Rhabdonatronobacter sediminivivens gen. nov., sp. nov. isolated from the sediment of Hutong Qagan Soda Lake

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Abstract
A novel Gram-stain-negative bacterium, designated as IM2376T, was isolated from the sediment of Hutong Qagan Lake in the Ordos, Inner Mongolia Autonomous Region of China. Phylogenetic analysis based on 16S rRNA gene sequence revealed that the strain IM2376T had the highest similarity with Roseinatronobacter thiooxidans DSM 13087T (96.2%) and Rhodobaca bogoriensis LBB1T (96.2%) of the family Rhodobacteraceae. Genomic relatedness analyses showed that strain IM2376T was clearly distinguished from other species in the family Rhodobacteraceae, with average nucleotide identities, average amino acid identities, and in silico DNA–DNA hybridization values not more than 74.1, 68.5, and 20.2%, respectively. The fatty acids were mainly composed of C18:1ω7c (64.9%), iso-C16:0 (16.3%), and C16:1ω7c/C16:1ω6c (6.0%). The major polar lipids were diphosphatidylglycerol, phosphatidylglycerol, and phosphatidylcholine. The predominant ubiquinone was Q-10 (94.9%). The genomic DNA G+C content was 66 mol%. Based on all these results, strain IM2376T was considered a novel species of a new genus in the family Rhodobacteraceae, for which the name Rhabdonatronobacter sediminivivens is proposed. The type strain of Rhabdonatronobacter sediminivivens is IM2376T (= CGMCC 1.17852T = KCTC 92134T).

Keywords Rhodobacteraceae · Rhabdonatronobacter · Soda lake · Whole-genome sequence

Abbreviations
DPG Diphosphatidylglycerol
PG Phosphatidylglycerol
PC Phosphatidylcholine
isDDH The in silico DNA–DNA hybridization
AAI The average amino acid identity

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ANI The average nucleotide identity
PHA Polyhydroxyalkanoate
PHB Polyhydroxybutyrate
sqr Sulfide-quinone reductase gene
fccA Cytochrome subunit of sulfide dehydrogenase gene
fccB Sulfide dehydrogenase [flavocytochrome c] flavoprotein chain gene
GTDB The Genome Taxonomy Database
ML The maximum-likelihood
NJ Neighbor-joining
ME Minimum evolution
TYGS The type (strain) genome server
OPNG The O-nitrophenyl-β-d-galactopyranoside
VP Voges Proskauer
tmRNA Transfer-messenger-RNA
CDS Coding sequence
Introduction

The family Rhodobacteraceae was first established by Garrity et al. (2005). Till date, approximately 200 genera are validly published and correctly named under this family (https://lpsn.dsmz.de/family/Rhodobacteraceae). Rhodobacteraceae are mainly of aquatic origin and are commonly found in marine environments (Pujalte et al. 2014). Some species of this family can synthesize bioplastic materials polyhydroxyalkanoates (PHAs) or more commonly polyhydroxybutyrate (PHB) as carbon reserve material (Boldareva et al. 2007; Hwang and Cho 2008; Li et al. 2017; Pujalte et al. 2014). Soda lakes could be a favorable environment for the isolation of strains of this family. Soda lake has high salinity and pH characteristics caused by the accumulation of sodium (bi)carbonate owing to evaporation (Jones and Grant 2000). Since soda lake is rich in hydrochloride and bicarbonate but poor in phosphorus, this environment is considered conducive for the accumulation of PHA or PHB (Chen et al. 2019). Besides, bacteria in this family often contain sulfide-quinone oxidoreductase (Ssqr) cytochrome subunit of sulfide dehydrogenase (fccA), or sulfide dehydrogenase [flavocytochrome c] flavoprotein chain (fccB) genes. These genes’ products are helpful in sulfur-containing wastewater or waste gas treatment (Yu et al. 2011). Isolation and identification of strains of this family from soda lakes would help in enriching the microbial resources and provide new-found assets for industrial development.

