Shewanella hafniensis sp. nov. and Shewanella morhuae sp. nov., isolated from marine fish of the Baltic Sea

Masataka Satomi,1,2 Birte Fonnesbech Vogel,3 Lone Gram3 and Kasthuri Venkateswaran2

1National Research Institute of Fisheries Science, Fisheries Research Agency, Yokohama, 236-8648, Japan
2California Institute of Technology, Jet Propulsion Laboratory, Biotechnology and Planetary Protection Group, 89-2, Oak Grove Dr., Pasadena, CA 91109, USA
3Danish Institute for Fisheries Research, Department of Seafood Research, Søltofts Plads, DTU bldg 221, DK-2800 Kgs. Lyngby, Denmark

Two novel species belonging to the genus Shewanella are described on the basis of their phenotypic characteristics, phylogenetic analyses of 16S rRNA and gyrB gene sequences and levels of DNA–DNA hybridization. A total of 47 strains belonging to two novel Gram-negative, psychrotolerant, H2S-producing bacterial species were isolated from marine fish (cod and flounder) caught from the Baltic Sea off Denmark. The phenotypic characteristics of strains belonging to group 1 (14 strains) indicated that these represented a non-sucrose-assimilating variant of Shewanella baltica with a DNA G+C content of 47·0 mol%. Strains of group 2 (33 isolates) did not utilize the carbon substrates assimilated by S. baltica except gluconate, N-acetylglucosamine and malate. Their DNA G+C content was 44·0 mol%. Phylogenetic analysis of the 16S rRNA gene sequence data placed the two novel species within the genus Shewanella. Group 1 strains showed greatest sequence similarity to Shewanella putrefaciens ATCC 8071T (99·0 %) and with S. baltica NCTC 10375T (98·3 %). However, gyrB gene sequence analysis showed these isolates to share only 90·0 % sequence similarity with S. putrefaciens ATCC 8071T and 93·9 % with S. baltica NCTC 10375T. Similarly, DNA–DNA hybridization experiments revealed DNA relatedness levels of 38 % between the group 1 isolates and S. putrefaciens ATCC 8071T and 43 % with S. baltica NCTC 10375T. The group 2 strains shared less than 97 % 16S rRNA gene sequence similarities with recognized Shewanella species. Comparisons between the two novel species indicated 16S rRNA gene sequence similarity of ~98 %, gyrB gene sequence similarity of ~89 % and DNA–DNA reassociation values of 20–34 %. Based on the evidence presented, two novel species, Shewanella hafniensis sp. nov. (type strain P010T = ATCC BAA-1207T = NBRC 100975T) and Shewanella morhuae sp. nov. (type strain U1417T = ATCC BAA-1205T = NBRC 100978T), are described.

Several physiologically and phylogenetically distinct microorganisms have been encountered while examining spoilage of Danish marine fish caught in the Baltic Sea (Fonnesbech Vogel et al., 2005). We have, in particular, focused on bacteria that reduce trimethylamine and produce hydrogen sulphide (H2S) as these are the main spoilage agents of chilled, stored fresh fish. These bacteria were non-fermentative, motile rods and initial screening tentatively identified them as members of the genus Shewanella, species of which are common in aquatic habitats. The phenotypic boundaries of and within this group are currently being redefined and the need for a more diagnostically informative pattern of phenotypic characteristics is pressing. Combining genetic and phenotypic analyses in a polyphasic taxonomic approach, 30 Shewanella species have been recognized at the time of writing (http://www.bacterio.cict.fr/s/shewanella.html).

The gene sequence of the 16S rRNA molecule has been used extensively to define phylogenetic relationships between...
organisms (Woese, 1987), but this molecule, at times, lacks
the specificity required for the differentiation of close
relatives (Fox et al., 1992; Venkateswaran et al., 1998). To
circumvent this limitation, the more rapidly evolving gyrB
gene has been employed as a high-resolution molecular
identification marker for distinguishing several species
(Satomi et al., 2003; Venkateswaran et al., 1998; Yamamoto

