

Agarivorans litoreus sp. nov., a novel gammaproteobacterium isolated from seawater and emended description of the genus *Agarivorans*

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Abstract A Gram-stain negative, aerobic, non-spore-forming, motile and rod-shaped or ovoid bacterial strain, designated GJSW-6^T, was isolated from a seawater collected at Geoje island on the South Sea, South Korea, and subjected to polyphasic taxonomic study. Strain GJSW-6^T was found to grow optimally at 30 °C, at pH 7.0–8.0 and in the presence of approximately 2.0 % (w/v) NaCl. Phylogenetic trees based on 16S rRNA gene sequences revealed that strain GJSW-6^T clustered with the type strains of two *Agarivorans* species, *Agarivorans albus* and *Agarivorans gilvus*, with which it exhibited sequence similarity values of 99.17 and 95.88 %, respectively. Sequence similarities to the type strains of the other recognized species were less than 93.04 %. Strain GJSW-6^T was found to contain Q-8 as the predominant ubiquinone and C_{16:0}, summed feature 3 (C_{16:1} ω7c and/or C_{16:1} ω6c) and C_{18:1} ω7c as the major fatty acids. The polar lipid profile of strain GJSW-6^T

containing phosphatidylethanolamine and phosphatidylglycerol as major components was similar to those of the type strains of *A. albus* and *A. gilvus*. The DNA G+C content of strain GJSW-6^T was determined to be 45.3 mol% and its mean DNA–DNA relatedness value with *A. albus* JCM 21469^T was 19 %. Differential phenotypic properties, together with the phylogenetic and genetic distinctiveness, revealed that strain GJSW-6^T is separated from two *Agarivorans* species. On the basis of the data presented, strain GJSW-6^T is considered to represent a novel species of the genus *Agarivorans*, for which the name *Agarivorans litoreus* sp. nov. is proposed. The type strain is GJSW-6^T (= KCTC 42116^T = NBRC 110444^T). An emended description of the genus *Agarivorans* is also proposed.

Keywords Seawater · Polyphasic taxonomy · Novel species · *Agarivorans litoreus*

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Introduction

The genus *Agarivorans* was proposed by Kurahashi and Yokota (2004) with the description of a single recognized species, *Agarivorans albus*, which was isolated from marine animals collected from the coast of the Kanto area in Japan. The second species of the genus, *Agarivorans gilvus*, was described from the surface of seaweed collected from the coast of Weihai

in China (Du et al. 2011). Phylogenetic analysis based on 16S rRNA gene sequences showed that the genus *Agarivorans* belongs to the order *Alteromonadales* of the class *Gammaproteobacteria* (Bowman and McMeekin 2005; Du et al. 2011). In this study, we describe a bacterial strain, designated GJSW-6^T, which was isolated from a seawater collected at Geoje island on the South Sea, South Korea. Comparative 16S rRNA gene sequence analysis indicated that strain GJSW-6^T is phylogenetically most affiliated to the genus *Agarivorans*. The aim of the present work was to determine the exact taxonomic position of strain GJSW-6^T by using a polyphasic characterization that included the determination of chemotaxonomic and other phenotypic properties, detailed phylogenetic investigations based on 16S rRNA gene sequences and DNA–DNA hybridization.

Materials and methods

Bacterial strains and culture conditions

Seawater was collected from Geoje island, an island located on the South Sea, South Korea and used as a source for the isolation of bacterial strains. Strain GJSW-6^T was isolated by the standard dilution plating technique at 25 °C on marine agar 2,216 (MA; Becton, Dickinson and Company) and cultivated routinely on MA at 30 °C. Strain GJSW-6^T was maintained on MA at 4 °C for short-term preservation and as a glycerol suspension (20 %, w/v in distilled water) at –80 °C for long-term preservation. Strain GJSW-6^T has been deposited in the Korean Collection for Type Cultures (KCTC; South Korea) and the NITE Biological Resource Centre (NBRC; Japan) under the accession numbers KCTC 42116^T and NBRC 110444^T, respectively.

