Description of *Shewanella glacialipiscicola* sp. nov. and *Shewanella algidipiscicola* sp. nov., isolated from marine fish of the Danish Baltic Sea, and proposal that *Shewanella affinis* is a later heterotypic synonym of *Shewanella colwelliana*

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Two novel species belonging to the genus *Shewanella* are described on the basis of a polyphasic taxonomic approach. A total of 40 strains of Gram-negative, psychrotolerant, H₂S-producing bacteria were isolated from marine fish (cod and plaice) caught in the Baltic Sea off Denmark. Strains belonging to group 1 (seven strains) were a lactate-assimilating variant of *Shewanella morhuae* with a G+C content of 44 mol%. The strains of group 2 (33 strains) utilized lactate, N-acetylglucosamine and malate but did not produce DNase or ornithine decarboxylase. Their G+C content was 47 mol%. Phylogenetic analysis of the 16S rRNA gene sequence data placed the two novel species within the genus *Shewanella*. Group 1 showed greatest sequence similarity with *S. morhuae* ATCC BAA-1205T (99.9%). However, gyrB gene sequence analysis and DNA–DNA hybridization differentiated these isolates from *S. morhuae*, with 95.6% sequence similarity and less than 57% DNA relatedness, respectively. Group 2 strains shared more than 99% 16S rRNA gene sequence similarity with the type strains of *Shewanella colwelliana* and *Shewanella affinis*, but gyrB sequence similarity (~85%) and the results of DNA hybridization (~28%) indicated that the new isolates represented a novel species. Furthermore, when compared to each other, the type strains of *S. colwelliana* and *S. affinis* had almost identical gyrB sequences and significantly high DNA reassociation values (76–83%), indicating that they belonged to the same species. Based on the conclusions of this study, we propose the novel species *Shewanella glacialipiscicola* sp. nov. (type strain T147T = LMG 23744T = NBRC 102030T) for group 1 strains and *Shewanella algidipiscicola* sp. nov. (type strain S13T = LMG 23746T = NBRC 102032T) for group 2 strains, and we propose that *Shewanella affinis* as a later heterotypic synonym of *Shewanella colwelliana*.

The majority of marine fish and seafood spoilage bacteria are reported to be members of the genus *Shewanella* (Shewan et al., 1960; Okuzumi et al., 1981; Gram et al., 1987; Stenstrom & Molin, 1990; Gram & Huss, 1996; Vogel et al., 1997, 2005). Most *Shewanella* species, particularly *Shewanella putrefaciens* and close relatives, are capable of reducing trimethylamine oxide (TMAO) to trimethylamine and producing hydrogen sulfide (H₂S), both of which are main components of the fishy odour present during low-temperature storage. Recently, it was reported that *Shewanella baltica* rather than *S. putrefaciens* is the dominant spoilage species producing H₂S in iced storage of marine fish caught in the Danish Baltic Sea (Vogel et al., 2005). Initial microbial diversity analysis of the bacterial community...
populations present on these fish resulted in the classification of several strains as belonging to the genus *Shewanella* based on biochemical characteristics (Vogel et al., 2005) and resulted in the description of two novel species (Satomi et al., 2006) based on molecular taxonomy. Furthermore, several of the closely related *Shewanella* isolates were physiologically and phylogenetically so distinct that they required further taxonomic analysis (Vogel et al., 2005). Such study will help to understand the microbial species diversity of marine fish and aid in developing countermeasures for fish spoilage.

Two groups of H$_2$S-producing organisms are described herein using a polyphasic taxonomic approach that includes phenotypic characterization, phylogenetic analysis of 16S rRNA and gyrB genes and DNA–DNA hybridization.

A total of 40 strains of novel H$_2$S-producing bacteria were isolated from cod and plaice caught between August 1995 and September 2001 from the Baltic Sea off Denmark. Bacterial isolation was carried out as reported by Vogel et al. (2005). Briefly, tissue samples were taken from the belly flap area of iced fish, homogenized, serially diluted in sterile peptone saline and poured-plate in iron agar (Oxoid CM964). Plates were then incubated at 25 °C for 3 days and black colonies, indicative of H$_2$S-producing bacteria, were picked, purified and stored for further characterization. Of 40 strains tested for phenotypic analysis, representative strains were selected for molecular taxonomy to determine their phylogenetic affiliation. The bacterial strains analysed in this study are shown in Supplementary Table S1, available in IJSEM Online. In addition to these newly described strains, type strains of closely related species were purchased from several established culture collections and were used as reference strains. All isolates were isolated in trypticase soy agar (TSA; Becton Dickinson) stabs 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; Becton Dickinson) incubated at 25 °C for 2–7 days. Representative strains have been deposited in the BCCM/LMG Bacteria Collection, Laboratorium voor Microbiologie, University of Ghent, Ghent, Belgium (LMG), and the National Institute of Technology and Evaluation, Biological Resource Center (NBRC), Japan (Supplementary Table S1).

