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ORIGINAL PAPER

Parerythrobacter lacustris sp. nov., a novel member of the family *Erythrobacteraceae* isolated from an inland alpine lake

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Abstract

A novel bacterium, designated as strain RS5-5^T, was isolated from lake water in northwestern China. Cells of the isolate were observed to be rod shaped and Gram stain negative. Its growth occurred at 4–37 ℃, pH 6.5–9.0 and in the presence of 0–5% (w/v) NaCl. Phylogenetic analysis based on 16S rRNA gene sequences showed that strain RS5-5^T was most closely related to *Qipengyuania sediminis* GDMCC 1.2497^T (97.5%), followed by *Erythrobacter dokdonensis* DSW-74^T (97.3%) and *Qipengyuania algicida* GDMCC 1.2535^T (97.0%). Phylogenomic analysis revealed that strain RS5-5^T formed a distinct branch with the genus *Parerythrobacter*. The sole quinone was ubiquinone-10, and the major fatty acids (≥ 10%) were unsaturated fatty acids including $C_{17:1}$ *ω6c*, summed feature 3 ($C_{16:1}$ *ω7c*/$C_{16:1}$ *ω6c*) and summed feature 8 ($C_{18:1}$ *ω7c*/$C_{18:1}$ *ω6c*). The polar lipids were phosphatidylethanolamine, diphosphatidylglycerol, phosphatidylglycerol, phosphatidylcholine, one unidentified sphingoglycolipid, three unidentified glycolipids, one unidentified aminoglycolipid, one unidentified aminolipid, two unidentified phospholipids and four unidentified polar lipids. Chemotaxonomic characteristics of strain RS5-5^T were coincident with those of the genus *Parerythrobacter* members. The average nucleotide identity, average amino acid identity and digital DNA–DNA hybridization values between strain RS5-5^T and two *Parerythrobacter* reference strains were in the ranges of 73.2–77.7%, 69.0–78.0% and 18.9–20.4%, respectively. The genomic DNA G + C content of strain RS5-5^T was 64.1%. The results of phenotypic, phylogenetic and genomic analyses suggested that strain RS5-5^T represents a novel species in the genus *Parerythrobacter*, for which the name *Parerythrobacter lacustris* sp. nov. is proposed. The type strain is RS5-5^T (= GDMCC 1.3163^T = KCTC 92277^T).

Keywords *Erythrobacteraceae* · *Alphaproteobacteria* · Whole genome sequencing · Phylogenetic analysis

Introduction

The genus *Parerythrobacter* belonging to the family *Erythrobacteraceae* was proposed by Xu et al. (2020) based on the core-genomic phylogeny, with two species *Erythrobacter jejuensis* and *Altererythrobacter lutipelagi* reclassified into the genus *Parerythrobacter* (https://lpsn.dsmz.de/genus/parerythrobacter). Members of the genus *Parerythrobacter* inhabit aquatic environments, such as seawater (Yoon et al. 2013) and tidal mudflat (Lee 2019). The cells of members of the genus *Parerythrobacter* are aerobic, rod shaped, Gram stain negative and non-motile. Genomic G + C contents of the genus *Parerythrobacter* are 60.2–60.6% calculated from genome sequences. The major polar lipids are diphosphatidylglycerol, phosphatidylglycerol, sphingoglycolipid, phosphatidylethanolamine and phosphatidylcholine, and the predominant isoprenoid quinone is ubiquinone-10 (Q-10). In

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this study, strain RS5-5^T was isolated from a surface water sample during an investigation of bacterial diversity in Sayram Lake located in northwestern China. Then a polyphasic taxonomic study including phenotypic, chemotaxonomic and genome-based approaches was applied to determine the taxonomic status of the strain RS5-5^T.