Agarivorans albus JCM 21469^T and *A. gilvus* DSM 26780^T, which were used as reference strains for phenotypic characterization, fatty acid and polar lipid analyses and DNA–DNA hybridization, were obtained from the Japan Collection of Microorganisms (JCM), Saitama, Japan and the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ), Braunschweig, Germany, respectively.

Cell biomass of strain GJSW-6^T for DNA extraction and for the analyses of isoprenoid quinones and

polar lipids was obtained from cultures grown for 2 days in marine broth 2,216 (MB; Becton, Dickinson and Company) at 30 °C, and cell biomass of *A. albus* JCM 21469^T and *A. gilvus* DSM 26780^T for DNA extraction and for polar lipid analysis was obtained from the same culture conditions. For cellular fatty acid analysis, cell mass of strain GJSW-6^T, *A. albus* JCM 21469^T and *A. gilvus* DSM 26780^T was harvested from MA plates after cultivation for 3 days at 30 °C. The physiological age of the cell masses was standardized by observing the development of colonies on the agar plates followed by harvesting them from the same quadrant on the agar plates according to the standard MIDI protocol (Sherlock Microbial Identification System, version 6.1).

Morphological, cultural, physiological and biochemical characterization

The cell morphology, Gram reaction, pH range for growth and anaerobic growth were determined as described by Park et al. (2013). Growth at 4, 10, 20, 25, 30, 35, 37 and 40 °C was measured on MA to determine the optimal temperature and temperature range for growth. Growth at various concentrations of NaCl (0, 0.5 and 1.0–8.0 %, at increments of 1.0 %) was investigated by supplementing with appropriate concentrations of NaCl in MB prepared according to the formula of the Becton, Dickinson and Company medium without NaCl. Growth in the absence of NaCl was also tested on R2A agar (Becton, Dickinson and Company). The requirement for Mg²⁺ ions was investigated by using MB, prepared according to the formula of the Becton, Dickinson and Company medium, comprising all of the constituents except MgCl₂ and MgSO₄. Catalase and oxidase activities were determined as described by Lányi (1987). Hydrolysis of casein, starch, hypoxanthine, L-tyrosine and xanthine was tested on MA using the substrate concentrations described by Barrow and Feltham (1993). Hydrolysis of aesculin and Tweens 20, 40, 60 and 80 and nitrate reduction were investigated as described previously (Lányi 1987) with the modification that artificial seawater was used for the preparation of media. Hydrolysis of gelatin and urea were investigated by using Nutrient gelatin and Urea agar base media (Becton, Dickinson and Company), respectively, with the modification that artificial seawater was used for the preparation of media. The

artificial seawater contained (l^{-1} distilled water): 23.6 g NaCl, 0.64 g KCl, 4.53 g $MgCl_2 \cdot 6H_2O$, 5.94 g $MgSO_4 \cdot 7H_2O$ and 1.3 g $CaCl_2 \cdot 2H_2O$ (Bruns et al. 2001). Utilization of various substrates for growth was tested according to Baumann and Baumann (1981), using supplementation with 1 % (v/v) vitamin solution (Staley 1968) and 2 % (v/v) Hutner's mineral salts (Cohen-Bazire et al. 1957). Susceptibility to antibiotics was tested on MA plates using antibiotic discs (Advantec) containing the following (μg per disc unless otherwise stated): ampicillin (10), carbenicillin (100), cephalothin (30), chloramphenicol (100), gentamicin (30), kanamycin (30), lincomycin (15), neomycin (30), novobiocin (5), oleandomycin (15), penicillin G (20 U), polymyxin B (100 U), streptomycin (50) and tetracycline (30). Enzyme activities were determined, after incubation for 8 h at 30 °C, by using the API ZYM system (bioMérieux); the strip was inoculated with cells suspended in artificial seawater from which $CaCl_2$ was excluded to avoid the formation of precipitates.

Molecular studies

Chromosomal DNA was extracted and purified according to the method described by Yoon et al. (1996), with the modification that RNase T1 was used in combination with RNase A to minimize contamination of RNA. The 16S rRNA gene was amplified by PCR as described previously (Yoon et al. 1998) using two universal primers (5'-GAGTTTGATCCTGGCTCAG-3' and 5'-ACGGTTACCTTGTTACGACTT-3'). Sequencing of the amplified 16S rRNA gene was performed as described by Yoon et al. (2003). Alignment of sequences was carried out with CLUSTAL W software (Thompson et al. 1994) and gaps at the 5' and 3' ends of the alignment were omitted from further analysis. Phylogenetic analysis was performed as described by Yoon et al. (2012).