All strains were tested at 25 °C for the following key characteristics: Gram reaction (Gregerson, 1978), motility and cell shape [phase-contrast microscopy after growth in veal infusion broth (Difco), for 24 h], cytochrome oxidase (BBL DrySlide oxidase; Becton Dickixon), catalase reaction (3 % H$_2$O$_2$), reduction of TMAO in TMAO medium (Gram et al., 1987) and production of H$_2$S from thiosulfate (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 (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.

API 20NE kits (bioMérieux) were also employed for assimilation tests according to the manufacturer’s instructions. Type strains of *S. putrefaciens*, *Shewanella affinis*, *S. baltica*, *Shewanella colwelliana*, *Shewanella hafniensis* and *Shewanella morrhuae* were included in each trial and served as controls. The genomic G + C content was determined by HPLC (Vogel et al., 1997). The ability to degrade gelatin (Frazier, 1926), DNA (Difco DNase test agar with methyl green) and ornithine (Difco) was also tested.

All of the new isolates were Gram-negative, motile rods, with positive oxidase and catalase reactions. They were unable to ferment glucose or produce indole but reduced nitrate and TMAO and produced H$_2$S. Based on these traits, the strains were tentatively classified as members of the genus *Shewanella* according to established procedures (Stenstrom & Molin, 1990). However, these characteristics were not sufficient to allow for a complete identification at the species level among the psychrotolerant shewanellae (Ziemke et al., 1997). Under optimum conditions, cells of these new isolates were 0.5–0.7 μm in diameter and 1.0–1.2 μm long. Colonies were round, undulate, beige and non-luminescent and had irregular margins on TSA plates incubated at 25 °C for 1 day. All strains were able to grow between 4 and 30 °C.

The first group (group 1; group C5 of Vogel et al., 2005) was composed of seven strains, including strain T147$^T$, and showed similar phenotypic traits to psychrotolerant *S. morrhuae* strains, but differed from *S. morrhuae* in that they assimilated lactate (Table 1). These strains were also distinguished from *S. putrefaciens*, *S. baltica* and *S. hafniensis* by their carbohydrate assimilation patterns, ability to grow at 37 °C and production of gelatinase. Furthermore, the G + C content of these strains was 44 mol%, which differs from that of *S. putrefaciens*, *S. baltica* and *S. hafniensis*. These results suggest that group 1 was phenotypically similar to, but nevertheless distinguishable from, known authentic *Shewanella* species. A second group (group 2; groups C1 and C2 of Vogel et al., 2005) encompassing 33 strains and represented by strain S13$^T$ grew well at 4 °C, cytochrome oxidase, positive oxidase and catalase reactions. They were unable to ferment glucose or produce indole but reduced nitrate and TMAO and produced H$_2$S. Based on these traits, the strains were tentatively classified as members of the genus *Shewanella* according to established procedures (Stenstrom & Molin, 1990). However, these characteristics were not sufficient to allow for a complete identification at the species level among the psychrotolerant shewanellae (Ziemke et al., 1997). Under optimum conditions, cells of these new isolates were 0.5–0.7 μm in diameter and 1.0–1.2 μm long. Colonies were round, undulate, beige and non-luminescent and had irregular margins on TSA plates incubated at 25 °C for 1 day. All strains were able to grow between 4 and 30 °C.

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The 16S rRNA and gyrB genes were amplified by PCR with universal primer sets as described by Weisburg et al. (1991) 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 5 mg ml\(^{-1}\)) for lysis. Extraction of 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 gene or \(\text{gyrB}\) sequences with existing sequences in public databases using the BLAST algorithm (Altschul et al., 1990). The multiple alignment calculation of nucleotide substitution rates (\(K_{\text{vac}}\) values; Kimura, 1980) and the 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. The topological robustness of the phylogenetic trees was evaluated by a bootstrap analysis through 1000 replications.