Materials and methods

Isolation of bacterial strain and culture conditions

The surface water sample was collected from Sayram Lake (81°04′E, 44°41′N), Xinjiang Uygur Autonomous Region, in August 2019. The sample was plated onto the surface of the R2A agar. After incubation for 2 weeks, one yellow-colored strain, designated as RS5-5^T, was picked and purified by subcultivation. Strain RS5-5^T was maintained in R2A broth with glycerol suspensions (20%, v/v) at − 80 °C for long-term preservation. *Parerythrobacter jejuensis* JCM 16677^T and *Parerythrobacter lutipelagi* NBRC 113275^T, obtained from the Japan Collection of Microorganisms (JCM) and the Biological Resource Center, National Institute of Technology and Evaluation (NBRC), were selected as reference strains.

16S rRNA gene sequence and phylogenetic analysis

Genomic DNA was extracted by using the bacterial genome DNA rapid extraction kit (Dongsheng Biotech, China, N1152) according to the manual, and the 16S rRNA gene was amplified and sequenced as described previously (Xu et al. 2007). The 16S rRNA gene sequence identity was analyzed by using the EzBioCloud database (https://www.ezbiocloud.net/). The 16S rRNA gene sequences of its relatives were obtained from GenBank and aligned by using CLUSTAL W (Thompson et al. 1994). The phylogenetic reconstructions were performed with MEGA X software (Kumar et al. 2018) based on three algorithms including maximum likelihood (Felsenstein 1981), maximum parsimony (Fitch 1971) and neighbor joining (Saitou and Nei 1987). The nucleotide substitution model was adopted by using the Kimura two-parameter model (Kimura 1980) and the bootstrap analysis was set as 1000 replications for obtaining confidence levels for the branch nodes (Felsenstein1985).

Genome sequencing and phylogenomic analysis

The draft genome of strain RS5-5^T was sequenced by Illumina sequencing technology and the HiSeq platform (Novogene Co., Ltd, Nanjing). The genome sequence was assembled using the gcType online server (Shi et al. 2021). Genomic annotation of strain RS5-5^T was carried out by using the Rapid Annotation using Subsystem Technology (RAST) platform (Overbeek et al. 2014), and genes involved in metabolic pathways were analyzed using the BlastKOALA (Kanehisa et al. 2016). The phylogenomic tree was constructed using the GTDBtk pipeline (Chaumeil et al. 2022; Parks et al. 2022). The average nucleotide identity (ANI) between strain RS5-5^T and the type strains *Parerythrobacter lutipelagi* NBRC 113275^T as well as *Parerythrobacter jejuensis* JCM 16677^T was calculated using EzBioCloud (https://www.ezbiocloud.net/, Chun et al. 2018). Average amino acid identity (AAI) was calculated using the Online tools of Genome-wide Identity Suite (Rodriguez-R and Konstantinidis 2016), and the digital DNA–DNA hybridization (*d*DDH) was determined by the Genome-to-Genome Distance Calculator (GGDC 3.0, https://ggdc.dsmz.de/ggdc.php#) with the recommended formula *2* (Meier-Kolthoff et al. 2022).