Materials and methods

Isolation and culture conditions

Strain IM2376T was isolated from the sediment of Hutong Qagan Lake in Ordos, Inner Mongolia Autonomous Region of the People’s Republic of China. The longitude and latitude of the sample site were 108° 58′ E, 39° 14′10″ N, and the altitude was 1270 m. The LN medium was used for strain isolation. This alkaline medium was modified from the NOM medium (Mou et al. 2012) with several inorganic components adjusted according to the environmental physicochemical parameters (Zhao et al. 2020), and it contains (per liter): 15 g NaCl, 4 g Na2CO3, 6 g NaHCO3, 2 g KCl, 0.5 g yeast extract, 0.2 g NH4Cl, 0.25 g fish peptone, 0.38 g sodium formate, 0.25 g sodium acetate, 0.25 g sodium pyruvate, 2 g MgSO4·7H2O, 0.05 g KH2PO4, 0.08 g CaCl2, 0.0046 g FeSO4·7H2O, 1 mL trace metal solution (SL-6), and 3 mL vitamins solution. The pH of the media was adjusted to 9.5 with NaOH. The composition of SL-6 solution was (per 100 mL): 0.1 g ZnSO4·7H2O, 0.03 g MnCl2·4H2O, 0.3 g H3BO3, 0.2 g CoCl2·6H2O, 0.01 g CuCl2·2H2O, 0.02 g NiCl2·6H2O, and 0.03 g Na2MoO4·H2O. The SL-6 solution was adjusted to final pH of 3–4 with HCl to prevent precipitation of metal salts and stored at 4 °C. The vitamins solution composed of (per liter): 13.0 mg 4-aminobenzoate, 3.0 mg d-(-)-biotin, 33.0 mg nicotinic acid, 17.0 mg hemicalcium D-(-)-pantethenate, 50.0 mg pyridoxamine hydrochloride, 33.0 mg thiamine chloride hydrochloride, 17.0 mg cyanocobalamin, 10.0 mg D, L-6,8-thiociotic acid, 10 mg riboflavin, and 4.0 mg folic acid.

The sediment sample was diluted and spread on the surface of the LN agar plates (with 1.5% agar) and then incubated at 37 °C for about 2 weeks until the colonies were observed. Subsequently, the colonies were sub-cultured thrice on LN agar plates with the dilution separation method to obtain the pure culture. The isolated strain IM2376T was stored in 20% (v/v) glycerol with 10% NaCl at – 80 °C.

Phylogenetic and phylogenomic analyses

The genomic DNA of strain IM2376T was extracted according to the method described by Marmur (1961) and Xu et al. (2007). The genome was sequenced using the Illumina Novaseq 6000 platform by the BioMarker technologies, PR China. The genome sequences were assembled using SPAdes 3.13.0 with default parameters (Nurk et al. 2013). The draft genome was annotated by the NCBI Prokaryotic Genome Annotation Pipeline (PGAP) version 4.12 (https://www.ncbi.nlm.nih.gov/genome/annotation_prok/). The 16S rRNA gene sequence similarity of the strain IM2376T was carried out through the BLAST program (http://blast.ncbi.nlm.nih.gov/Blast.cgi) (Johnson et al. 2008) and the EzBioCloud webserver (Yoon et al. 2017a). The 120 conserved single-copy genes in the IM2376T genome were obtained by employing the Genome Taxonomy Database (GTDB) (Chaumeil et al. 2019; Parks et al. 2020, 2018). Multiple sequence alignments were performed using the CLUSTAL W program (Larkin et al. 2007). Furthermore, the phylogenetic tree was constructed based on the 16S rRNA gene and the 120 conserved single-copy proteins in the MEGA X software (Sudhir et al. 2018) with the Maximum-likelihood (ML) (Felsenstein 1981), Neighbor-Joining (NJ) (Saitou 1987), and the Minimum Evolution (ME) (Felsenstein 1981) methods. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) were shown next to the branches (Felsenstein 1985). The G+C content was calculated from the whole-genome sequence. The OrthoANI algorithm was used to calculate the Average Nucleotide Identity (ANI) value (Yoon et al. 2017b). The genome sequence data were uploaded to the Type (Strain) Genome Server (TYGS), a free bioinformatics...
platform (https://tygs.dsmz.de) for the genome-to-genome distance analysis in accordance with in silico DNA-DNA hybridization (isDDH) (Meier-Kolthoff and Göker 2019). The average amino acid identity (AAI) was also calculated using the AAI calculator (http://enve-omics.ce.gatech.edu/aaic.ui/index) (Rodriguez-R and Konstantinidis 2014).