In a previous report we found that the majority of H2S-
producing strains isolated from Baltic fish were identified as
Shewanella baltica (Fonnesbech Vogel et al., 2005). How-
ever, a number of strains differed from the Shewanella
species included in that report (S. baltica, Shewanella algae,
Shewanella putrefaciens, Shewanella oneidensis, Shewanella
colwelliana and Shewanella affinis) based on phenotypic
testing and 16S rRNA gene sequence analysis. A detailed
taxonomic characterization of these H2S-producing organ-
isms is warranted with regard to our understanding of
potential human pathogens (related to S. algae) and of
organisms important in fish spoilage (S. baltica). In the
present study we characterize two of the non-identifiable
groups from the previous report (Fonnesbech Vogel et al.,
2005) using phenotypic characterization, phylogenetic
analysis of 16S rRNA and gyrB gene sequences and DNA–
DNA hybridization, and two novel species are described.

A total of 47 strains of novel H2S-producing bacteria were
isolated from cod, plaice or flounder caught between August
1995 and September 2001 from the Baltic Sea off Denmark.
Bacterial isolation was carried out as reported elsewhere
(Fonnesbech Vogel et al., 2005). Briefly, samples were taken
from the belly flap area and pour-plated in iron agar (Oxoid
CM964) from which H2S-producing bacteria were isolated.

Of the 47 strains tested for phenotypic analysis, representa-
tive strains were selected for further molecular characteriza-
tion in order to determine their phylogenetic affiliation
(Table 1). In addition to these newly described strains, the
type strains of closely related species were purchased from
several established culture collections and were used as
reference strains. All isolates were maintained in stabs on
trypticase soy agar (TSA) at room temperature for short-
term analysis and in a medium containing skimmed milk
powder and glycerol at −80 °C for long-term storage. Liquid
cultures were grown in trypticase soy broth (TSB; BD
Biosciences) and were incubated at 25 °C for 2–7 days.
Representative strains have been deposited in two public
culture collections, namely the American Type Culture
Collection (ATCC) and the National Institute of Technology
and Evaluation, Biological Resource Center (NBRC), Japan.

All strains were tested at 25 °C for Gram reaction
(Gregerson, 1978), motility and cell shape [phase-contrast
microscopy after growth in vital infusion broth (Difco; 0344-
17-6) for 24 h], cytochrome oxidase (BBL DrySlide oxidase,
231746; BD Biosciences), catalase-reaction (3 % H2O2),
reduction of trimethylamine oxide (TMAO) in TMAO
medium (Gram et al., 1987) and production of H2S from
thiosulphate (Gram et al., 1987). Fermentation of glucose
was tested in O-F medium (Merck) at 25 °C. Growth at
various temperatures (4, 37 and 42 °C) and in 6 % NaCl
(Fonnesbech Vogel et al., 1997) and assimilation of several
carbon and energy sources (citrate, gluconate, glucose,
lactate and sucrose; Ziemke et al., 1998) were used to
differentiate the Shewanella isolates further. Type strains of
S. putrefaciens, S. baltica and S. algae were included in each
trial and served as controls. The genomic G + C content was
determined by HPLC (Fonnesbech Vogel et al., 1997). The

