis of the phylogenetic position

Phylogenetic analyses based on the 16S rDNA sequence (Fig. 2) revealed that the bacteria studied are members of the γ -Proteobacteria, clustering robustly within the genus *Shewanella*. According to detailed analyses such as that shown in Fig. 2, the three 16S

Table 2. 16S rDNA nucleotide sequence similarity to strain OS217^T among *Shewanella* species

Strain	Accession no.	Similarity (%)
OS217 ^T	AJ311964	(100)
OS220	AJ457093	99.0
OS226	AJ457092	99.0
<i>S. baltica</i>		
NCTC 10735 ^T	AJ000214	96.1
OS195	AJ000216	96.4
OS155	AJ000215	96.0
' <i>S. massilia</i> '	AJ006084	96.2
<i>S. putrefaciens</i> LMG 2268 ^T	X81623	96.2
' <i>S. saccharophilus</i> ' GC-29	AF033028	95.5
<i>S. oneidensis</i>		
ATCC 700550 ^T	AF005251	96.1
SP-7	AF039054	94.8
<i>S. frigidimarina</i> ACAM 591 ^T	U85903	95.0
<i>S. japonica</i> KMM 3299 ^T	AF145921	94.1

rDNA sequences of the studied strains formed a robust clade that itself never formed a larger robust clade with the sequence of an already recognized species of *Shewanella* (except with all *Shewanella* sequences, which then defines the genus). Accordingly, phylogenetic analyses suggest that the three strains form a novel species of *Shewanella*. The 16S rDNA sequence similarity of strain OS217^T with OS220 and OS226 was 99.0 %. Strains OS220 and OS226 had a high 16S rDNA sequence similarity, of 99.9 %. Similarity to related sequences was highest with strains of *S. baltica* (96.0–96.4 %), *Shewanella putrefaciens* (96.2 %), *Shewanella oneidensis* (94.8–96.1 %) and *Shewanella frigidimarina* (95.0 %) (Table 2).

DNA–DNA hybridization between strains OS217^T and OS226 showed 88.3 % DNA relatedness, indicating that they are members of the same species (Wayne *et al.*, 1987). This finding is consistent with the analysis of the 16S rDNA sequences. Therefore, all three strains can be perceived as members of the same species.

The G + C content ranged from 46.8 (OS217^T) to 48.1 (OS226) mol % (Table 1). The G + C contents of the related species *S. baltica*, *S. putrefaciens*, *S. oneidensis*, *S. frigidimarina* and *S. japonica* range from 40 to 47 mol % (Venkateswaran *et al.*, 1999). *S. baltica*, having a G + C content of 45.7–46.8 mol %, was closest in G + C content to OS217^T (Ziemke *et al.*, 1998).

Cellular fatty acid profiles

The fatty acid profiles for strains OS217^T and OS226 showed similar patterns (Table 3); for comparison, the fatty acid profile is given of *S. baltica* OS155, grown under the same conditions as the novel strains. For the novel strains, the dominant fatty acids were 16:1 ω 7c (mean $\pm$ SD for OS217^T and OS226, 31.8 $\pm$ 0.7 %), 15:0 iso (12.0 $\pm$ 1.0 %) 16:0 (11.4 $\pm$ 2.7 %) and 13:0 iso

Table 3. Fatty acid composition of strains OS217^T and OS226 in comparison with related *Shewanella* species

Values are percentages of total fatty acids; major components are listed in bold. Taxa are identified as: 1–2, *S. denitrificans* sp. nov. strains OS217^T (1) and OS226 (2); 3, *S. baltica* OS155 (described as *S. baltica* by Ziemke *et al.*, 1998; data generated under the same conditions as for *S. denitrificans*); 4, *S. putrefaciens* ATCC 8071^T; 5, *S. frigidimarina* (means for eight strains); 6, *S. oneidensis* ATCC 700550^T (data for taxa 4–6 from Venkateswaran *et al.*, 1999); 7, *S. japonica* KM 3299^T (data from cultures grown at 28 °C from Ivanova *et al.*, 2001). ND, Not detected. Detailed fatty acid composition data are available as supplementary material in IJSEM Online (<http://ijs.sgmjournals.org/>).

Fatty acid	1	2	3	4	5	6	7
Straight-chain fatty acids							
14:0	3.9	3.0	2.2	2.3	3.7	2.6	4.2
15:0	4.4	5.3	7.8	3.2	2.5	4.7	1.1
16:0	13.3	9.5	4.3	19.1	11.8	14.8	16.6
17:0	0.8	0.7	0.6	1.5	1.2	2.8	0.7
18:0	0.3	0.2	ND	2.1	0.1	1.1	0.7
Terminally branched fatty acids							
13:0-iso	9.3	9.8	12.4	2.5	6.3	2.5	7.5
14:0-iso	0.6	0.8	1.6	0.3	0.6	2.3	0.8
15:0-iso	11.3	12.7	14.3	21.1	9.0	25.4	19.6
16:0-iso	ND	ND	0.2	0.1	ND	1.4	0.2
17:0-iso	0.7	0.8	0.5	1.7	0.3	1.7	1.6
Monounsaturated fatty acids							
15:1 ω 6c	1.0	1.4	2.2	0.2	1.2	0.3	0.1
16:1 ω 7c	31.3	32.3	24.1	29.6	51.1	23.3	23.4
16:1 ω 9c	1.7	1.7	1.6	3.5	2.2	2.1	ND
17:1 ω 6c	ND	0.4	1.4	0.9	ND	1.5	1.4
17:1 ω 8c	4.8	6.6	11.0	6.7	3.0	8.0	0.1
18:1 ω 7c	1.7	1.1	0.8	6.0	5.3	5.7	5.8
18:1 ω 9c	1.0	1.0	0.8	3.8	1.7	2.9	1.6

