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Sandaracinobacteroides sayramensis sp. nov., a yellow-pigmented bacterium isolated from lake water

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Abstract

A Gram-negative, non-motile, facultatively anaerobic, rod-shaped bacterium, designated strain RS1-74^T, was isolated from the surface water of Sayram Lake, Xinjiang Uygur Autonomous Region, China. The strain was able to grow optimally at 30 °C and pH 7.0–7.5, and in the presence of 0–0.5% (v/w) NaCl. Catalase and oxidase activities were present. H_2S was produced. Chemotaxonomic analysis showed Q-10 was the sole respiratory quinone. The polar lipids were composed of phosphatidylethanolamine, diphosphatidylglycerol, two glycolipids, phosphatidylglycerol, sphingoglycolipid and two unidentified lipids. Summed feature 3 ($C_{16:1}\,\omega7c$ and/or $C_{16:1}\,\omega6c$) and summed feature 8 ($C_{18:1}\,\omega7c$ and/or $C_{18:1}\,\omega6c$) were the predominant fatty acids. Phylogenetic analysis based on 16S rRNA gene sequence showed that strain RS1-74^T was closely related to '*Sandaracinobacter neustonicus*' JCM 30734 (98.65%), '*Sandaracinobacter sibiricus*' RB16-17 (98.42%) and *Sandaracinobacteroides hominis* SZY PN-1^T (97.09%). The genomic DNA G+C content was 66.45mol%. The average nucleotide identity and DNA–DNA hybridization values among the genomes of strain RS1-74^T and '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T were 78.2 and 77.22%, and 22.2 and 20.40%, respectively. Based on the physiological, biochemical, phylogenetic and genomic data, strain RS1-74^T represents a novel species within the genus *Sandaracinobacteroides*, for which the name *Sandaracinobacteroides sayramensis* sp. nov. is proposed, with type strain RS1-74^T (=KCTC 82674^T=MCCC 1K06282^T).

The genus *Sandaracinobacter* [1] belongs to the family *Sphingosinicellaceae*, order *Sphingomonadales*, class *Alphaproteobacteria*, phylum *Pseudomonadota* and was first proposed and emended by Yurkov *et al.* [1, 2]. At the time of writing (October 2022), The genus *Sandaracinobacter* contains two species: '*Sandaracinobacter sibiricus*' RB16-17^T (formerly *Erythromicrobium sibiricum*) and '*Sandaracinobacter neustonicus*' JCM 30734 [3]. They were isolated from freshwater microbial mats in hydrothermal vents and sea microlayer water, respectively. Members of the genus *Sandaracinobacter* are Gram-negative and strictly aerobic or facultatively anaerobic. Cells contain carotenoid pigments, are catalase- and oxidase-positive, and reproduce by binary division. They contain the quinones Q-9, Q-10, and Q-11, or sole quinone Q-10.

The novel genus named *Sandaracinobacteroides* was proposed by Qu *et al.* [4, 5]. Cells of the type strain of the type species *Sandaracinobacteroides hominis* SZY PN-1^T are rod-shaped and yellow-pigmented and were isolated from a human skin sample. Based on the results of phenotypic, phylogenetic and genomic analyses, Qu *et al.* proposed that *Sandaracinobacteroides* resembled and was closely related to the genus *Sandaracinobacter*. The aim of the present work is to determine the taxonomic position of novel strain RS1-74^T, which was isolated from a cold-water lake, where environmental conditions were characterized by low temperature, low nutrients and strong UV radiation.

ISOLATION AND ECOLOGY

The surface lake water sample was collected from Sayram lake (44° 29′ N 81° 10′ E), Xinjiang Uygur Autonomous Region, north-west China, in August 2019. The sample was spread on Reasoner's 2A (R2A) agar medium [6], and incubated at 30 °C for

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Keywords: Alphaproteobacteria; Phylogenetic analysis; *Sandaracinobacteroides*; Sayram lake; whole genome sequencing.
Abbreviations: ANI,, average nucleotide identity ;; dDDH,, digital DNA-DNA hybridization;; KEGG,, Kyoto Encyclopedia of Genes and Genomes;; ND,, no data available;.
The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain RS1-74^T is MW564019. The GenBank/EMBL/DDBJ accession number for draft genome sequence of strain RS1-74^T is JAKLSQ000000000.
Four supplementary figures and two supplementary tables are available with the online version of this article.