Approximately 1.4 kbp nucleotide sequences of 16S rRNA genes and 1.1 kbp nucleotide sequences of the \(\text{gyrB}\) genes 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 neighbour of the group 1 (T147\(^T\)) strains was *S. morrhuae* ATCC BAA-1205\(^T\), with sequence similarity of 99.9%. The sequences of the group 2 (S13\(^T\)) strains shared more than 99% similarity with *S. colwelliana* ATCC 39565\(^T\) (99.4%) and *S. affinis* ATCC BAA-642\(^T\) (99.6%). In the case of the genus *Shewanella*, Venkateswaran et al. (1999) and Satomi et al. (2003) have reported that analysis of \(\text{gyrB}\) sequences is useful, since the resolution of the 16S rRNA gene sequence is insufficient to evaluate their phylogenetic position. Fig. 2 shows the phylogenetic tree constructed based on \(\text{gyrB}\) sequences. The group 1 strains clustered with *S. morrhuae*, sharing 95.6% sequence similarity, and the group 2 strains were positioned monophyletically, apart from both *S. affinis* (85.6%) and *S. colwelliana* (85.6%), clearly delineating them as a distinct species. The \(\text{gyrB}\) sequences of *S. affinis* and *S. colwelliana* were almost identical; there is only one base difference, and the deduced amino acid sequences were identical between the two type strains, indicating that they were probably members of the same species. The taxonomic status of the group 1 strains was still unresolved, since they shared 99.2 and 95.6% similarity with *S. morrhuae* based on 16S rRNA gene and \(\text{gyrB}\) sequences, respectively. Such similarity values are not sufficient to distinguish closely related species according to established procedures (Stackebrandt & Goebel, 1994; Satomi et al., 2003; Venkateswaran et al., 1999). Therefore, DNA–DNA hybridization was carried out to confirm the novelty of these isolates.

Table 1. Phenotypic characteristics of the new isolates and the type strains of *Shewanella* species

<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>
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</thead>
<tbody>
<tr>
<td>G+C content (mol%)</td>
<td>Vogel et al. (1997)</td>
<td>44</td>
<td>44</td>
<td>44</td>
<td>47</td>
<td>45</td>
<td>46</td>
<td>47</td>
<td>46</td>
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<tr>
<td>Growth at:</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>4 °C</td>
<td></td>
<td>50% marine agar</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>100</td>
<td>−</td>
</tr>
<tr>
<td>37 °C</td>
<td></td>
<td>50% marine agar</td>
<td>0</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>70</td>
<td>−</td>
</tr>
<tr>
<td>Growth in 6% NaCl</td>
<td>Vogel et al. (1997)</td>
<td>0</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>100</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Gelatinase</td>
<td>Gelatin agar</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>+</td>
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<td>DNase</td>
<td>DNase test agar</td>
<td>100</td>
<td>+</td>
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<td>0</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Ornithine decarboxylase</td>
<td>Decarboxylase agar</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Assimilation of:</td>
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<tr>
<td>Lactate</td>
<td>Vogel et al. (2005)</td>
<td>100</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>100</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Sucrose</td>
<td>Vogel et al. (2005)</td>
<td>0</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>0</td>
<td>−</td>
<td>−</td>
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<tr>
<td>Gluconate</td>
<td>API 20NE</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>0</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Glucose</td>
<td>API 20NE</td>
<td>0</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>0</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Arabinose</td>
<td>API 20NE</td>
<td>57</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>0</td>
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<tr>
<td>N-Acetylgalactosamine</td>
<td>API 20NE</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>100</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Maltose</td>
<td>API 20NE</td>
<td>0</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>0</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Capric acid</td>
<td>API 20NE</td>
<td>0</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>3</td>
<td>−</td>
<td>−</td>
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<tr>
<td>Malate</td>
<td>API 20NE</td>
<td>100</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>100</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Citrate</td>
<td>API 20NE</td>
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<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>0</td>
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<td>−</td>
</tr>
</tbody>
</table>
DNA–DNA hybridization was performed 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). Supplementary Table S2 shows the results of DNA–DNA hybridization between strains T147T and S13T and the type strains of closely related Shewanella species. Within each of the groups themselves, DNA relatedness values were significantly higher, with the group 1 and group 2 strains exhibiting relatedness values of 85 and 81–91 %, respectively. Strains T147T and U718 showed DNA–DNA hybridization values of 53–57 % with S. morhuae strains and less than 22 % with S. putrefaciens ATCC 8071T and S. baltica NCTC 10735T. Similarly, the group 2 strains exhibited ~24 and ~28 % DNA relatedness with S. affinis ATCC BAA-642T and S. colwelliana ATCC 39565T, respectively. The DNA–DNA hybridization results strongly support the claim that isolates of group 1 (T147T) and group 2 (S13T) represent novel species within the genus Shewanella (Wayne et al., 1987).

Interestingly, S. affinis ATCC BAA-642T and S. colwelliana ATCC 39565T had a DNA–DNA hybridization value of 76–83 %. This supported the results of gyrB and 16S rRNA gene sequence analysis, though some phenotypic differences exist between the two strains, such as growth at 4 °C and in 6 % NaCl and gluconate assimilation (Table 1). However, Ivanova et al. (2004) reported that DNA relatedness values were only 45–52 % between S. affinis ATCC BAA-642T and S. colwelliana ATCC 39565T. The gyrB and 16S rRNA gene sequence analyses and DNA–DNA hybridization newly performed in this study show no evidence to separate the two species genetically. Based on these results, S. affinis ATCC BAA-642T and S. colwelliana ATCC 39565T received from the ATCC in March 2005 should be considered members of the same species.