Phenotypic characteristics

Cellular morphology was observed using a transmission electron microscope (JEM1230, JEOL, Japan). The motility test was assessed by using R2A broth with 0.25% (w/v) agar for 2 weeks. The temperature range (4, 10, 15, 25, 30, 37, and 40 °C) for growth was determined in the R2A broth. Growth at different pH values (5.0–10.5 at 0.5 pH units interval) was measured using appropriate biological buffers at 50 mM concentration monohydrate for pH 5.0–6.0, 1,4-piperazinediethanesulfonic acid for pH 6.5–7.0, N-[tris(hydroxymethyl)methyl] glycine for pH 7.5–8.5, 3-(cyclohexylamino)-2-hydroxy-1-propanesulfonic acid for pH 9.0–10.5 in R2A broth at 25 ℃. The NaCl range for growth was tested at 0–7.5% (w/v) NaCl with the interval of 0.5% in the R2A broth. Oxidase and catalase activity was examined using the oxidase reagent kit (bioMérieux) and 3.0% (v/v) H_2O_2 solution. Hydrolysis of starch, gelatin, CM-cellulose (carboxymethyl cellulose) and Tweens 20, 40, 60 and 80 (1.0%, w/v) and production of H_2S were according to the methods described by Xamxidin et al. (2016). Pigments were extracted using acetone/methanol (7:2, v/v) and determined using 300–800 nm wavelength scanning (SP-756P UV/Vis scanning spectrophotometer, Shanghai Spectrum Instruments Co., Ltd). The flexirubin-type pigment was tested using the color change of the colonies when immersed in a 20% (w/v) KOH solution (Bernardet et al. 2002). Acid production was examined by MOF medium supplemented with 1% (w/v) alcohols or carbohydrates (Leifson 1963). The medium contained (per liter distilled water): 5 g NaCl, 2.5 g $MgCl_2{\cdot}2H_2O$, 1.0 g $MgSO_4{\cdot}7H_2O$, 0.5 g KCl, 0.25 g $CaCl_2$, trace $FeSO_4$, 0.5 g $(NH_4)_2SO_4$, 1.0 g casitone (Difco), 0.1 g yeast extract (Difco), 0.5 g Tris and 0.01 g phenol red (pH 8.0). Other physiological and biochemical tests were assessed using API 20NE, API ZYM kit (bioMérieux) and

GENIII Microplate (Biolog) according to the manufacturer's instructions.

Chemotaxonomic characterization

Cellular fatty acids of strains RS5-5^T, *Parerythrobacter lutipelagi* NBRC 113275^T and *Parerythrobacter jejuensis* JCM 16677^T were analyzed by the protocol of MIDI (method: TSBA6) with cells collected at the mid-exponential phase. Respiratory quinones of strain RS5-5^T were extracted from 400 mg freeze-dried cell material with chloroform/methanol (2:1, v/v), identified by TLC (thin layer chromatography) and then identified by an HPLC–MS system (Agilent 1200 and Thermo Finnigan LCQ DECA XP MAX mass spectrometer) (Minnikin et al. 1984). For polar lipid analyses, cells of strain RS5-5^T were collected and lyophilized following the cultivation in R2Abroth at 25 °C for 5 days, their polar lipids were extracted according to the procedure described by Minnikin et al. (1984), separated by two-dimensional TLC and identified by spraying reagents including molybdophosphoric acid, ammonium molybdate reagent, ninhydrin and α-naphthol–sulfuric acid (Tindall 1990).

Results and discussion

Genetic features and phylogenetic relationship

The 16S rRNA gene sequence identity analysis showed that strain RS5-5^T was closely related to *Qipengyuania sediminis* GDMCC 1.2497^T (97.5%) (Feng et al. 2015), *Erythrobacter dokdonensis* DSW-74^T (97.30%) (Yoon et al. 2006) and *Qipengyuania algicida* GDMCC 1.2535^T (97.0%) (Kristyanto et al. 2017; Xu et al. 2020). The phylogenetic relation of strain RS5-5^T needed to be further investigated by using additional analyses including the phylogenomic reconstruction and overall genome relatedness index calculation (Table S1).

The genomic size of strain RS5-5^T was 3.06 Mb with a total of 12 contigs and the G + C content was 64.1%. The genome of strain RS5-5^T contained 49 RNA genes (3 rRNA genes and 46 tRNA genes) and 3048 coding sequences. Genome annotation by RAST results showed that RS5-5^T with closely related strains shared many common subsystem features including membrane transport, stress response, respiration, metabolism of carbohydrates, DNA, RNA, protein, etc. (Table S2). In addition, the genomic G + C content of strain RS5-5^T was higher than that of *Parerythrobacter lutipelagi* NBRC 113275^T and *Parerythrobacter jejuensis* JCM 16677^T (60.2–60.6%).