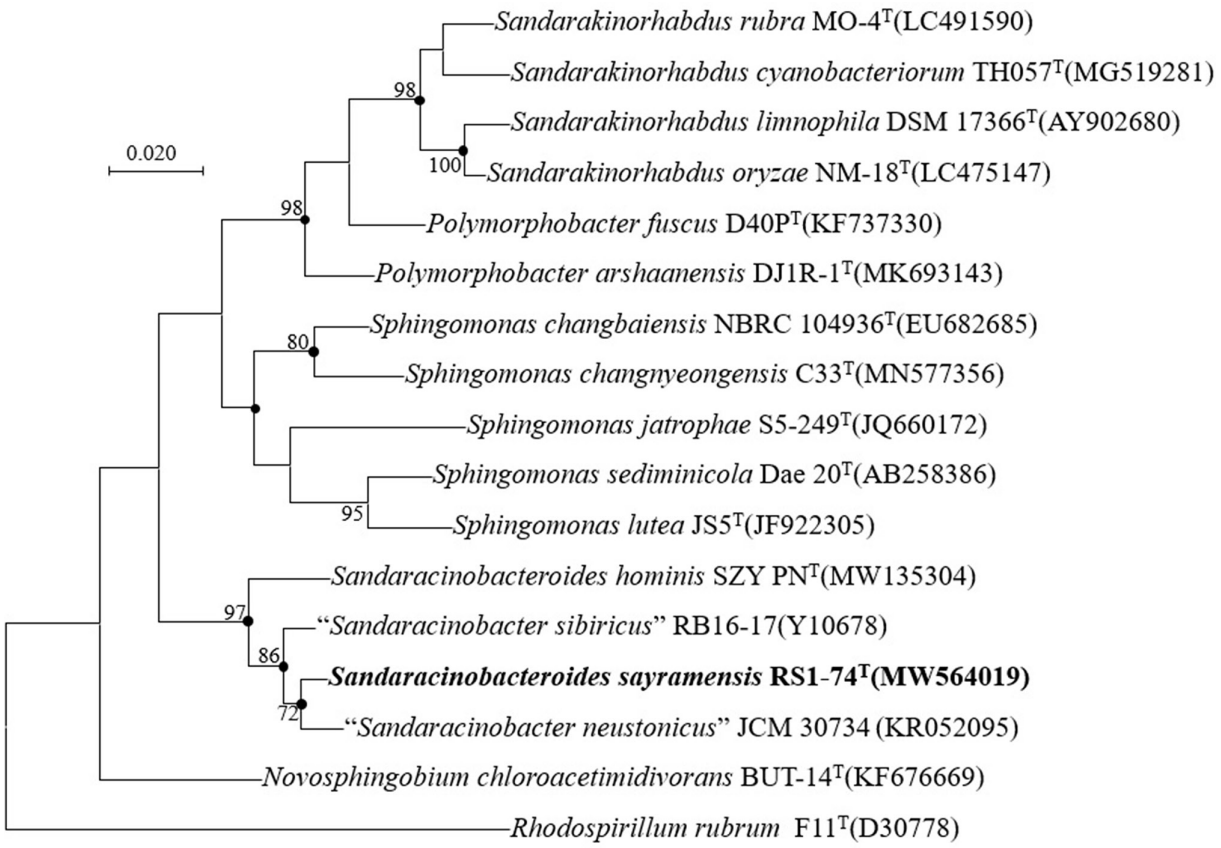

Fig. 1. Maximum-likelihood phylogenetic tree based on 16S rRNA gene sequences showing the relationships between RS1-74^T and related taxa. Bootstrap was expressed higher than 50% at the branch points. Filled circles indicate branches that were recovered with all three methods (neighbour-joining, maximum-likelihood and maximum-parsimony). Bar, 0.02 sequence divergence. *Rhodospirillum rubrum* F11^T (D30778) was used as an outgroup.

2 weeks. A yellow round colony was designed as RS1-74^T. Strain RS1-74^T was purified by consecutively streaking and stored in R2A medium with 30% (v/v) glycerol at −80 °C for further study.

