Flaviramulus ichthyoenteri sp. nov., an N-acylhomoserine lactone-degrading bacterium isolated from the intestine of a flounder (Paralichthys olivaceus), and emended descriptions of the genus Flaviramus and Flaviramus basaltis

Yunhui Zhang, Kaihao Tang, Xiaochong Shi and Xiao-Hua Zhang

Correspondence
Xiao-Hua Zhang
xhzhang@ouc.edu.cn
College of Marine Life Sciences, Ocean University of China, Qingdao 266003, PR China

A Gram-stain-negative, strictly aerobic, yellow-pigmented, rod-shaped and N-acylhomoserine lactone-degrading bacterium, designated strain Th78T, was isolated from the intestine of a cultured flounder (Paralichthys olivaceus). Phylogenetic analysis based on 16S rRNA gene sequences indicated that strain Th78T belonged to the genus Flaviramus (family Flavobacteriaceae) and showed the highest 16S rRNA gene sequence similarity to Flaviramus basaltis H35T (96.70 %). Optimal growth occurred in the presence of 2–3 % (w/v) NaCl, at pH 7.0–8.0 and at 28 °C. The major fatty acids were iso-C15 : 0 3-OH, iso-C15 : 1 G and iso-C17 : 0 3-OH. The major polar lipids were phosphatidylethanolamine, one unidentified aminolipid and three unidentified polar lipids. Menaquinone 6 (MK-6) was the only respiratory quinone. The DNA G + C content of strain Th78T was 31.5 mol%. On the basis of polyphasic analysis, strain Th78T is considered to represent a novel species of the genus Flaviramus, for which the name Flaviramus ichthyoenteri sp. nov. is proposed. The type strain is Th78T (= JCM 18634T = KCTC 32142T = DSM 26285T). Emended descriptions of the genus Flaviramus and Flaviramus basaltis are also proposed.

In numerous Gram-negative bacteria, N-acylhomoserine lactones (AHLs) are employed as the major signal molecules in cell-to-cell communication termed quorum sensing (QS) (Whitehead et al., 2001; Williams, 2007). AHLs regulate various biological phenomena when they accumulate to a crucial threshold of concentration. Considering that many virulence factors of pathogenic bacteria are controlled by QS, signal molecules as well as other elements involved in QS become important targets in the biological control of pathogenicity (Kaufmann et al., 2008; Antunes et al., 2010). These strategies involve chemical inhibitors and AHL-degrading enzymes existing in a wide range of bacteria (Czajkowski & Jafra, 2009). Here we report a novel AHL-degrading strain Th78T isolated from the intestine of cultured flounder (Paralichthys olivaceus) and investigated in a taxonomic study using a polyphasic approach. Strain Th78T is described as a novel species of the genus Flaviramus in the family Flavobacteriaceae (phylum Bacteroidetes). At the time of writing, the genus Flaviramus, described by Einen & Øvreås (2006), contains the single species Flaviramus basaltis isolated from seafloor basalt.

A flounder was collected from a fish farm in Shandong Province, China, in 2010. For the isolation of intestinal bacteria, the surface of the fish was cleaned with 75 % alcohol and a piece of intestinal tissue was sampled aseptically without removing the intestinal contents. Strain Th78T was isolated from the tissue homogenate by the dilution plating technique on marine agar 2216 (MA; Becton Dickinson) at 28 °C and purified by streaking three times on MA. Cultures of strain Th78T were maintained at 16 °C for short-term preservation and in sterile 0.85 % (w/v) saline supplemented with 15 % (v/v) glycerol at −80 °C for long-term preservation. Flaviramus basaltis DSM 18180T, Mariniflexile gromovii LMG 22578T and Gaetbulibacter saemankumensis KCTC 12379T were used as reference strains in phenotypic analyses.

The genomic DNA of strain Th78T was extracted and the 16S rRNA gene was obtained by PCR amplification with

Abbreviations: AHL, N-acylhomoserine lactone; AL, aminolipid; C6-HSL, N-decanoyl-L-homoserine; QS, quorum sensing; PE, phosphatidylethanolamine.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain Th78T is JX412958.

A supplementary figure is available with the online version of this paper.