Table 1. Source and isolation of Shewanella strains tested in this study

<table>
<thead>
<tr>
<th>Strain</th>
<th>Source, location and year of isolation</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. affinis ATCC BAA-642T</td>
<td>Marine invertebrate, Sea of Japan, 1997</td>
</tr>
<tr>
<td>S. algae IAM 14159T</td>
<td>Red alga, Japan, 1990</td>
</tr>
<tr>
<td>S. baltica NCTC 10735T</td>
<td>Oil brine, Japan, 1998</td>
</tr>
<tr>
<td>S. colwelliana ATCC 39565T</td>
<td>Estuarine aquaculture unit containing juvenile</td>
</tr>
<tr>
<td></td>
<td>oysters, Chesapeake Bay, MD, USA, 1988</td>
</tr>
<tr>
<td>S. denitrificans DSM 15013T</td>
<td>Baltic Sea, 1986</td>
</tr>
<tr>
<td>S. frigulimaris ACM 591T</td>
<td>Congelation ice, Prydz Bay, Antarctica</td>
</tr>
<tr>
<td>S. oneidensis ATCC 700550T</td>
<td>Oneida Lake sediment, NY, USA, 1998</td>
</tr>
<tr>
<td>S. putrefaciens ATCC 8071T</td>
<td>Butter, UK, 1931</td>
</tr>
<tr>
<td>S. hafniensis sp. nov. (group 1)</td>
<td>Cod, Baltic Sea, Denmark, 2001</td>
</tr>
<tr>
<td>P010T (=ATCC BAA-1207T=NBRC 100975T)</td>
<td></td>
</tr>
<tr>
<td>P14 (=NBRC 100976)</td>
<td>Cod, Baltic Sea, Denmark, 2001</td>
</tr>
<tr>
<td>R1418 (=ATCC BAA-1208=NBRC 100977)</td>
<td>Flounder, Baltic Sea, Denmark, 2001</td>
</tr>
<tr>
<td>S. morlhae sp. nov. (group 2)</td>
<td></td>
</tr>
<tr>
<td>U1417T (=ATCC BAA-1205T=NBRC 100978T)</td>
<td>Cod, Baltic Sea, Denmark, 1996</td>
</tr>
<tr>
<td>T214 (=NBRC 100979)</td>
<td>Cod, Baltic Sea, Denmark, 1996</td>
</tr>
<tr>
<td>U212 (=NBRC 100980)</td>
<td>Cod, Baltic Sea, Denmark, 1996</td>
</tr>
<tr>
<td>U1414 (=ATCC BAA-1206=NBRC 100981)</td>
<td>Cod, Baltic Sea, Denmark, 1996</td>
</tr>
</tbody>
</table>
ability to degrade gelatin (Frazier, 1926), DNA (Difco DNase test agar with methyl green; 0220-17-5) and ornithine (Difco decarboxylase base Moeller; 289020) was also tested.

All of the new isolates were non-fermentative, Gram-negative, motile rods, with positive oxidase and catalase reactions and the ability to reduce TMAO and produce H₂S. Under optimum growth conditions, cells were 0.5–0.7 µm in diameter and 1.0–1.2 µm in length. Colonies were round, undulate, beige coloured, non-luminescent and had irregular margins when grown on TSA plates incubated at 25 °C for 1 day. All strains were able to grow between 4 and 25 °C. Based on these traits the strains were classified as belonging to the genus *Shewanella*, but these characteristics do not allow for species differentiation, for instance between *S. putrefaciens* and *S. algae* (Fonnesbech Vogel et al., 1997), or for differentiation between some of the psychrophilic *shewanellae* (Ziemke et al., 1997).

The first group (group 1; group A3 of Fonnesbech Vogel et al., 2005) of 14 strains included the proposed type strain P01⁷ and were phenotypically similar to the psychrotolerant *S. baltica* NCTC 10735⁵. However, unlike the type strain of *S. baltica*, group 1 strains were unable to utilize sucrose as a sole carbon source (Table 2). Strains of this group degraded gelatin, DNA and ornithine. The DNA G+C content of these strains was 47 mol%. In combination, phenotypic results for these strains were similar but distinguishable from those of *S. baltica*. A second group (group 2; groups C3 and C4 of Fonnesbech Vogel et al., 2005) encompassing 33 strains and represented by the proposed type strain U1417² grew well at 4 °C, but only assimilated three of the carbohydrates tested (Table 2). This group was phenotypically different from the type strains of *S. putrefaciens* (ATCC 8071¹), *S. oneidensis* (ATCC 700550⁵) *Shewanella frigidimarina* (ACAM 591¹; Bowman et al., 1997), *Shewanella denitrificans* (DSM 15013¹; Brettar et al., 2002), *Shewanella livingstonensis* (LMG 19866¹; Bozal et al., 2002) and *S. colwelliana* (ATCC 39565⁵). Strains of group 2 did not grow in 6% NaCl but degraded gelatin, DNA and ornithine. DNA G+C content for these strains was 44 mol%, indicating that they were different from *S. frigidimarina* (40–43 mol%), *S. denitrificans* (47 mol%) and *S. colwelliana* (47 mol%). Although the phenotypic traits of group 2 strains were somewhat similar to those of *S. putrefaciens*, they differed in several characteristics (Table 2): they liquefied gelatin, assimilated gluconate, did not utilize lactate or sucrose as sole carbon source and did not grow at 37 °C.