16S rRNA GENE PHYLOGENY

Genomic DNA was extracted using the Bacterial Genome DNA Rapid Extraction Kit (Dongsheng Biotech) based on the manufacturer's instructions. PCR amplification of the 16S rRNA gene was performed as described by Xu *et al.* [7]. The almost-complete 16S rRNA gene sequence (1473 bp) of strain RS1-74^T was compared with closely related sequences of reference organisms via the NCBI website (www.ncbi.nlm.nih.gov/BLAST) and the 16S rRNA gene sequences of similar type strains were downloaded from the EzBioCloud website (www.ezbio-cloud.net/identify) [8]. The results showed that strain RS1-74^T had the highest 16S rRNA gene similarity of 98.65% to '*Sandaracinobacter neustonicus*' JCM 30734 and relatively high similarities of 98.42 and 97.09% to '*Sandaracinobacter sibiricus*' RB16-17 and *Sandaracinobacteroides hominis* SZY PN-1^T. Phylogenetic analysis based on 16S rRNA gene sequences was conducted with the MEGA X program package [9], using the neighbour-joining [10], maximum-parsimony [11] and maximum-likelihood [12] methods with Kimura two-parameter model [13]. Bootstrap analysis was performed with 1000 replications [14]. *Rhodospirillum rubrum* F11^T (D30778) was selected as an outgroup. The maximum-likelihood phylogenetic tree (Fig. 1) showed that RS1-74^T formed a monophyletic group with '*Sandaracinobacter neustonicus*' JCM 30734, '*Sandaracinobacter sibiricus*' RB16-17 and *Sandaracinobacteroides hominis* SZY PN-1^T. This topology was also supported by the neighbour-joining and maximum parsimony trees. Based on the phylogenetic analysis, strain RS1-74^T could be identified as a representative strain of a novel species in the genus *Sandaracinobacteroides*. '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T were used as experimental control type strains, and '*Sandaracinobacter neustonicus*' JCM 30734 was obtained from JCM (Japan Collection of Microorganisms). *Sandaracinobacteroides hominis* SZY PN-1^T was provided by Qu *et al.* [4]. The experimental data of strain '*Sandaracinobacter sibiricus*' RB16-17 were from Yurkov [15].

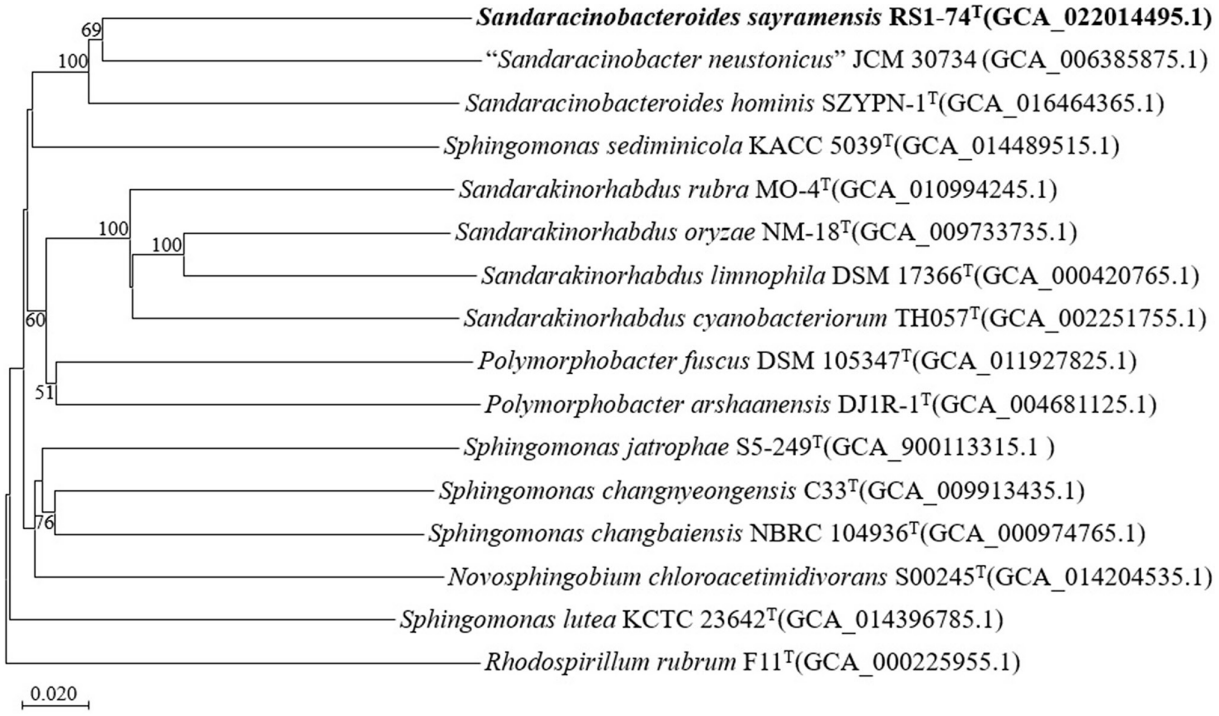

Fig. 2. Phylogenomic tree of strain RS1-74^T and its closest neighbours. Tree inferred with FastME 2.1.6.1 [32] from GBDP distances calculated from genome sequences. The branch lengths are scaled in terms of GBDP distance formula d_5. The numbers above branches are GBDP pseudo-bootstrap support values>50% from 100 replications, with average branch support of 57.9%. The tree was rooted at the midpoint [33].