(9.6±0.4%). This fatty acid composition fits well within the typical pattern of *Shewanella* (Venkateswaran *et al.*, 1999) and shows similarities to those of related *Shewanella* species such as *S. baltica*, *S. putrefaciens* and *S. japonica*. Detailed fatty acid composition data are available as supplementary material in IJSEM Online (<http://ijs.sgmjournals.org/>).

Conclusion

According to phylogenetic analyses based on 16S rDNA sequences, the three strains described, OS217^T, OS220 and OS226, belong to the genus *Shewanella* and form a novel species. The closest relatives were *S. baltica*, *S. putrefaciens*, *S. oneidensis*, *S. frigidimarina* and *S. japonica*. Physiological features and fatty acid profiles support the phylogenetic analysis that suggests a novel species of the genus *Shewanella*. Physiological features that differentiate this novel species from closely related *Shewanella* species are given in Table 1. There is a broad spectrum of features that differentiate the novel species from related *Shewanella* species. Growth optima for temperature and salinity are different from *S. putrefaciens*, *S. oneidensis* and *S. japonica*. Enzymic activities such as amylase, gelatinase, lipase and chitinase are different among the novel species and related *Shewanella* species. In terms of utilization of substrates, the novel species is different

for galactose, sucrose, maltose, succinate, fumarate, citrate, mannitol and malate. In terms of utilization of electron acceptors under anaerobic conditions, there are differences for denitrification of nitrite to dinitrogen and reduction of iron oxide, trimethylamine-oxide and thiosulphate. The physiological features that can be used to distinguish the novel species from *S. baltica* are amylase production, utilization of sucrose, citrate and malate and the use of iron oxide, trimethylamine-oxide and thiosulphate as electron acceptors. *S. putrefaciens* can be distinguished from the novel species by growth at 37 °C, amylase and gelatinase activity, utilization of galactose and the use of the electron acceptors (iron oxide, trimethylamine-oxide, thiosulphate). *S. frigidimarina* is different due to amylase and lipase activity, utilization of sucrose, cellobiose, mannitol and the use of electron acceptors. It can be distinguished from *S. japonica* by growth at 4 °C and at 6% salinity, lipase activity and the utilization of galactose, fructose and cellobiose.

Based on these analyses, we suggest strain OS217^T as the type strain of the novel species *Shewanella denitrificans* sp. nov. because this strain displayed most of the features typical of the strains isolated. On the basis of 16S rDNA sequence comparison, DNA–DNA hybridization and the phenotypic features, all of the strains described are considered to belong to the novel species *S. denitrificans*.

Description of *Shewanella denitrificans* sp. nov.

Shewanella denitrificans (de.ni.tri'fi.cans. N.L. v. *denitrifico* to denitrify; N.L. part. adj. *denitrificans* denitrifying, referring to the capacity for vigorous denitrification).

Cells are Gram-negative, polarly flagellated with two flagella, rod-shaped (straight or curved rods: width, 0.5–0.8 µm; length, 2.0–3.0 µm) and oxidase- and catalase-positive. Colonies are circular, transparent and unpigmented to slightly yellow or brownish on ZoBell agar or marine agar. Growth is facultatively anaerobic, chemoheterotrophic and occurs at 4–30 °C, with optimum growth at 20–25 °C. Sugars such as glucose are not metabolized with production of acid. Dominant fatty acids are 16:1ω7c, 15:0 iso, 16:0 and 13:0 iso. Of marine or estuarine origin. NaCl supports growth, but is not required for growth; strains do not tolerate high salinity (> 6%). Growth occurs under anoxic conditions in the presence of nitrate, nitrite and sulphite, but not in the presence of trimethylamine-oxide, ferric iron or thiosulphate as electron acceptors. Able to use an ample spectrum of carbohydrates such as D-glucose, N-acetylglucosamine, aesculin, maltose, starch and glycogen. Assimilates glucose, N-acetylglucosamine and maltose. β-Glucosidase, protease, aminopeptidase, phosphatase (alkaline) and leucine arylamidase activities are present. Starch, gelatin, Tween 80 and lecithin are hydrolysed. The G+C content ranges from 46.8 to 48.1 mol%. The type strain is strain OS217^T (= DSM 15013^T = LMG 21692^T).

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