The 16S rRNA and gyrB genes were PCR-amplified with universal primer sets as described by Weisburg et al. (1991)

---

**Table 2. Phenotypic characteristics of *Shewanella hafniensis* sp. nov. and *Shewanella morhuae* sp. nov. strains and other closely related *shewanellae***

Species/strains: 1, *S. hafniensis* (14 strains); 2, *S. morhuae* (33 strains); 3, *S. putrefaciens* ATCC 8071; 4, *S. baltica* NCTC 10337; 5, *S. algae* IAM 14159; 6, *S. oneidensis* ATCC 700550; 7, *S. affinis* ATCC BAA-642; 8, *S. colwelliana* ATCC 39565. Cells of all strains are Gram-negative, rod-shaped, motile and produce H₂S. All strains are also positive for cytochrome oxidase, catalase, DNase and ornithine decarboxylase, hydrolyse aesculin, and reduce nitrate to nitrite as well as TMAO. All strains are non-fermentative, do not produce arginine dihydrolase or indole, do not hydrolyse urea or ONPG (2-nitrophenyl β-D-galactopyranoside) and do not assimilate phenylacetic acid, mannose, mannitol or adipic acid. +, Positive; −, negative; numbers refer to percentages of strains that are positive for the particular characteristic.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Reference/medium/ID kit</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>DNA G+C content (mol%)</td>
<td>Fonnesbech Vogel et al. (1997)</td>
<td>47</td>
<td>44</td>
<td>45</td>
<td>46</td>
<td>53</td>
<td>45</td>
<td>45</td>
<td>46</td>
</tr>
<tr>
<td>Growth at:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 °C</td>
<td>50 % Marine agar</td>
<td>100</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>37 °C</td>
<td>50 % Marine agar</td>
<td>0</td>
<td>0</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>42 °C</td>
<td>50 % Marine agar</td>
<td>0</td>
<td>0</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Growth in 6 % NaCl</td>
<td>Fonnesbech Vogel et al. (1997)</td>
<td>100</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gelatin hydrolysis</td>
<td>API 20NE</td>
<td>100</td>
<td>91</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Assimilation of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lactate</td>
<td>Fonnesbech Vogel et al. (2005)</td>
<td>100</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Sucrose</td>
<td>Fonnesbech Vogel et al. (2005)</td>
<td>0</td>
<td>24</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Gluconate</td>
<td>API 20NE</td>
<td>100</td>
<td>100</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Glucose</td>
<td>API 20NE</td>
<td>100</td>
<td>0</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Arabinose</td>
<td>API 20NE</td>
<td>21</td>
<td>61</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>N-Acetylglucosamine</td>
<td>API 20NE</td>
<td>100</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Malate</td>
<td>API 20NE</td>
<td>100</td>
<td>0</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Capric acid</td>
<td>API 20NE</td>
<td>71</td>
<td>0</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Malate</td>
<td>API 20NE</td>
<td>100</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Citrate</td>
<td>API 20NE</td>
<td>100</td>
<td>0</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
</tr>
</tbody>
</table>
and Yamamoto & Harayama (1995) and subsequently sequenced. To extract DNA, cells were cultured in TSB and collected by centrifugation. Cell pellets were suspended in TE buffer (pH 8.0) and treated with SDS (final concentration, 10 mg ml$^{-1}$) for lysis. Procedures for extracting chromosomal DNA and subsequent purification steps were carried out according to standard methods (Johnson, 1981; Sambrook et al., 1989). The identity of a given PCR product was verified by bidirectional sequencing analysis. The phylogenetic relationships of organisms covered in this study were determined by comparison of individual 16S rRNA or gyrB gene sequences with other existing sequences in the public databases using the BLAST algorithm (Altschul et al., 1990). Multiple alignment calculation of nucleotide substitution rates ($K_{nu}$ values) described by Kimura (1980) and construction of phylogenetic trees by the neighbour-joining method (Saitou & Nei, 1987) were performed using the CLUSTAL W program (Thompson et al., 1994). Alignment gaps, primer regions for PCR amplification and unidentified base positions were not taken into consideration for the calculations. Topological robustness of the phylogenetic trees was evaluated by a bootstrap analysis of 1000 replications. GenBank nucleotide accession numbers for the 16S rRNA and gyrB gene sequences are shown in Figs 1 and 2, respectively.