DNA–DNA hybridization was performed fluorometrically by the method of Ezaki et al. (1989) using photobiotin-labelled DNA probes in microdilution wells. Hybridization was performed with five replications for each sample. The highest and lowest values obtained in each sample were excluded and the means of the remaining three values are quoted as DNA–DNA relatedness values. The DNAs of strain GJSW-6^T and *A. albus* JCM 21469^T were used individually as labelled DNA probes for reciprocal hybridization.

Chemotaxonomic characterization

Isoprenoid quinones were extracted and analysed as described by Komagata and Suzuki (1987), using reversed-phase HPLC and a YMC ODS-A (250 × 4.6 mm) column. The isoprenoid quinones were eluted by a mixture of methanol/isopropanol (2:1, v/v) using a flow rate of 1 ml min⁻¹ at room temperature and detected by UV absorbance at 275 nm. Fatty acids were saponified, methylated and extracted using the standard protocol of the Microbial Identification System (version 6.1). The fatty acids were analysed by GC (Hewlett Packard 6890) and identified using the TSBA6 database of MIDI (Sasser 1990). Polar lipids were extracted according to the procedures described by Minnikin et al. (1984), and separated by two-dimensional TLC using chloroform/methanol/water (65:25:3.8, by vol.) for the first dimension and chloroform/methanol/acetic acid/water (40:7.5:6:1.8, by vol.) for the second dimension as described by Embley and Wait (1994). Individual polar lipids were identified by spraying the plates with 10 % ethanolic molybdophosphoric acid, molybdenum blue, ninhydrin and α -naphthol reagents (Minnikin et al. 1984; Komagata and Suzuki 1987) and with Dragendorff's reagent (Sigma).

The DNA G+C content was determined by the method of Tamaoka and Komagata (1984) with the modification that DNA was hydrolysed and the resultant nucleotides were analysed by reversed-phase HPLC equipped with a YMC ODS-A (250 × 4.6 mm) column. The nucleotides were eluted by a mixture of 0.55 M $NH_4H_2PO_4$ (pH 4.0) and acetonitrile (40:1, v/v), using a flow rate of 1 ml min⁻¹ at room temperature and detected by UV absorbance at 270 nm.

Results and discussion

Morphological, cultural, physiological and biochemical characteristics

Strain GJSW-6^T was found to be aerobic, Gram-stain negative, non-spore-forming and rod-shaped or ovoid. Strain GJSW-6^T was observed to grow optimally at 30 °C and at pH 7.0–8.0. It was found to grow in the presence of 0–5.0 % (w/v) NaCl with an optimum of approximately 2.0 % (w/v) NaCl. Strain GJSW-6^T was found not to require NaCl for growth, whereas the type strains of two *Agarivorans* species, *A. albus* and

Table 1 Differential characteristics of strain GJSW-6^T and the type strains of two *Agarivorans* species

Characteristic	1	2	3
NaCl requirement	–	+ ^a	+ ^a
Nitrate reduction	+	+ ^a	– ^a
Utilization of			
D-Cellobiose	+	+	–
D-Fructose	+	+	–
D-Galactose	+	+	–
D-Glucose	+	+	–
D-Mannose	+	+	–
D-Xylose	+	+	–
Acetate	+	+	–
Citrate	+	–	–
Succinate	–	w	–
L-Glutamate	+	–	–
Enzyme activity (API ZYM)			
Esterase (C 4)	w	–	–
Esterase lipase (C 8)	–	–	+
Acid phosphatase	–	w	+
Naphthol-AS-BI-phosphohydrolase	–	w	+
Susceptibility to			
Ampicillin	+	–	–
Carbenicillin	+	+	–
Cephalothin	+	+	–
Kanamycin	–	+	–
Neomycin	–	+	–
Novobiocin	–	+	+
Penicillin G	+	+	–
Polymyxin B	–	–	+
Streptomycin	+	–	–
DNA G+C content (mol%)	45.3	49.5 ^a	48.5 ^a