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two universal primers, B8F (5′-AGAGTTTGATCTGGCTCAG-3′) and B1510 (5′-GGTTACCTGTTAGACCTT-3′) (Weisburg et al., 1991). For cloning and sequencing of the 16S rRNA gene, the PCR product was purified by TIANgel Midi purification kit (TIANGEN Biotech), ligated into the pUCm-T vector (TaKaRa) and sequenced at BGI (Qingdao, China). The almost complete 16S rRNA gene (1484 nt) was manually checked for the evaluation of quality and gaps. Pairwise similarity values between strain Th78T and closely related type strains were calculated using the EzTaxon-e server (http://eztaxon-e.ezbiocloud.net/; Kim et al., 2012). The 16S rRNA gene sequences of related strains were downloaded from the NCBI database (http://www.ncbi.nlm.nih.gov) and aligned using the clustal x program (Thompson et al., 1997) with manual modification. Phylogenetic trees based on the neighbour-joining, maximum-likelihood and maximum-parsimony algorithms were reconstructed using MEGA version 5.0 (Tamura et al., 2011). The genetic distance matrices were estimated by Kimura’s two-parameter model (Kimura, 1980). The topology of the phylogenetic trees was evaluated by the bootstrap resampling method of Felsenstein (1981) with 1000 replicates.

Comparative phylogenetic analysis of the 16S rRNA gene sequence indicated that strain Th78T had the highest pairwise similarity with Flaviramulus basaltis H35T (96.7 %), Mariniflexile aquimaris HWR-17T (96.5 %) and Gaethuli-bacter lutimaris D1-y4T (96.4 %). The similarities between strain Th78T and related species of the genera Mariniflexile and Gaethulibacter were in the ranges of 95.8–96.5 % and 93.8–96.4 %, respectively. Phylogenetic analyses based on neighbour-joining (Fig. 1), maximum-likelihood and maximum-parsimony algorithms showed that strain Th78T formed a distinct cluster with Flaviramulus basaltis H35T.

Cell morphology of strain Th78T was studied by transmission electron microscopy (JEM-1200EX; JEOL) after cells at different growth phases were collected from MA and negatively stained with 1 % (w/v) phosphotungstic acid. Gram-staining and flagellum staining were performed according to Beveridge et al. (2007). Gliding motility was observed by the hanging-drop technique and production of flexirubin-type pigments was estimated by a colour shift following exposure to 20 % (w/v) KOH (Bernardet et al., 2002). Cell pigments were extracted with acetone and the absorption spectrum was recorded at 300–900 nm with a UNIC 2802S UV/VIS spectrophotometer. Salinity and pH range supporting growth were investigated in 96-well microplates by measuring the optical densities at 590 nm. The temperature range supporting growth were investigated in 96-well microplates by measuring the optical densities at 590 nm.

For cellular fatty acid analysis, strain Th78T and the three reference strains according to standard methods (method 2), oxidase and lecithinase and hydrolysis of starch, casein, gelatin (method 2), agar, cellulose (method 2, filter paper) and Tween 20, 40 and 80 (method 2). DNase agar (Qingdao 96 Hope Bio-technology Co.) prepared with sterile seawater was used to detect the DNase activity. Chitin (1 %, w/v), CM-cellulose (1 %, w/v) and sodium alginate (2 %, w/v) were added to MA plates to determine their degradation by the formation of clear zones around colonies observed directly or after flooding with appropriate solutions (Teather & Wood, 1982). Other physiological and biochemical properties and enzyme activities of strain Th78T were investigated using API 20E, API 20NE, API 50CH and API ZYM strips (bioMérieux) and the GN2 MicroPlate kit (Biorad) according to the manufacturers’ instructions except that sterile seawater was used to prepare the inoculum.

Cells of strain Th78T were rod-shaped (0.3–0.5 μm in diameter and 1.4–3.6 μm in length, in exponential phase) (Fig. S1, available in IJSEM Online). In contrast to Flaviramulus basaltis DSM 18180T, no branched and curled cells were observed in the stationary phase. Cells contained non-diffusible yellow pigments which had a typical carotenoid absorption spectrum (Tindall et al., 2007) with a maximum absorption peak at 455 nm. No flexirubin-type pigment was detected. Growth occurred at 4–37 ºC, with optimum growth at 28 ºC, and no growth was observed at 0 ºC or 42 ºC. Seawater was not required for growth. Unlike strain Th78T, none of the three reference strains showed AHL-degrading ability. Other physiological and biochemical characteristics are summarized in the species description and in Table 1.