Nucleotide sequences of 16S rRNA genes (1413 bp) and gyrB genes (1077 bp) were used for phylogenetic analyses. A phylogenetic tree based on the 16S rRNA gene (Fig. 1) indicated that the new isolates clustered with members of the genus *Shewanella*. Based on 16S rRNA gene sequences, the nearest neighbours of the group 1 strains (represented by P010$^T$) were *S. putrefaciens* ATCC 8071$^T$ and *S. baltica* NCTC 10735$^T$ with sequence similarities of 99 and 98.3 %, respectively. By contrast, the sequences of the group 2 strains (represented by U1417$^T$) shared less than 97 % similarity with recognized *Shewanella* species, the closest neighbour being *S. frigidimarina* ACAM 591$^T$ (96-6 %). These values suggested that the phylogenetic distances between the group 2 isolates and recognized *Shewanella* species was enough to clarify them as representing a distinct species (Stackebrandt & Goebel, 1994), but it was unclear whether the group 1 strains were distinguishable from *S. putrefaciens* as a different species. However, the topology based on the gyrB gene showed these latter strains to cluster monophyletically, distinct from *S. baltica*, *S. oneidensis* or *S. putrefaciens*, and clearly delineating them as representing a distinct species (Fig. 2). Sequence similarity values used to separate species based on the gyrB gene vary depending on the genus (Satomi et al., 2002, 2003, 2004; Venkateswaran et al., 1999) and, therefore, DNA–DNA hybridization experiments were carried out to confirm the novelty of these isolates.

DNA–DNA hybridization was studied by microplate hybridization methods (Ezaki et al., 1989) with photobiotin labelling and colorimetric detection, using 1,2-phenylenediamine (Sigma) as the substrate and streptavidin–peroxidase conjugate (Boehringer Mannheim) as the colorimetric substrate (Satomi et al., 1997). Table 3 shows the results of DNA–DNA hybridization between the putative novel species and type strains of closely related *Shewanella* species. Strain P010$^T$ showed a DNA–DNA hybridization value of 38 % with *S. putrefaciens* ATCC 8071$^T$ and 43 % with *S. baltica* NCTC 10735$^T$. Similarly, the group 2 strains exhibited levels of DNA–DNA relatedness of 9–34 % with several *S. putrefaciens* ATCC 8071$^T$, *S. frigidimarina* ACAM 591$^T$ and *S. baltica* NCTC 10735$^T$. Furthermore, strains of groups 1 and 2 shared only 20–34 % DNA–DNA relatedness. Within each of the groups themselves, DNA–DNA relatedness values were significantly higher, with groups 1 and 2 exhibiting relatedness values of 80–92 and 78–83 %, respectively. This strongly supports the suggestion that the isolates of groups 1 and 2 (respectively represented by strains P010$^T$ and U1417$^T$) represent novel species within the genus *Shewanella* (Wayne, 1988).

Of the genotypic analyses performed, 16S rRNA gene sequence analysis was the least discriminatory for the
isolates tested. The more rapidly evolving gyrB gene allowed for distinct clustering of the tested strains into two distinct species, results which are in strong agreement with those from DNA–DNA hybridization analyses. Based on the polyphasic data presented, the strains isolated from the Baltic Sea Danish marine fish were determined to represent two novel species within the genus *Shewanella*, for which the names *Shewanella hafniensis* sp. nov. and *Shewanella morhuae* sp. nov. are proposed.

**Description of *Shewanella hafniensis* sp. nov.**

*Shewanella hafniensis* [haf.ni.en’sis. M.L. fem. adj. *hafniensis* pertaining to Hafnia, the medieval name of København (Copenhagen), the capital of Denmark].