Based on the findings of the polyphasic taxonomic study, it was determined that some of the strains isolated from marine fish from the Danish Baltic Sea represent two novel species within the genus Shewanella, Shewanella glacialipiscicola.

**Fig. 1.** Phylogenetic tree of the genus *Shewanella* based on 16S rRNA gene sequences. The tree was constructed using the neighbour-joining method and genetic distances were computed by Kimura's model. The scale bar indicates a genetic distance of 0.01. Numbers at nodes indicate percentages of occurrence in 1000 bootstrapped trees; only values greater than 40 % are shown. *Pseudoalteromonas tetraodonis* IAM 14160T was included as an outgroup. GenBank accession numbers are given in parentheses.
sp. nov. (represented by strain T147\textsuperscript{T}) and Shewanella algidipiscicola sp. nov. (represented by strain S13\textsuperscript{T}). In addition, Shewanella affinis Ivanova et al. 2004 should be considered as a later heterotypic synonym of Shewanella colwelliana (Weiner et al. 1988) Coyne et al. 1990.

**Description of Shewanella glacialipiscicola sp. nov.**

*Shewanella glacialipiscicola* (gla\textsuperscript{ci}a.li.pis\textsuperscript{ci}.co\textsuperscript{la}. L. adj. glacialis icy; L. n. piscis fish; L. suff. -cola dweller; N.L. n. glacialipiscicola iced fish dweller).

Mesophilic, aerobic and chemoheterotrophic. Cells are Gram-negative rods, 0.5–0.7 μm in diameter and 1.0–1.2 μm long, motile by means of polar flagella. None of the strains are capable of growing at concentrations of 6 % (w/v) NaCl. The temperature range for growth is 4–30°C, with 25°C being optimal. Growth does not occur at temperatures above 37°C. Colonies are round, undulate, white–dull and non-luminescent and have irregular margins on marine agar 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 H\textsubscript{2}S. Cells hydrolyse gelatin and aesculin, reduce nitrate and are positive for the production of DNase and ornithine decarboxylase, but do not produce acetoin, arginine dihydrolase, indole, urease or β-galactosidase. Cells utilize lactate, gluconate, N-acetylglucosamine and malate readily as energy sources.

D-Glucose, citrate, sucrose, mannose, mannitol, adipic acid and phenylacetate are not utilized as sole carbon sources, but more than half of the strains tested assimilate arabinose. Cells do not grow on minimal media, indicating the presence of a required growth factor. The DNA G+C content is 44 mol%.

The type strain is T147\textsuperscript{T} (= LMG 23744\textsuperscript{T} = NBRC 102030\textsuperscript{T}), isolated from cod from Danish waters of the Baltic Sea. Strain U718 (= LMG 23745 = NBRC 102031) is a reference strain.

**Description of Shewanella algidipiscicola sp. nov.**

*Shewanella algidipiscicola* (al.gi\textsuperscript{di}.pis\textsuperscript{ci}.co\textsuperscript{la}. L. adj. algidus cold; L. n. piscis fish; L. suff. -cola dweller; N.L. n. algidipiscicola cold-fish dweller).

Mesophilic, aerobic and chemoheterotrophic. Cells are Gram-negative rods, 0.5–0.7 μm in diameter and 1.0–1.2 μm long, motile by means of polar flagella. Capable of growing at 6 % (w/v) NaCl. The temperature range for growth is 4–37°C, with 25°C being optimal. Growth does not occur at temperatures above 42°C. Colonies are round, undulate, white–dull and 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 or hydrolyse gelatin, but reduce TMAO and produce H\textsubscript{2}S. Cells reduce nitrate and are positive for the production of DNase and
ornithine decarboxylase, but do not produce acetoin, arginine dihydrolase, indole, urease or β-galactosidase. Cells are unable to use most of the carbon substrates tested, although lactate, N-acetylgalactosamine and malate are readily utilized as energy sources. D-Glucose, glucuronate, maltose, citrate, sucrose, mannose, mannotol, adic acid and phenylacetate are not utilized as sole carbon sources, but several strains assimilate arabinose and capric acid. Cells do not grow on minimal media, indicating the presence of a required growth factor. The DNA G+C content is 47 mol%.

The type strain is S13T (LMG 23746T = NBRC 102032T), isolated from plaice from Danish waters of the Baltic Sea. Strains Q14 (LMG 23477 = NBRC 102033), Q213 and W01 are reference strains.

Acknowledgements

The technical assistance of Anemone Bundvald is acknowledged. Shariff Osman is acknowledged for critically reviewing the manuscript.

References