**Physiological characteristics**

The LN medium with various NaCl concentrations (0, 0.17, 0.34, 0.51, 0.68, 0.86, 1.03, 1.20, 1.36, 1.54, 1.71, 1.88, and 2.05 M) was used to test the (optimum) salinity for growth. The pH range for growth (5–10.5, at an interval of 0.5 pH unit) was also determined in the LN medium with the addition of the following buffers: MES (pH 5.0–6.7), PIPES (pH 6.5–7.0), Tricine (pH 7.4–8.8), CHES (pH 9.0–10.1), and CAPS (pH 9.7–11.1). The temperature range for growth was ascertained by incubating at 4, 15, 20, 25, 35, 37, 42, and 50 °C. The strain was cultivated in LN medium at 37 °C for 2 days to examine the cell morphology by scanning electron microscopy (SU8010, Hitachi) and motility by light microscopy (BX51, Olympus).

The following substances were used to test the utilization as sole carbon and energy source (2 g/L for sugars, alcohols, and organic acids while 1 g/L for amino acids) in LN medium with 0.1 g/L yeast extract (without the fish peptone, sodium formate, sodium acetate, and sodium pyruvate): galactose, starch, trehalose, mannitol, D-xylulose, D-maltose, sucrose, D-glucose, D-mannose, L-rhamnose, lactose, arabinose, cellobiose, fructose, sorbose, glycerol, sorbitol, acetate, malate, pyruvate, DL-lactate, succinate, fumarate, citrate, ornithine, arginine, glutamate, glycine, histidine, cysteine, isoleucine, valine, lysine, and aspartate. Biochemical tests were performed in LN medium (containing 0.001 g/L yeast extract) according to the methods described by Xu et al. (2007) and Mata et al. (2002), and encompassed the activity of oxidase, catalase and urease, the reduction of nitrate and nitrite, the production of H2S and indole, as well as the O-nitrophenyl-β-D-galactopyranoside (OPNG) and Voges Proskauer (VP) test. The antibiotic sensitivity test was conducted on LN agar plate with the following antibiotic discs (μg per disc unless otherwise noted): Nitrofurantoin (300), Erythromycin (15), Bacitracin B (10 Units), Rifampicin (5), Ciprofloxacin (5), Novobiocin (5), Neomycin (30), Norfloxacin (10), Cefoxitin (30), Tetracycline (30), Tobramycin (10), Amoxicillin (10), Cefotaxime (30), Vancomycin (30), Chloramphenicol (30), Penicillin G (10 Units), and Streptomycin (10).

**Chemotaxonomic characterization**

The LN medium with various NaCl concentrations (0, 0.17, 0.34, 0.51, 0.68, 0.86, 1.03, 1.20, 1.36, 1.54, 1.71, 1.88, and 2.05 M) was used to test the (optimum) salinity for growth.

Gas Chromatography–Mass Spectrometry (GC–MS) were performed by following the previously described method (Kuy kendall et al. 1988). The frozen dry cells (about 200 mg) were used to extract isoprenoid quinones with chloroform/methanol (2:1, by vol.). The extracted isoprenoid quinones were measured by reversed-phase High-Performance Liquid Chromatography (HPLC) (Wu et al. 2009). The polar lipids analysis was done using one- and two-dimensional Thin-Layer Chromatography (TLC) by following the method described by Kamekura and Kates (1988).

**Results and discussion**

**Morphology, physiology, and biochemical analysis**

The cells of strain IM2376T were non-motile and had no flagellum (Fig. S1, Table 1). The strain IM2376T was sensitive to Nitrofurantoin, Erythromycin, Bacitracin B, Rifampicin, Ciprofloxacin, Novobiocin, Neomycin, Norfloxacin, Cefoxitin, Tetracycline, Tobramycin, Amoxicillin, Cefotaxime, and Vancomycin, while resistant to Chloramphenicol, Penicillin G, and Streptomycin. Other features of strain IM2376T are indicated in the species description. The detailed features comparison between strain IM2376T and its close species are listed in Table 1.