Strains: 1, GJSW-6^T; 2, *A. albus* JCM 21469^T; 3, *A. gilvus* DSM 26780^T. Data of reference strains obtained from this study unless otherwise indicated. All strains are positive for flagellar motility; catalase and oxidase activity*; growth at 37 °C; hydrolysis of* aesculin and agar; utilization of maltose and [L-malate and pyruvate] (weak for *A. albus* JCM 21469^T); activity of alkaline phosphatase, leucine arylamidase and β-galactosidase; and susceptibility to chloramphenicol and tetracycline. All strains are negative for Gram-staining; hydrolysis of gelatin and urea[‡]; utilization of L-arabinose, sucrose, D-trehalose, benzoate, formate and salicin; activity of lipase (C 14), valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase; and susceptibility to gentamicin, lincomycin and oleandomycin

Symbol: +, positive reaction; –, negative reaction; w, weakly positive reaction

^a Data of *A. albus* JCM 21469^T and *A. gilvus* DSM 26780^T taken from Kurahashi and Yokota (2004) and Du et al. (2011), respectively

A. gilvus, required NaCl for growth (Table 1). While strain GJSW-6^T was found to be able to utilize citrate and L-glutamate, the type strains of the two

Agarivorans species were unable to utilize these substrates (Table 1). Strain GJSW-6^T was found to be susceptible to ampicillin and streptomycin and resistant to novobiocin, whereas the type strains of the two *Agarivorans* species showed inverse results (Table 1). Strain GJSW-6^T was also found to be susceptible to carbenicillin, cephalotin, chloramphenicol, penicillin G and tetracycline, but resistant to gentamicin, kanamycin, lincomycin, neomycin, oleandomycin and polymyxin B.

Morphological, cultural, physiological and biochemical characteristics of strain GJSW-6^T are given in the species description (see below), Table 1 and Supplementary Fig. 1.

Phylogenetic analysis and DNA–DNA relatedness

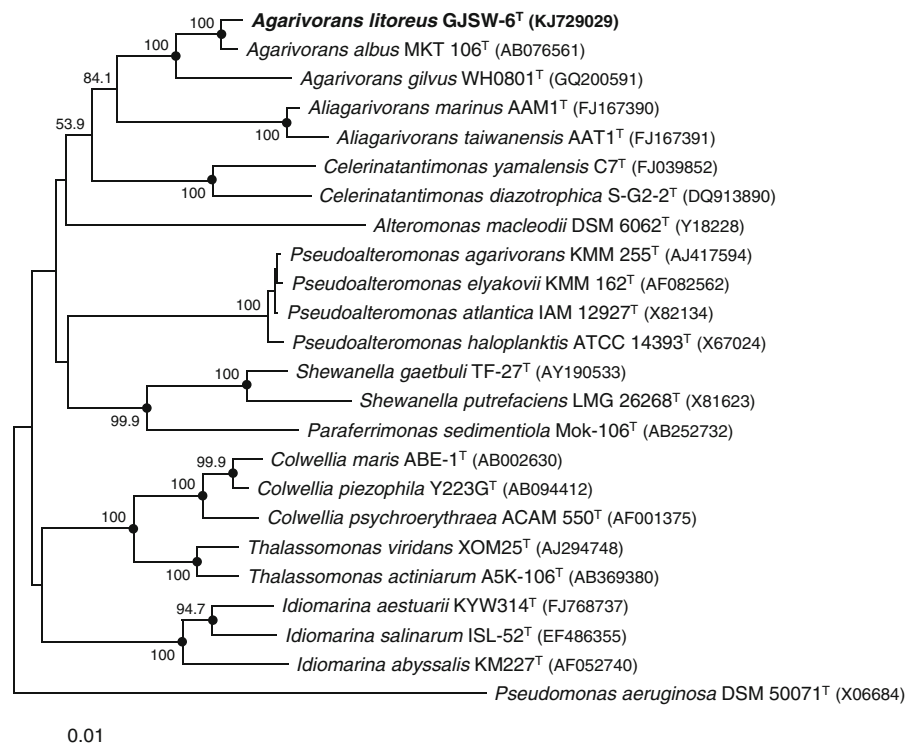
The almost-complete 16S rRNA gene sequence (1467 nucleotides; GenBank/EMBL/DDBJ accession number KJ729029) of strain GJSW-6^T, approximately 95 % of the *Escherichia coli* 16S rRNA sequence, was determined in this study. In the neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, strain GJSW-6^T clustered with the type strain of *A. albus* with a bootstrap resampling value of 100 %, and this cluster joined the type strain of *A. gilvus* with a bootstrap resampling value of 100 % (Fig. 1). The relationships among strain GJSW-6^T and the type strains of *A. albus* and *A. gilvus* were maintained in the trees constructed using the maximum-likelihood and maximum-parsimony algorithms (Fig. 1). Strain GJSW-6^T exhibited 16S rRNA gene sequence similarity values of 99.17 and 95.88 % to *A. albus* MKT 106^T and *A. gilvus* WH0801^T, respectively, and of less than 93.04 % to the type strains of the other recognized species.