GENOME FEATURES

The genome sequence of strain RS1-74^T was obtained using Solexa PE150 sequencing technology and the HiSeq platform (Novogene). The sequencing data was assembled and the genome annotation was performed using the gcType online server (http://gctype.wdcm.org/index) [16]. The online tool BlastKOALA (www.kegg.jp/blastkoala/) [17] was used to reveal the metabolic pathways. The average nucleotide identity (ANI) values according to the minimal standards proposed by Chun *et al.* [18] were calculated using the ANI Calculator (http://enveomics.ce.gatech.edu/ani/). Digital DNA–DNA hybridization (dDDH) values were calculated online by using the Genome-to-Genome Distance Calculator (GGDC 3.0, http://ggdc.dsmz.de/distcalc2.php) [19] with default settings. The closest neighbours' genomes were downloaded from the NCBI database (www.ncbi.nlm.nih.gov/genome/). The genome of strain RS1-74^T was submitted to the Type (Strain) Genome Server (https://tygs.dsmz.de) and whole genome-based taxonomic analysis was performed according to the manufacturer's instructions [20] in order to obtain the phylogenomic tree.

The genome sequence generated 3758165 bp of clean data with 99.91% completeness and 0.65% contamination. The G+C content of strain RS1-74^T was 66.45mol% from whole-genome sequence data. The ANI values of RS1-74^T with '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T were 78.20 and 77.22%, far lower than the ANI species identification threshold (94–96%) [21]. The digital DDH values between strain RS1-74^T and '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T were 22.2 and 20.40%, also below the 70% standard for the description of prokaryotic species [22]. The whole-genome sequence-based (Fig. 2) and whole-proteome-based phylogenetic trees (Fig. S3, available in the online version of this article) showed that strain RS1-74^T clustered with the rest of the *Sandaracinobacteroides* species and that it shared a common ancestor with '*Sandaracinobacter neustonicus*' JCM 30734, therefore indicating that strain RS1-74^T represents novel species of gene *Sandaracinobacteroides*.

For gene function prediction, the obtained genome sequences were annotated by the Rapid Annotation of microbial genomes using Subsystem Technology (RAST) for further comparative analyses. The gene content of strain RS1-74^T and reference strains had some genes in common and some differences (Table S6). As the results of KEGG analysis, strain RS1-74^T and reference strains '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T had 50, 55 and 57 complete pathways, respectively, which included carbohydrate metabolism, energy metabolism, lipid metabolism, nucleotide metabolism, amino acid metabolism, metabolism of cofactors and vitamins, and bio-synthesis of terpenoids and polyketides. Strain RS1-74^T had putative gene clusters for cobalamin, cobalamin, phenylalanine, and tyrosine biosynthesis. Meanwhile, the dTDP-L-rhamnose

and tryptophan biosynthesis pathway was present in RS1-74^T and '*Sandaracinobacter neustonicus*' JCM 30734, but absent from *Sandaracinobacteroides hominis* SZY PN-1^T (Fig. S5).

PHYSIOLOGY AND CHEMOTAXONOMY

Cell size, shape and flagellum were studied using transmission electron microscopy (JEM-1230, JEOL) after incubating on R2A medium at 30 °C for 5 days. Motility was assessed in R2A medium with 0.5% agar for 2 weeks. The growth temperature was assessed range at 4, 15, 20, 25, 30, 37, 42 and 45 °C. The pH range for growth was examined between pH 5.0 and 10.5 (at increments of pH 0.5) using biological buffers MES (for pH 5.5 and 6.0), PIPES (for pH 6.5 and 7.0), Tricine (for pH 7.5–8.5) and CAPSO (for pH 9.0–10.0) at a concentration of 50 mM. The range of NaCl concentration for growth was studied using R2A medium containing 0, 0.5, 1.0, 1.5, 2, 3, 4, 5, 7.5, 10 and 12 NaCl (%, w/v) according to Chen *et al.* [23]. Hydrolysis of soluble starch (1%, w/v), cellulose (0.1%, w/v) and 1% (v/v) Tweens (40, 60, 80) were determined as described by Xamxidin *et al.* [24]. H_2S production was tested in a liquid medium with added 0.5% (w/v) thiosulphate. Anaerobic growth was tested with the AnaeroPack System (Mitsubishi Gas Chemical) on R2A plates supplemented with $NaNO_3$ (20 mM), $NaNO_2$ (10 mM), Na_2SO_3 (5 mM), $Na_2S_2O_3$ (20 mM) or Na_2SO_4 (20 mM) as growth factors over 15 days, respectively. Acid production was tested using marine oxidation/fermentation medium [25] supplemented with a final concentration of 1.0% (w/v) substrates. The results were read after 2 weeks of cultivation. Biochemical characteristics were determined using API 20NE, API ZYM strips (all from bioMérieux), and the GEN III MicroPlate (Biolog) according to the manufacturers' protocols. Flexirubin-type pigments were investigated by using the colour shift test with a 20% (w/v) KOH solution [26]. Pigments were extracted from 5-day-old cultures using a methanol–acetone mixture (7:2, v/v). Components of the pigments were scanned for optical absorbance in SP-756P and using a UV/Vis scanning spectrophotometer (Shanghai Spectrum Instruments). Detection of pigmentation and bacteriochlorophyll *a* was according to Xu *et al.* [27].