The whole genome-based phylogeny tree reconstructed using GTDBtk showed that strain RS5-5^T formed a reliable clade with *Parerythrobacter lutipelagi* NBRC 113275^T, which branched from *Parerythrobacter jejuensis* JCM 16677^T (Fig. 1) Moreover, the AAI, ANI and *d*DDH values of strain RS5-5^T with *Parerythrobacter lutipelagi* NBRC 113275^T and *Parerythrobacter jejuensis* JCM 16677^T were 69.0–78.1%, 73.2–77.7% and 18.9–20.4%, respectively, which were lower than the thresholds for species delineation (Konstantinidis and Tiedje 2005; Goris et al. 2007; Richter and Rosselló-Móra 2009; Stackebrandt and Goebel 1994). Thus, it is strongly suggested that strain RS5-5^T could be classified as a novel species of the genus *Parerythrobacter*.

Biochemical features

Cells of strain RS5-5^T were rod shaped (0.4–0.6 μm × 1.0–1.6 μm), non-flagellated (Fig. S2) and Gram stain negative. Colonies of strain RS5-5^T were yellow, which was consistent with *Parerythrobacter lutipelagi* NBRC 113275^T and *Parerythrobacter jejuensis* JCM 16677^T. The temperature, pH and NaCl range for growth were 4–37 °C, 6.5–9.0 and 0–5% (optimum 25 °C, pH 8.0, 0%). Compared with two reference strains, strain RS5-5^T grew optimally in NaCl-free medium. Moreover, strain RS5-5^T could produce acids from cellobiose and xylan, which were different from *Parerythrobacter lutipelagi* NBRC 113275^T and *Parerythrobacter jejuensis* JCM 16677^T. Detailed results and other physiological and biochemical characteristics of strain RS5-5^T are given in the species description, and similarities and differences with reference strains are described in Table 1. All negative traits from API ZYM, API 20NE kits and acid production are listed in Table S4, and the unavailability of carbon sources (GENIII Microplate) is listed in Table S5.

Chemotaxonomic features

Q-10 was determined as the sole respiratory quinone for strain RS5-5^T, which is in accord with that found in members of the family *Erythrobacteraceae* (Xu et al. 2020). The dominant cellular fatty acids (> 10%) of strain RS5-5^T were $C_{17:1}$ *ω6c* and summed feature 8 ($C_{18:1}$ *ω7c*/$C_{18:1}$ *ω6c*), which were similar to *Parerythrobacter jejuensis* JCM 16677^T and *Parerythrobacter lutipelagi* NBRC 113275^T, while the amount percentages of $C_{17:1}$ *ω6c* (40.1%) and summed feature 8 in strain RS5-5^T were obviously different from those in *Parerythrobacter lutipelagi* NBRC 113275^T. Furthermore, the amount percentage of summed feature 3 in strain RS5-5^T was 16.7%, which was higher than in the *Parerythrobacter lutipelagi* NBRC 113275^T (6.2%) and *Parerythrobacter jejuensis* JCM 16677^T (3.4%). The detailed amount percentages of fatty acids are listed in Table S3. The polar lipid profiles of strain RS5-5^T and reference strains all included phosphatidylethanolamine (PE), phosphatidylglycerol (PG), diphosphatidylglycerol (DPG),