Mesophilic, aerobic, chemoheterotrophic Gram-negative rods that are motile by means of polar flagella. Cells are 0.5–0.7 μm in diameter and 1.0–1.2 μm in length. Growth occurs at 0–6% (w/v) NaCl and the temperature range for growth is 4–25 °C (25 °C being optimal). Growth does not occur at temperatures >37 °C. Colonies are round, undulate, white-dull, non-luminescent and have irregular margins on TSA plates incubated at 25 °C for 24 h. Cells are positive for oxidase and catalase reactions. They are unable to ferment glucose but reduce TMAO and produce H2S. Cells reduce nitrate, hydrolyse gelatin and are positive for the production of DNase and ornithine decarboxylase. D-Glucose, gluconate, lactate, maltose, N-acetylglucosamine, malate and citrate are readily utilized as energy sources. Sucrose is not utilized as an energy source. Cells do not grow on minimal media, indicative of a required growth factor. The DNA G+C content is 47 mol%.

The type strain, P010T (=ATCC BAA-1207T=NBRC 100975T), was isolated from cod from the Baltic Sea off Denmark. Strains P14 (=NBRC 100976) and R1418 (=ATCC BAA-1208=NBRC 100977) are reference strains.

**Description of *Shewanella morhuae* sp. nov.**

*Shewanella morhuae* (mo.ru’ae. N.L. gen. n. *morhuae* of *Gadus morhua*, the Atlantic cod).

Mesophilic, aerobic, chemoheterotrophic Gram-negative rods that are motile by means of polar flagella. Cells are 0.5–0.7 μm in diameter and 1.0–1.2 μm in length. None of

---

**Table 3. DNA–DNA reassocation values of *S. hafniensis* sp. nov. and *S. morhuae* sp. nov. strains with closely related shewanellae**

<table>
<thead>
<tr>
<th>Strain</th>
<th>DNA–DNA reassocation (%) with labelled DNA from:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>1.  <em>S. hafniensis</em> P010T</td>
<td>100</td>
</tr>
<tr>
<td>2.  <em>S. hafniensis</em> P14</td>
<td>92</td>
</tr>
<tr>
<td>3.  <em>S. hafniensis</em> R1418</td>
<td>80</td>
</tr>
<tr>
<td>4.  <em>S. morhuae</em> U1417T</td>
<td>25</td>
</tr>
<tr>
<td>5.  <em>S. morhuae</em> T214</td>
<td>23</td>
</tr>
<tr>
<td>6.  <em>S. morhuae</em> U212</td>
<td>20</td>
</tr>
<tr>
<td>7.  <em>S. morhuae</em> U1414</td>
<td>34</td>
</tr>
<tr>
<td>8.  <em>S. putrefaciens</em> ATCC 8071T</td>
<td>38</td>
</tr>
<tr>
<td>9.  <em>S. baltica</em> NCTC 10735T</td>
<td>43</td>
</tr>
<tr>
<td>10. <em>S. frigidimarina</em> ACAM 591T</td>
<td>NT</td>
</tr>
</tbody>
</table>

NT, Not tested.
the strains is able to grow at 6% (w/v) NaCl. The temperature range for growth is 4–25 °C (25 °C being optimal). Growth does not occur at temperatures >37 °C. Colonies are round, undulate, white-dull, non-luminescent and have irregular margins on TSA plates incubated at 25 °C for 24 h. Cells are positive for oxidase and catalase reactions. Unable to ferment glucose but reduce TMAO and produce H2S. Cells reduce nitrate, hydrolyse gelatin and are positive for the production of DNase and ornithine decarboxylase. Cells are unable to use most of the carbon substrates tested, although gluconate, N-acetylglucosamine and malate are readily utilized as energy sources. D-Glucose, citrate and succrose are not utilized as sole carbon sources, but more than half of the strains tested assimilate arabinose. Cells do not grow on minimal media, indicative of a required growth factor. The DNA G + C content is 44 mol%.

The type strain, U1417T (=ATCC BAA-1205T=NBRC 100978T), was isolated from cod from the Baltic Sea off Denmark. Strains T214 (=NBRC 100979), U122 (=NBRC 100980) and U1414 (=ATCC BAA-1206=NBRC 100981) are reference strains.

Acknowledgements

Our sincere thanks go to Hans Trüper for guidance in naming the novel bacterial species. The technical assistance of Anemone Bundvad is acknowledged. Shariff Osman is acknowledged for helping to deposit the strains in the ATCC and James Bruckner for critically reading the manuscript.

References