For analysis of the whole-cell fatty acid composition, strain RS1-74^T and the reference strains were cultured in R2A medium at 30 °C for 5 days, centrifuged, and freeze-dried. Fatty acids were then analysed according to the standard protocol of the Microbial Identification System (MIDI). The respiratory quinones were extracted using chloroform–methanol (2:1, v/v) and identified using the HPLC-MS system (Agilent 1200) [28]. Polar lipids were prepared as described by Kates *et al.* [29], separated by two-dimensional TLC, and identified as described by Minnikin *et al.* [30] using spray reagents specific for each one according to Liu *et al.* [31].

In conclusion, the predominant cellular fatty acids (>10% of the total fatty acids) of strain RS1-74^T were summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*, 10.3%) and summed feature 8 ($C_{18:1}$ *ω7c* and/or $C_{18:1}$ *ω6c*, 71.0%). Bacteriochlorophyll *a* was not detected but the carotenoid pigment was present in both tested strains. The sole respiratory quinone of strain RS1-74^T was Q-10, which was consistent with the respiratory quinone of the reference strains '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T, and in line with all other members of the family *Sphingomonadaceae*. The results showed that the polar lipids detected in strain RS1-74^T mainly contained phosphatidylethanolamine (PE), diphosphatidylglycerol (DPG), sphingoglycolipid (SGL), two unidentified glycolipids (GL1–2), phosphatidylglycerol (PG) and two unidentified polar lipids (L1–2) (Fig. S2). Strain RS1-74^T, '*Sandaracinobacter neustonicus*' JCM 30734 and *Sandaracinobacteroides hominis* SZY PN-1^T exhibited similar polar lipid profiles, and they all had PE, PG, SGL and several unidentified lipids. DPG was not detected in '*Sandaracinobacter neustonicus*' JCM 30734; furthermore, unidentified aminolipids and phospholipids were detected in this strain. In addition, *Sandaracinobacteroides hominis* SZY PN-1^T contained a different sphingoglycolipid (SGL2) from the other strains. Strain RS1-74^T differed from the reference strains primarily in the presence and proportions of some minor unidentified polar lipids.

In terms of genome features, the DNA G+C contents of '*Sandaracinobacter neustonicus*' JCM 30734, '*Sandaracinobacter sibiricus*' RB16-17 and *Sandaracinobacteroides hominis* SZY PN-1^T were 65.31, 68.5 and 65.0 mol%, respectively, and similar to strain RS1-74^T (66.45 mol%). Peaks in absorption spectra for the cellular pigments are observed at 397, 450 (major peak) and 470 nm. The results indicated the presence of carotenoids in the cells of strains RS1-74^T and '*Sandaracinobacter neustonicus*' JCM 30734, similar to *Sandaracinobacteroides hominis* SZY PN-1^T. Bacteriochlorophyll *a* was absent, contrary to '*Sandaracinobacter sibiricus*' RB16-17. Flexirubin-type pigments were not detected in any of the strains. Strain RS1-74^T is distinguishable from the type strains of its closely related species by phenotypic characteristic differences, such as NaCl tolerance, pH range (optimum) for growth, hydrolysis of starch and Tweens 80 and 60, and positive catalase and oxidase activities, enzyme activities in API tests, utilization of substrates, and acid production (Table 1). Compared to the reference strains, strain RS1-74^T had some differences in the percentage of some fatty acids (Table S4); for example, the content of $C_{16:0}$ 2-OH in strain RS1-74^T was significantly higher than that of the reference strains. Consequently, based on the phenotypic, chemotaxonomic, phylogenetic and whole-genome results, strain RS1-74^T represents a novel taxonomic unit of the genus *Sandaracinobacteroides*, for which the name *Sandaracinobacteroides sayramensis* sp. nov.is proposed.