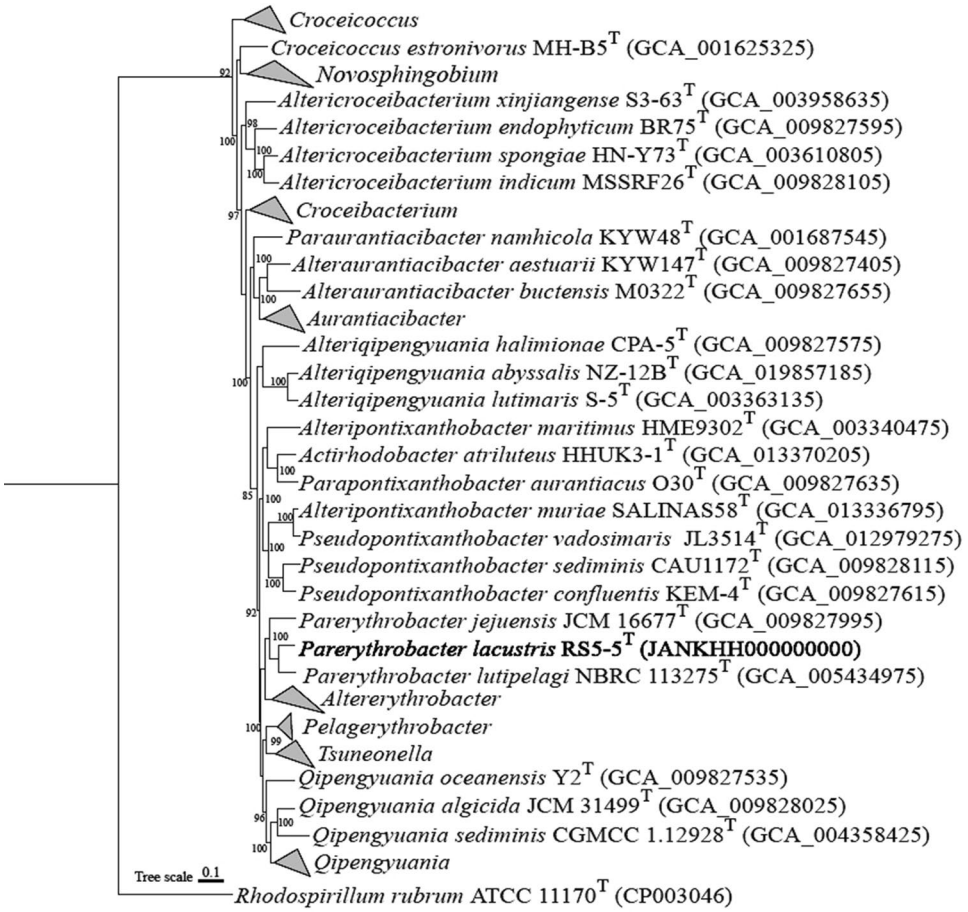

Fig. 1 The phylogenomic tree based on 120 marker gene sequences showing the relationship of strain RS5-5^T with representative members of the genus *Parerythrobacter*. *Rhodospirillum rubrum* ATCC 11170^T (CP 003046) was selected as the outgroup. Bar, 0.1 substitutions per nucleotide position. Bootstrap values shown for branches with more than 50% support. Visualization of phylogenetic tree using https://www.chiplot.online/tvbot.html

phosphatidylcholine (PC) and sphingoglycolipid (SGL). Two unidentified phospholipids (PL), three unidentified glycolipids (GL), one unidentified aminoglycolipid (AGL) and unidentified aminolipid (AL) were detected in strain RS5-5^T, but were absent in two reference strains (Fig.S3).

Conclusions

The genotypic, phylogenetic, chemotaxonomic and other phenotypic characteristics of strain RS5-5^T were closely related, but also different from *Parerythrobacter jejuensis* JCM 16677^T *and Parerythrobacter lutipelagi* NBRC 113275^T. Strain RS5-5^T should be classified within the genus *Parerythrobacter* as representing a novel species, for which the name *Parerythrobacter lacustris* sp. nov. is proposed.

Emended description of the genus *Parerythrobacter*

In addition to the characteristics described for the genus *Parerythrobacter* by Xu et al. (2020), some species do not necessarily require NaCl for growth. The summed feature 3 (C16:1 ω7*c*/C16:1 ω6*c*) is present as the major component. The DNA G+C contents range from 60 - 64% (by genome).

Description of *Parerythrobacter lacustris* sp. nov.

Parerythrobacter lacustris (la.cus'tris. N.L. masc./fem. adj. *lacustris*, referring to the site from which the type strain was isolated: from L. gen. masc. n. *lacus*, a lake).