Strain GJSW-6^T exhibited DNA–DNA relatedness value of 19 ± 7.6 % to *A. albus* JCM 21469^T.

Chemotaxonomic characteristics

The predominant isoprenoid quinone detected in strain GJSW-6^T was determined to be ubiquinone-8 (Q-8) which is compatible with that of the genus *Agarivorans* (Kurahashi and Yokota 2004). In Table 2, the fatty acid profile of strain GJSW-6^T is compared with those of the type strains of *A. albus* and *A. gilvus*, which were grown and analysed under identical conditions. The major fatty acids (>10 % of the total

Fig. 1 Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing the positions of strain GJSW-6^T, the type strains of *Agarivorans* species and representatives of some other related taxa. Bootstrap values (expressed as percentages of 1,000 replications) of > 50 % are shown at branching points. Filled circles indicate that the corresponding nodes were also recovered in the trees generated with the maximum-likelihood and maximum parsimony algorithms. *Pseudomonas aeruginosa* DSM 50071^T (GenBank accession number, X06684) was used as an outgroup. Scale bar, 0.01 substitutions per nucleotide position



fatty acids) detected in strain GJSW-6^T were C_{16:0} (27.9 %), summed feature 3 (C_{16:1} ω7c and/or C_{16:1} ω6c, 27.5 %) and C_{18:1} ω7c (19.0 %). The fatty acid profile of strain GJSW-6^T was similar to those of the type strains of *A. albus* and *A. gilvus*, although there were differences in the proportions of some fatty acids (Table 2). The major polar lipids found in strain GJSW-6^T were phosphatidylethanolamine and phosphatidylglycerol; minor amounts of diphosphatidylglycerol, an unidentified aminolipid, an unidentified phospholipid and an unidentified lipid were also present (Supplementary Fig. 2). The polar lipid profile of strain GJSW-6^T was similar to those of the type strains of *A. albus* and *A. gilvus* in that phosphatidylethanolamine and phosphatidylglycerol are major polar lipids (Supplementary Fig. 2).

The DNA G+C content of strain GJSW-6^T was determined to be 45.3 mol%, a value lower than those reported for *Agarivorans* species (Table 1).

Conclusion

The results obtained from the phylogenetic and chemotaxonomic analyses are sufficient to prove that

strain GJSW-6^T is a member of the genus *Agarivorans* (Fig. 1; Table 2; Supplementary Fig. 2; Kurahashi and Yokota 2004; Du et al. 2011). Strain GJSW-6^T could be distinguished from the type strains of *A. albus* and *A. gilvus* by differences in several phenotypic characteristics, including NaCl requirement, nitrate reduction, utilization of some substrates, activity of some enzymes and susceptibility to some antibiotics (Table 1). These differences, in combination with the phylogenetic and genetic distinctiveness of strain GJSW-6^T, suggest that the novel strain is separated from other species of the genus *Agarivorans* (Wayne et al. 1987; Stackebrandt and Goebel 1994). On the basis of the data presented, therefore, strain GJSW-6^T is considered to represent a novel species of the genus *Agarivorans*, for which the name *Agarivorans litoreus* sp. nov. is proposed.