Table 1. Differential phenotypic characteristics of strain RS1-74^T and its related species

Strains: 1, RS1-74^T (this study); 2, '*Sandaracinobacter neustonicus*' JCM 30734 (this study); 3, *Sandaracinobacteroides hominis* SZY PN-1^T (this study and [4]). +, Positive reaction; –, negative reaction; ND, no data.

Characteristic	1	2	3
Isolation source	Lake water	Seawater	Human skin
Salt tolerance (%, w/v) (optimum)	0.5–1.5 (0–0.5)	0–1.0 (0.5–1.0)	0–1.0 (0)
pH range (optimum) for growth	7.5 (6–10)	6.5–7.0 (6–8)	6.0–8.0 (7.0)
Oxidase activity	+	+	–
Hydrolysis of:			
Starch	–	+	+
Gelatin	–	+	–
Tween 60	+	+	ND
Tween 80	–	+	–
H_2S production	+	–	–
Acid production from:			
D-Fructose	–	+	
Maltose	–	+	+
D-Ribose	–	+	–
D-Xylose	+	+	–
Glucose	–	+	–
Galactose	–	–	–
Utilization of:			
D-Fructose	+	–	–
D-Xylose	–	+	–
Trehalose	–	–	–
Citric acid	–	–	–
Sucrose	–	–	–
API 20NE tests:			
Arginine dihydrolase	–	+	–
Hydrolysis (β-glucosidase) aesculin	+	+	+
Assimilation of *N*-acetylglucosamine	+	–	–
Assimilation of trisodium citrate	+	–	–
API ZYM tests:			
Alkaline phosphatase	+	+	+
Valine arylamidase	+	–	–
β-Glucosidase	+	–	+
Major polar lipids	PE, PG, DPG, SGL1, GL (1–2), L (1–2)	PE, PG, SGL, AL, PL (1–2), L	PE, PG, DPG, L (1–7), GL (1–4) SGL (1–2)
DNA G+C content (mol%, by genome analysis)	66.45	65.31	65.0

* AL, aminolipid; PE, phosphatidylethanolamine; DPG, diphosphatidylglycerol; GL, glycolipid; PG, phosphatidylglycerol; PL, phospholipid; SGL, sphingoglycolipid; L, unidentified lipid.

DESCRIPTION OF *SANDARACINOBACTEROIDES SAYRAMENSIS* SP. NOV.

Sandaracinobacteroides sayramensis (say.ram.en'sis. N.L. masc. adj. *sayramensis*, referring to the Sayram lake in China, from where the type strain was isolated).