Polar lipids were extracted from strain Th78T and Flaviramulus basaltis DSM 18180T according to Minnikin et al. (1984), and separated by two-dimensional TLC on silica gel 60 F254 plates (Merck). The identification of individual lipids was performed by spraying the plates with appropriate detection reagents (Komagata & Suzuki, 1987). For cellular fatty acid analysis, strain Th78T and the three reference strains were grown in MB at 28 ºC until they reached the mid-exponential phase. Fatty acid methyl esters were prepared and analysed according to the
standard protocol of MIDI (Sherlock Microbial Identification System, version 6.0), and identified by the TSBA6.0 database of the Microbial Identification System (Sasser, 1990). The respiratory quinones of strain Th78T were extracted with chloroform/methanol (2:1, v/v), separated by TLC and identified by HPLC as described by Xie & Yokota (2003). Genomic DNA of strain Th78T was extracted according to the procedure of Moore et al. (1999) and the G+C content was determined according to Mesbah et al. (1989).

The polar lipids profile of strain Th78T comprised phosphatidylethanolamine (PE), one unidentified amino-lipid (AL) and the three unidentified lipids (L1, L2 and L3), which was remarkably similar to the polar lipids profile of Flaviramulus basaltis DSM 18180T (Fig. 2). The cellular fatty acid profile of strain Th78T and three reference strains are listed in Table 2. The predominant fatty acids (>10 % of the total fatty acids) of strain Th78T were iso-C_{15:0} 3-OH, iso-C_{15:1} G and iso-C_{17:0} 3-OH. Only minor differences existed in the relative proportions between strain Th78T and Flaviramulus basaltis DSM 18180T, while the differences between strain Th78T and the other two reference strains were more apparent. The only respiratory quinone of strain Th78T was MK-6, in accordance with all members of the family Flavobacteriaceae (Bernardet et al., 2002). The DNA G+C content of strain Th78T was 31.5 %, which was quite close to the value of Flaviramulus basaltis H35T but lower than those of species of the genera Mariniflexile (Jung & Yoon, 2013) and Gaetbulibacter (Park et al., 2012).

Though the major features of strain Th78T including chemotaxonomic characteristics and DNA G+C content are significantly in line with the type and only species of the genus Flaviramulus, strain Th78T could be distinguished from Flaviramulus basaltis DSM 18180T by a number of obvious differences including cell morphology, oxidase activity, degradation of C6-HSL and hydrolysis of gelatin, DNA and Tween 40. Based on the phylogenetic analysis as well as the phenotypic and biochemical data, strain Th78T is proposed to represent a novel species of the genus Flaviramulus, for which the name Flaviramulus ichthyoenteri sp. nov. is proposed. In addition, emended descriptions of the genus Flaviramulus and the species Flaviramulus basaltis are also proposed on the basis of new data obtained in this study.

**Fig. 1.** Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing the phylogenetic position of strain Th78T and the type strains of closely related members of the family Flavobacteriaceae. Bootstrap percentages (>70 %) based on 1000 replicates are shown at branch points. *Cryomorpha ignava* ACAM 647T (GenBank accession no. NR027184) was used as an outgroup. Bar, 0.02 substitutions per nucleotide position.
Table 1. Differential characteristic between strain Th78<sup>T</sup> and the type strains of phylogenetically closely related species

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell shape</td>
<td>Rod</td>
<td>Rod/branched/curl</td>
<td>Rod</td>
<td>Rod</td>
</tr>
<tr>
<td>Cell size (µm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>1.4–3.6</td>
<td>1–3</td>
<td>2–3</td>
<td>3–4.5</td>
</tr>
<tr>
<td>Diameter</td>
<td>0.3–0.5</td>
<td>0.2–0.3</td>
<td>0.4–0.5</td>
<td>0.4–0.5</td>
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<tr>
<td>Growth at:</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>0 °C</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>42 °C</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>pH 5.5</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Requirement for sea-salt</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Oxidase</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Degradation of C6-HSL</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Nitrate reduction (API 20E)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Acetoin production (API 20E)</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Hydrolysis of:</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Gelatin</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
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<tr>
<td>Starch</td>
<td>+</td>
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<td>–</td>
<td>+</td>
</tr>
<tr>
<td>DNA</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Tween 40</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Tween 80</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Enzyme activity (API ZYM)</td>
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<tr>
<td>Cystine arylamidase</td>
<td>+</td>
<td>–</td>
<td>–</td>
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<td>Trypsin</td>
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<td>+</td>
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<td>α-Chymotrypsin</td>
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<td>+</td>
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<td>α-Glucosidase</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>β-Glucosidase</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>α-Mannosidase</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>α-Fucosidase</td>
<td>+</td>
<td>–</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>DNA G+C content (mol%)</td>
<td>31.5</td>
<td>31.4</td>
<td>35.7</td>
<td>34.8</td>
</tr>
</tbody>
</table>