Description of *Agarivorans litoreus* sp. nov.

Agarivorans litoreus (li.to're.us. L. masc. adj. *litoreus* belonging to the seashore).

Cells are Gram-stain negative, non-spore-forming and rod-shaped or ovoid, approximately 0.2–0.6 μm in diameter and 0.5–3.0 μm in length. Motile by means of

Table 2 Cellular fatty acid compositions (%) of strain GJSW-6^T and the type strains of two *Agarivorans* species

Fatty acid	1	2	3
Straight-chain			
C _{12:0}	5.3	6.7	4.4
C _{14:0}	4.5	4.2	2.6
C _{16:0}	27.9	30.1	28.4
C _{17:0}	tr	0.7	tr
C _{18:0}	0.8	1.2	1.1
Unsaturated			
C _{18:1} ω7c	19.0	30.7	34.0
Branched			
iso-C _{16:0}	3.6	–	tr
iso-C _{18:0}	2.5	–	tr
iso-C _{19:0}	–	1.3	–
Hydroxy			
C _{15:0} 2-OH	–	0.6	–
C _{16:0} 3-OH	1.1	1.1	0.6
10-Methyl-C _{19:0}	tr	0.7	tr
Summed features ^a			
2	5.5	6.1	5.2
3	27.5	16.4	21.9

Strains: 1, GJSW-6^T; 2, *A. albus* JCM 21469^T; 3, *A. gilvus* DSM 26780^T. All data obtained from this study. Fatty acids that represented < 0.5 % in all strains were omitted. tr, traces (< 0.5 %). –, not detected

^a Summed feature 2 contained C_{14:0} 3-OH and/or iso-C_{16:1} I; summed feature 3 contained C_{16:1} ω7c and/or C_{16:1} ω6c

a single polar flagellum. Colonies on MA are circular, smooth, glistening, sunken into agar, yellowish white in colour and 1.0–1.5 mm in diameter after incubation for 3 days at 30 °C. Optimal growth occurs at 30 °C; growth occurs at 4 and 37 °C, but not at 40 °C. Optimal pH for growth is between 7.0 and 8.0; growth occurs at pH 5.5, but not at pH 5.0. Growth occurs in the presence of 0–5.0 % (w/v) NaCl with an optimum of approximately 2.0 % (w/v) NaCl. Mg²⁺ ions are required for growth. Anaerobic growth does not occur on MA and on MA supplemented with nitrate. Catalase and oxidase positive. Nitrate is reduced to nitrite. Aesculin, casein, starch and Tweens 20, 40, 60 and 80 are hydrolysed but gelatin, hypoxanthine, L-tyrosine, urea and xanthine are not. D-Cellobiose, D-fructose, D-galactose, D-glucose, maltose, D-mannose, D-xylose, acetate, citrate, L-malate, pyruvate and L-glutamate are utilized as carbon and energy sources, but L-arabinose, sucrose, D-trehalose, benzoate, formate, succinate and

salicin are not. In assays with the API ZYM system, alkaline phosphatase, leucine arylamidase and β-galactosidase activities are present and esterase (C 4) activity is weakly present, but esterase lipase (C 8), lipase (C 14), valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase activities are absent. The predominant ubiquinone is Q-8. The major fatty acids (>10 % of the total fatty acids) are C_{16:0}, summed feature 3 (C_{16:1} ω7c and/or C_{16:1} ω6c) and C_{18:1} ω7c. The major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. The DNA G+C content of the type strain is 45.3 mol%.

The type strain, GJSW-6^T (= KCTC 42116^T - = NBRC 110444^T), was isolated from a seawater off Geoje island, an island located on the South Sea, South Korea. The GenBank/EMBL/DDBJ accession number of the 16S rRNA gene sequence of strain GJSW-6^T is KJ729029.

Emended description of the genus *Agarivorans* Kurahashi and Yokota 2004

The description of the genus *Agarivorans* is as given by Kurahashi and Yokota (2004) with the following amendments. The common major polar lipids are phosphatidylethanolamine and phosphatidylglycerol. The DNA G+C content is 45.3–49.5 mol%.

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