A Gram-negative bacterium with rod-shaped cells (1.3–2.0 µm long and 0.8–1.1 µm wide), non-motile and flagellated (Fig. S1). After 5 days of incubation on R2A medium, bright yellow round colonies of 1–2 mm in diameter with whole colony edge and smooth surface are observed. In R2A medium, NaCl concentration, pH and temperature growth ranges are 0–1.5% (w/v), pH 6.0–10.5 and 4–40 °C, respectively. Optimum growth occurrs with 0–1.5% (w/v), at pH 7.0–7.5 and at 30 °C. The type strain has oxidase and catalase activity, and produces H_2S from thiosulphate. Hydrolyses tyrosine, Tweens 40 and 60, but not Tween 80, gelatin, starch or CM-cellulose. No anaerobic growth occurs on R2A supplemented with potassium nitrate sodium nitrite and sodium sulphite, but growth under anaerobic conditions with sodium sulphate and sodium thiosulphate. In the API ZYM system, activities of alkaline phosphatase, leucine arylamidase, valine arylamidase, trypsin, cystine arylamidase, α-chymotrypsin, acid phosphatase, naphthol-AS-BI-phosphohydrolase, β-galactosidase, β-glucosidase and *N*-acetyl-β-glucosaminidase are present, but activities of esterase (C4), esterase lipase (C8), lipase (C14), α-galactosidase, β-glucuronidase, α-glucosidase, α-mannosidase and α-fucosidase are absent. In API 20 NE tests, positive for the hydrolysis of aesculin (β-glucosidase), β-galactosidase, assimilation of D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetyl-glucosamine, maltose, potassium gluconate, adipic acid, malate and trisodium citrate, but negative for other results. Acids are produced from D-ribose and D-xylose. According to the Biolog GEN III MicroPlate test, positive results for *N*-acetyl-D-glucosamine, D-fructose, 1% sodium lactate, rifamycin SV, glycyl-L-proline, lincomycin, guanidine HCL, vancomycin, tetrazolium blue, nalidixic acid, potassium tellurite, β-hydroxy-D,L-butyric acid, propionic acid, acetic acid and aztreonam; weakly positive results for dextrin, D-fucose, D-galactose, D-glucose-6-PO_4, D-fructose-6-PO_4, gelatin, L-alanine, L-aspartic acid, L-glutamic acid, D-galacturonic acid, L-galactonic acid lactone, D-glucuronic acid, mucic acid, tetrazolium violet, methyl pyruvate, D-lactic acid methyl ester, lithium chloride, Tween 40 and acetoacetic acid, but negative results for maltose, trehalose, cellobiose, gentiobiose, sucrose, turanose, stachyose, raffinose, lactose, melibiose, methyl β-D-glucoside, D-salicin, *N*-acetyl-β-dmannosamine, *N*-acetyl-D-galactosamine, *N*-acetyl neuraminic acid, α-D-glucose, D-mannose, D-galactose, 3-methyl glucose, L-fucose, L-rhamnose, inosine, fusidic acid, D-serine, D-sorbitol, D-mannitol, D-arabitol, *myo*-inositol, glycerol, D-aspartic acid, D-serine, troleandomycin, minocycline, gelatin, L-alanine, L-arginine, L-histidine, L-pyroglutamic acid, L-serine, niaproof 4, pectin, D-gluconic acid, quinic acid, D-saccharic acid, *p*-hydroxyphenylacetic acid, L-lactic acid, citric acid, α-keto-glutaric acid, D-malic acid, L-malic acid, bromo-succinic acid, γ-amino-butryric acid, α-keto-butyric acid, formic acid, sodium butyrate, sodium bromate. The sole menaquinone is Q-10. Summed feature 3 ($C_{16:1}\omega7c$ and/or $C_{16:1}\omega6c$), summed feature 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$) are the predominant fatty acids (>10% of the total cellular fatty acids). The major polar lipids are diphosphatidylglycerol, two glycolipids, phosphatidylglycerol, phosphatidylethanolamine, sphingoglycolipid and two unidentified lipids (Fig. S2).

The type strain, RS1-74^T (=KCTC 82674^T=MCCC 1K06282^T), was isolated from lake water of Xinjiang Uygur Autonomous Region, China . The DNA G+C content of the type strain is 66.45mol%.

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

References

1. Yurkov VV, Gorlenko VM. *Erythrobacter sibiricus* sp. nov. a new freshwater aerobic species containing bacteriochlorophylla[J]. *microbiology* 1990.
2. Yurkov V, Stackebrandt E, Buss O, Vermeglio A, Gorlenko V, *et al*. Reorganization of the genus *Erythromicrobium*: description of "*Erythromicrobium sibiricum*" as *Sandaracinobacter sibiricus* gen. nov., sp. nov., and of "*Erythromicrobium ursincola*" as *Erythromonas ursincola* gen. nov., sp. nov. *Int J Syst Bacteriol* 1997;47:1172–1178.
3. Lee I, Jang GI, Cho Y, Yoon SJ, Pham HM, *et al*. *Sandaracinobacter neustonicus* sp. nov., isolated from the sea surface microlayer in the Southwestern Pacific Ocean, and emended description of the genus *Sandaracinobacter*. *Int J Syst Evol Microbiol* 2020;70:4698–4703.
4. Qu PH, Luo HM, Feng JH, Li S, Chen C, *et al*. *Sandaracinobacteroides hominis* gen. nov., sp. nov., isolated from human skin. *Arch Microbiol* 2021;203:5067–5074.
5. Oren A, Garrity GM. Valid publication of new names and new combinations effectively published outside the IJSEM. *Int J Syst Evol Microbiol* 2022;72:005260.
6. Reasoner DJ, Geldreich EE. A new medium for the enumeration and subculture of bacteria from potable water. *Appl Environ Microbiol* 1985;49:1–7.
7. Xu XW, Wu YH, Zhou Z, Wang CS, Zhou YG, *et al*. *Halomonas sacharevitans* sp. nov., *Halomonas arcis* sp. nov. and *Halomonas subterranea* sp. nov., halophilic bacteria isolated from hypersaline environments of China. *Int J Syst Evol Microbiol* 2007;57:1619–1624.