**Chemotaxonomic characterization**

The primary fatty acids of strain IM2376T were C18:1ω7c (64.9%), iso-C16:0 (16.3%), and C16:1ω6c (6.0%). The details of the fatty acid categories are listed in Table S1. The major polar lipids were diphosphatidylglycerol, phosphatidylethanolamine, phosphatidylcholine, and one unknown aminophospholipid (Fig. S2). Phospholipids were also detected, but no glycolipid was found. The quinones were Q-10 (94.9%) and Q-11 (5.1%).

**Phylogenetic and phylogenomic analyses**

The 16S rRNA gene (1503 bp) and whole-genome sequence of strain IM2376T were obtained. The genome size was 4.063 Mb. The genomic DNA G+C content was 66 mol% which was higher than that of the reference species (59–62 mol%, Table 1). The strain IM2376T had 1 16S rRNA gene, 1 23S rRNA gene, 3 5S rRNA genes, 41 tRNAs, and 3 ncRNAs. Three clustered regularly interspaced short palindromic repeat sequences (CRISPRs) arrays were predicted. A total of 3671 coding sequences (CDSs) were predicted in the whole genome.

The 16S rRNA gene sequences similarity analysis showed that strain IM2376T was closely related to *Roseinatronobacter thiooxidans* DSM 13087T (96.2%), followed by
Rhodobaca bogoriensis LBB1T (96.2%), and Pararhodobacter aggregans D1-19T (96.1%). The OrthoANI and isDDH values between strain IM2376T and these reference strains were 73.5–74.1% and 19.4–20.9%, respectively (Table 2). These values were lower than the threshold values for the species boundary, i.e., 95–96% for ANI and 70% for isDDH (Goris et al. 2007; Meier-Kolthoff et al. 2013; Richter and Rosselló-Móra 2009). Besides, the AAI values (66.5–69.3%) were between 60% and 80% in the specified range of the genus-level boundary (Luo et al. 2014). The ML trees based on 16S rRNA sequences and 120 conserved single-copy genes from the whole-genome sequences showed that strain IM2376T formed a distinct clade (bootstrap value > 75%, Fig. 1a, b), separated from Roseibaca ekhonensis EL-50T, R. bogoriensis LBB1T, Rhodobaca barguzinensis VKM B-2406T, R. thiooxidans DSM 13087T, and Roseinatronobacter monicus ROS 35T. The NL and ME trees also supported the stability of the ML trees (bootstrap value > 75%, Fig. S3a, b, and Fig. S4a, b). The phenotypic, chemotaxonomic, and phylogenetic properties suggested that strain IM2376T represented a novel species of a new genus within the family Rhodobacteraceae, for which the name Rhabdonatronobacter sediminivivens gen. nov., sp. nov. was proposed.

| Characteristics | 1 | 2 | 3 | 4 | 5 | 6 |
|-----------------|---|---|---|---|---|---|
| Cell size (µm)  | 0.50–1.06×1.00–2.27 | 0.80–1.20×1.20–4.00 | 1.0×1.5 | 0.8–1×1.1–1.5 | 0.5–0.8×0.8–2.2 | 0.5–0.7×1.2–1.7 |
| Cell shape      | Short rod | Rod | Short rod | Short rod | Rod with elongated ends | Short rod |
| NaCl range for growth (M) | 0–2.05 | 0–0.68 | 0.17–1.37 | 0.17–0.51 | 0.1–2 | 0–1.37 |
| Optimum NaCl for growth (M) | 0.34–0.68 | 0.43 | 0.34–0.51 | 0.4–0.6 | 0.4–0.6 | 0.4–0.6 |
| Temperature range for growth (°C) | 4–42 | 10–30 | 10–45 | 30–43 | Mesophilic | Mesophilic |
| Optimum temperature for growth (°C) | 37 | 16 | 23–35 | 39 | 30 | 25–30 |
| pH range for growth | 5.5–10.5 | 5.5–9.5 | 7.5–9 | 7.5–10 | 8.5–10.4 | 8–10 |
| Optimum pH for growth | 7.0–8.0 | 7.0–9.5 | 8.2 | 9 | 10 | 8.5–9.5 |