Fig. 2. Total polar lipids of strain Th78<sup>T</sup> (a) and Flaviramulus basaltis DSM 18180<sup>T</sup> (b) separated by two-dimensional TLC and detected with 10% ethanolic molybdenophosphoric acid. PE, phosphatidylethanolamine; AL, unidentified aminolipid; L1–3, unidentified lipids.
Table 2. Cellular fatty acid contents (%) of strain Th78T and the type strains of phylogenetically closely related species

<table>
<thead>
<tr>
<th>Fatty acid</th>
<th>1</th>
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<th>4</th>
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<tbody>
<tr>
<td>Straight chain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C14:0</td>
<td>TR</td>
<td>TR</td>
<td>1.0</td>
<td>TR</td>
</tr>
<tr>
<td>C16:0</td>
<td>5.7</td>
<td>4.1</td>
<td>10.3</td>
<td>4.3</td>
</tr>
<tr>
<td>C18:0</td>
<td>4.3</td>
<td>2.5</td>
<td>8.8</td>
<td>1.4</td>
</tr>
<tr>
<td>Branched</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso-C17:0</td>
<td>TR</td>
<td>TR</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>iso-C17:0</td>
<td>1.1</td>
<td>1.4</td>
<td>1.1</td>
<td>TR</td>
</tr>
<tr>
<td>iso-C18:0</td>
<td>8.6</td>
<td>14.3</td>
<td>13.1</td>
<td>20.5</td>
</tr>
<tr>
<td>iso-C19:0</td>
<td>14.9</td>
<td>15.9</td>
<td>14.4</td>
<td>11.6</td>
</tr>
<tr>
<td>iso-C16:0</td>
<td>1.3</td>
<td>TR</td>
<td>1.2</td>
<td>TR</td>
</tr>
<tr>
<td>iso-C16:1 G*</td>
<td>1.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>anteiso-C15:0</td>
<td>3.0</td>
<td>4.7</td>
<td>4.9</td>
<td>8.3</td>
</tr>
<tr>
<td>anteiso-C15:1 A*</td>
<td>1.2</td>
<td>1.3</td>
<td>1.2</td>
<td>TR</td>
</tr>
<tr>
<td>iso-C17:109c</td>
<td>TR</td>
<td>TR</td>
<td>TR</td>
<td>1.4</td>
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<tr>
<td>Unsaturated</td>
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</tr>
<tr>
<td>C15:0:06c</td>
<td>TR</td>
<td>1.1</td>
<td>1.8</td>
<td>TR</td>
</tr>
<tr>
<td>C17:0:06c</td>
<td>TR</td>
<td>TR</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>C20:0:06,9,12,15c</td>
<td>TR</td>
<td>2.1</td>
<td>4.5</td>
<td>-</td>
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<tr>
<td>Hydroxy</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>C15:0:2-OH</td>
<td>1.6</td>
<td>1.7</td>
<td>1.4</td>
<td>1.8</td>
</tr>
<tr>
<td>C15:0:3-OH</td>
<td>1.3</td>
<td>2.9</td>
<td>1.7</td>
<td>1.3</td>
</tr>
<tr>
<td>C16:0:3-OH</td>
<td>1.5</td>
<td>1.7</td>
<td>TR</td>
<td>1.3</td>
</tr>
<tr>
<td>C17:0:2-OH</td>
<td>1.1</td>
<td>1.2</td>
<td>1.3</td>
<td>2.1</td>
</tr>
<tr>
<td>iso-C15:0:3-OH</td>
<td>17.9</td>
<td>14.6</td>
<td>5.1</td>
<td>8.1</td>
</tr>
<tr>
<td>iso-C16:0:3-OH</td>
<td>6.5</td>
<td>5.7</td>
<td>4.3</td>
<td>2.7</td>
</tr>
<tr>
<td>iso-C17:0:3-OH</td>
<td>13.1</td>
<td>13.0</td>
<td>10.0</td>
<td>14.3</td>
</tr>
<tr>
<td>Summed feature†</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>9.4</td>
<td>6.9</td>
<td>5.5</td>
<td>12.3</td>
</tr>
<tr>
<td>5</td>
<td>TR</td>
<td>TR</td>
<td>1.3</td>
<td>-</td>
</tr>
</tbody>
</table>