8. Kim O-S, Cho Y-J, Lee K, Yoon S-H, Kim M, *et al*. Introducing EzTaxon-e: a prokaryotic 16S rRNA gene sequence database with phylotypes that represent uncultured species. *Int J Syst Evol Microbiol* 2012;62:716–721.
9. Kumar S, Stecher G, Li M, Knyaz C, Tamura K. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Mol Biol Evol* 2018;35:1547–1549.
10. Saitou N, Nei M. The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* 1987;4:406–425.
11. Fitch WM. Toward defining the course of evolution: minimum change for a specific tree topology. *Syst Zool* 1971;20:406.
12. Felsenstein J. Evolutionary trees from DNA sequences: a maximum likelihood approach. *J Mol Evol* 1981;17:368–376.
13. Kimura M. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J Mol Evol* 1980;16:111–120.
14. Felsenstein J, Joseph F. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 1985;39:783–791.
15. Yurkov V. *Sandaracinobacter*. In: *Bergey's Manual of Systematics of Archaea and Bacteria*. 2015. pp. 1–5.
16. Wu L, Ma J. The Global Catalogue of Microorganisms (GCM) 10K type strain sequencing project: providing services to taxonomists for standard genome sequencing and annotation. *Int J Syst Evol Microbiol* 2019;69:895–898.
17. Kanehisa M, Sato Y, Morishima K. BlastKOALA and GhostKOALA: KEGG tools for functional characterization of genome and metagenome sequences. *J Mol Biol* 2016;428:726–731.
18. Chun J, Oren A, Ventosa A, Christensen H, Arahal DR, *et al*. Proposed minimal standards for the use of genome data for the taxonomy of prokaryotes. *Int J Syst Evol Microbiol* 2018;68:461–466.
19. Meier-Kolthoff JP, Carbasse JS, Peinado-Olarte RL, Göker M. TYGS and LPSN: a database tandem for fast and reliable genome-based classification and nomenclature of prokaryotes. *Nucleic Acids Res* 2022;50:D801–D807.
20. Meier-Kolthoff JP, Göker M. TYGS is an automated high-throughput platform for state-of-the-art genome-based taxonomy. *Nat Commun* 2019;10:2182.
21. Richter M, Rosselló-Móra R. Shifting the genomic gold standard for the prokaryotic species definition. *Proc Natl Acad Sci* 2009;106:19126–19131.
22. Moore WEC, Stackebrandt E, Kandler O, Colwell RR, Krichevsky MI, *et al*. Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. *Int J Syst Evol Microbiol* 1987;37:463–464.
23. Chen C, Han S, Zhu Z, Fu G, Wang R, *et al*. *Idiomarina mangrovi* sp. nov., isolated from rhizosphere soil of a mangrove *Avicennia marina* forest. *Int J Syst Evol Microbiol* 2019;69:1662–1668.
24. Xamxidin M, Wu YH, Jian SL, Zhou YD, Wang CS, *et al*. *Aquaticitalea lipolytica* gen. nov., sp. nov., isolated from Antarctic seawater. *Int J Syst Evol Microbiol* 2016;66:2657–2663.
25. Leifson E. Determination of carbohydrate metabolism of marine bacteria. *J Bacteriol* 1963;85:1183–1184.
26. Bernardet J-F, Nakagawa Y, Holmes B. Proposed minimal standards for describing new taxa of the family *Flavobacteriaceae* and emended description of the family. *Int J Syst Evol Microbiol* 2002;52:1049–1070.
27. Xu XW, Wu YH, Wang CS, Wang XG, Oren A, *et al*. *Croceicoccus marinus* gen. nov., sp. nov., a yellow-pigmented bacterium from deep-sea sediment, and emended description of the family Erythrobacteraceae. *Int J Syst Evol Microbiol* 2009;59:2247–2253.
28. Kroppenstedt RM. Separation of bacterial menaquinones by HPLC using reverse phase (RP18) and a silver loaded Ion exchanger as stationary phases. *J Liq Chromatogr* 1982;5:2359–2367.
29. Kates M, Lipidology T. *Isolation, Analysis and Identification of Lipids*. 2nd ed. Amsterdam: Elsevier; 1986.
30. Minnikin DE, O'Donnell AG, Goodfellow M, Alderson G, Athalye M, *et al*. An integrated procedure for the extraction of bacterial isoprenoid quinones and polar lipids. *J Microbiol Methods* 1984;2:233–241.
31. Liu Q, Xamxidin M, Sun C, Cheng H, Meng F-X, *et al*. *Marinobacter fuscus* sp. nov., a marine bacterium of Gammaproteobacteria isolated from surface seawater. *Int J Syst Evol Microbiol* 2018;68:3156–3162.
32. Lefort V, Desper R, Gascuel O. FastME 2.0: a comprehensive, accurate, and fast distance-based phylogeny inference program. *Mol Biol Evol* 2015;32:2798–2800.
33. Farris JS. Estimating phylogenetic trees from distance matrices. *Am Nat* 1972;106:645–668.