| Characteristics | 1 | 2 | 3 | 4 | 5 | 6 |
|-----------------|---|---|---|---|---|---|
| Cell size (µm)  | 0.50–1.06×1.00–2.27 | 0.80–1.20×1.20–4.00 | 1.0×1.5 | 0.8–1×1.1–1.5 | 0.5–0.8×0.8–2.2 | 0.5–0.7×1.2–1.7 |
| Cell shape      | Short rod | Rod | Short rod | Short rod | Rod with elongated ends | Short rod |
| NaCl range for growth (M) | 0–2.05 | 0–0.68 | 0.17–1.37 | 0.17–0.51 | 0.1–2 | 0–1.37 |
| Optimum NaCl for growth (M) | 0.34–0.68 | 0.43 | 0.34–0.51 | 0.4–0.6 | 0.4–0.6 | 0.4–0.6 |
| Temperature range for growth (°C) | 4–42 | 10–30 | 10–45 | 30–43 | Mesophilic | Mesophilic |
| Optimum temperature for growth (°C) | 37 | 16 | 23–35 | 39 | 30 | 25–30 |
| pH range for growth | 5.5–10.5 | 5.5–9.5 | 7.5–9 | 7.5–10 | 8.5–10.4 | 8–10 |
| Optimum pH for growth | 7.0–8.0 | 7.0–9.5 | 8.2 | 9 | 10 | 8.5–9.5 |

| Utilization as sole carbon and energy source: | | | | | | |
|---------------------------------------------|---|---|---|---|---|---|
| Pyruvate | + | + | + | + | + | + |
| Aspartate | + | + | + | + | + | + |
| Succinate | + | + | + | + | + | + |
| Fructose | – | + | + | + | + | + |
| Glutamate | – | + | + | + | + | + |
| Citrate | – | + | + | + | + | + |
| Major polar lipids** | DPG, PG, PE, PC, APL, L1 | DPG, PG, PE, PC | ND | ND | ND | ND |
| G+C content (mol%) | 66 | 61 | 60 | 59 | 62 | 59 |

Table 2 Overall genome relatedness index (%) of strain IM2376T with the closely related species within the family Rhodobacteraceae

| Strain | isDDH | ANI | AAI |
|--------|-------|-----|-----|
| Rhodobaca barguzinensis VKM b-2406T | 20.9 | 73.73 | 69.25 |
| Rhodobaca bogoriensis LBB1T | 20.9 | 73.87 | 69.22 |
| Roseibaca ekhonensis EL-50T | 19.4 | 73.51 | 66.51 |
| Roseinatronobacter thiooxidans DSM 13087T | 19.6 | 74.06 | 68.65 |
| Roseinatronobacter monicus ROS 35T | 19.8 | 73.76 | 68.78 |

** DPG, diphostatidylglycerol; PG, phosphatidyl glycerol; PE, phosphatidyl ethanolamine; PC, phosphatidyl choline; APL, unidentified aminophospholipid, L1, unidentified lipid. ND: no data. +, positive; -, negative

Rhodobaca bogoriensis LBB1T (96.2%), and Pararhodobacter aggregans D1-19T (96.1%). The OrthoANI and isDDH values between strain IM2376T and these reference strains were 73.5–74.1% and 19.4–20.9%, respectively (Table 2). These values were lower than the threshold values for the species boundary, i.e., 95–96% for ANI and 70% for isDDH (Goris et al. 2007; Meier-Kolthoff et al. 2013; Richter and Rosselló-Móra 2009). Besides, the AAI values (66.5–69.3%) were between 60% and 80% in the specified range of the genus-level boundary (Luo et al. 2014). The ML trees based on 16S rRNA sequences and 120 conserved single-copy genes from the whole-genome sequences showed that strain IM2376T formed a distinct clade (bootstrap value > 75%, Fig. 1a, b), separated from Roseibaca ekhonensis EL-50T, R. bogoriensis LBB1T, Rhodobaca barguzinensis VKM B-2406T, R. thiooxidans DSM 13087T, and Roseinatronobacter monicus ROS 35T. The NL and ME trees also supported the stability of the ML trees (bootstrap value > 75%, Fig. S3a, b, and Fig. S4a, b). The phenotypic, chemotaxonomic, and phylogenetic properties suggested that strain IM2376T represented a novel species of a new genus within the family Rhodobacteraceae, for which the name Rhabdonatronobacter sediminivivens gen. nov., sp. nov. was proposed.
Description of *Rhabdonatronobacter* gen. nov.