*Double bond position indicated by a capital letter is unknown. Different letter designation indicates that the bond is at a different location than for other monounsaturated fatty acids of the same chain length and branch pattern.
†As indicated by Montero-Calasanz et al. (2013), summed features are groups of two or three fatty acids that are treated together for the purpose of evaluation in the MIDI system and include both peaks with discrete equivalent chain lengths (ECLs) as well as those where the ECLs are not reported separately. Summed feature 3 comprises C16:1ω7c and/or C16:1ω6c; summed feature 5 comprises C18:2ω6,9c and/or anteiso-C18:0.

Emended description of the genus *Flaviramulus* Einen and Øvreas 2006

The description is as given by Einen & Øvreås (2006) with the following amendment. The polar lipids of the two analysed type strains consist of phosphatidylethanolamine, one unidentified aminolipid and three unidentified lipids.

**Emended description of Flaviramulus basalis**

Einen and Øvreås 2006

The description is as given by Einen & Øvreås (2006) with the following amendment. In the API ZYM strip, alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, β-glucosidase and N-acetyl-β-glucosaminidase activities are present; lipase (C14), cysteine arylamidase, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, x-fucosidase and x-mannosidase activities are absent. The polar lipids consist of phosphatidylethanolamine, one unidentified aminolipid and three unidentified lipids.

**Description of Flaviramulus ichthyoenteri**

Einen and Øvreås 2006

*Flaviramulus ichthyoenteri* (ich.thy.o'en't.e.ri. Gr. n. ichthys fish; Gr. n. enteron gut; N.L. gen. n. ichthyoenteri of fish gut).

Cells are Gram-stain-negative, strictly aerobic, gliding rods (approx. 0.3–0.5 μm in diameter and 1.4–3.6 μm in length in the exponential phase). Colonies on MA are bright yellow, convex and translucent with an entire margin, 0.8–1.2 mm in diameter after incubation for 4 days at 28°C. Growth occurs at 4–37°C (optimum, 28°C), at pH 7.0–9.0 (optimum, pH 7.0–8.0) and in the presence of 0.5–6% NaCl (optimum, 2–3%). Carotenoid pigments are produced but flexirubin-type pigments are not. Positive for oxidase and catalase activities and hydrolysis of starch, sodium algin, Tween 20 and Tween 80; negative for hydrolysis of cellulose (CM-cellulose and filter paper), chitin, casein, DNA, Tween 40, gelatin and lecithin. In the API 20E and 20NE strips, there are positive results for β-galactosidase activity, acetoin production and asaculin hydrolysis; there are negative results for arginine dihydrolyase, lysine decarboxylase, ornithine decarboxylase, trypsin and z-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α-glucosidase, N-acetyl-β-glucosaminidase and x-fucosidase activities are present; lipase (C14), α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase and x-mannosidase activities are absent. In the API 50CH strip, acid is produced from D-arabinose, D-galactose, N-acetyl-D-glucosamine, N-acetyl-D-glucosamine, gentiobiose, L-fucose and potassium 5-ketogluconate, but not from other substrates. The following substrates are utilized in the GN2 Microplate: z-cyclodextrin, glyco-
z-ketoglutaric acid, z-ketovaleric acid, d-saccharic acid, sebacic acid, succinic acid, L-alanine, L-alanyl glycine, and L-proline; the other substrates are not utilized. The major polar lipids are phosphatidylethanolamine, one unidentified aminolipid and three unidentified lipids. The major fatty acids (>10% of the total) are iso-C₁₅ : 0 3-OH, iso-C₁₅ : 1 G and iso-C₁₇ : 0 3-OH. The complete fatty acid composition is given in Table 2.

The type strain is Th78 T (JCM 18634 T = KCTC 32142 T = DSM 26285 T), isolated from the intestine of a cultured flounder in Shandong Province, China. The DNA G+C content of the type strain is 31.5%.

Acknowledgements

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References


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