*Rhabdonatronobacter* (Rhab.do.na.tro.no.bac ter. Gr. fem. n. rhabdos, rod; N.L. neut. n. natron, soda, sodium carbonate (derived from the Arabic n. natrun or natron); N.L. masc. n. bacter, short rod; N.L. masc. n. Rhabdonatronobacter, short rod from soda lake).

Cells are Gram-stain negative, non-motile, short rod, or oval. The major respiratory quinone is Q-10. The major fatty acids are C_{18:1}ω7c and iso-C_{16:0}. The major polar lipids are diphosphatidylglycerol (DPG), phosphatidylglycerol (PG), and phosphatidylcholine (PC). According to 16S rRNA sequences similarity analysis, the genus belongs to the family *Rhodobacteraceae*, order *Rhodobacterales*, class Alphaproteobacteria. The type species is *Rhabdonatronobacter sediminivivens*.

Description of *Rhabdonatronobacter sediminivivens* sp. nov.

*Rhabdonatronobacter sediminivivens* (se.di.mi.ni.vi’ven.s. L. neut. n. sedimeninis, sediment; L. pres. part. vivens, living; N.L. part. adj. sediminivivens, living in the sediment).

The cells are short rod or oval, non-motile, without flagellum. The cells are Gram-stain negative. Colonies on optimum agar plate are pink, circular, convex, smooth-edged, and of 1.0–2.0 mm diameter. The optimum condition for growth is 0.34–0.68 M (range of 0–2.05 M) NaCl, 37 °C (range of 4–42 °C), pH 7.0–8.0 (range of 5.5–10.5). The oxidase and catalase activity are positive. The hydrolysis of gelatin, Tween 80, and casein is positive. Starch hydrolysis is negative. Nitrate and nitrite reduction are positive. H₂S is produced while indole is not. No urease activity. The OPNG and VP test is positive. The following compounds are utilized as the sole carbon and energy source: galactose, trehalose, mannitol, D-xylose, D-maltose, sucrose, D-glucose, D-mannose, L-rhamnose, arabinose, cellobiose, glycerol, acetate, malate, pyruvate, DL-lactate, succinate, histidine, cysteine, isoleucine, aspartate, while starch, lactose, fructose, sorbose, sorbitol, fumarate, citrate, ornithine, arginine, glutamate, glycine, valine, lysine, and aspartate were not used. The major fatty acids are composed of C_{18:1}ω7c (64.9%), iso-C_{16:0} (16.3%), and C_{16:1}ω6c/C_{16:1}ω7c (6.0%). The major quinones are ubiquinone Q-10 (94.9%) and Q-11 (5.1%). The major polar lipids are diphosphatidylglycerol, phosphatidylglycerol,
phosphatidylethanolamine, phosphatidyglycerol, and one unknown aminophospholipid. Phospholipids are also detected, but no glycolipid is found. The genomic DNA G + C content of the type strain is 66 mol% (calculated from the genome sequence).

The type strain IM2376T (=CGMCC 1.17852T = KCTC 92134T) was isolated from a soda lake.

The GenBank accession number for the 16S rRNA gene sequence is MW750412. The whole-genome has been deposited in GenBank under the accession number JACBXS000000000.

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Author contributionsHX designed and supervised the study. HZ, DZ, SZ, QX and JZ collected the samples. QX isolated the strain. HZ and MY performed the microbial culture and identification. HZ, DZ and SZ performed bioinformatic and statistical analyses. HZ and DZ prepared the figures and tables. HZ drafted the manuscript, and then HX, DZ, QX and SK participated in revisions. All the authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

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