Cells are Gram stain negative, non-motile, aerobic, rod shaped (0.4–0.6 μm in width and 1.0–1.6 μm in length) and non-spore-forming. Colonies are circular, convex, smooth, slimy and yellow after 5 days of incubation at 25 °C on R2A agar. Growth occurs at 4–37 °C, NaCl (0–5%, w/v) and pH 6.0–9.0, with optimal growth at 25 °C, 0% NaCl and pH 8.0. Cells are positive for oxidase and catalase, but negative for H_2S production; hydrolyze gelatin, tyrosine and starch, but not CM-cellulose and Tweens 20, 40, 60 and 80. Flexirubin-type pigments are absent, but carotenoid pigments are present. In the API 20NE tests, positive for hydrolysis of aesculin and gelatin, β-galactosidase (PNPG) activity, assimilation of glucose, maltose, adipic acid, malate and potassium gluconate and weakly positive for assimilation of arabinose, mannitol, trisodium citrate and phenylacetic acid. In the API ZYM kit, positive for alkaline phosphatase esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, cystine arylamidase and α-chymotrypsin activities, and weakly positive for lipase (C14), trypsin, acid phosphatase,

Table 1 Differential characteristics between strain RS5-5^T and closely related reference strains

Characteristic	1	2	3
Source	Lake water	Tidal mudflat[§]	Seawater[#]
Ranges and optimum for growth			
pH	6.5–9.0 (8.0)	6.0–10.0 (7.0)[§]	6.0–10.0 (7.0–8.0)[#]
Temperature (°C)	4–37 (25)	10–30 (30)[§]	15–37 (30)[#]
NaCl (w/v, %)	0–5 (0)	0.5–5 (0.5)[§]	2–5 (2–4)[#]
Hydrolysis of			
Tyrosine	+	−	+
Starch	+	−	+
Gelatin	+	+	−
Tween 80	−	+	+
API 20NE test			
Assimilation of D-glucose, L-maltose and potassium gluconate	+	−	−
API ZYM test			
Acid phosphatase	+	−	+
Cystine arylamidase	+	−	−
α-galactosidase	−	−	+
β-galactosidase and α-glucosidase	+	+	−
Acid production from			
Cellobiose	w	−	−
D-Glucose	−	+	+
D-Mannose	−	+	−
Xylan	+	−	−
DNA G+C content (%)	64.1	60.6	60.2

All data were obtained from this study unless stated otherwise. 1, RS5-5^T; 2, *Parerythrobacter lutipelagi* NBRC 113275^T; 3, *Parerythrobacter jejuensis* JCM 16677^T

+ positive, w weakly positive, − negative

[§]Data obtained from Lee (2019)

[#]Data obtained from Yoon et al. (2013)

naphthol-AS-BI-phosphohydrolase, β-galactosidase and α-glucosidase. Produce acid from xylan and cellobiose (weak), but not from a-lactose, fructose, mannitol, mannitol, maltose, raffinose, sorbose, sucrose, L-arabinose, D-glucose, D-galactose, D-mannose, D-ribose, L-rhamnose and D-xylose. Positive for GENIII Microplate substrates including D-serine, D-fructose-6-PO_4, glucuronamide, acetoacetic acid and acetic acid. The major quinone is ubiquinone 10 (Q-10), the major fatty acids (≥ 10%) were unsaturated fatty acids including $C_{17:1}$ $\omega6c$, summed feature 3 ($C_{16:1}$ $\omega7c$/$C_{16:1}$ $\omega6c$) and summed feature 8 ($C_{18:1}$ $\omega7c$/$C_{18:1}$ $\omega6c$), and the polar lipids were diphosphatidylglycerol, phosphatidylglycerol, sphingoglycolipid, phosphatidylcholine, phosphatidylethanolamine, one unidentified aminoglycolipid, three unidentified glycolipids, one unidentified aminolipid, two unidentified phospholipids and four unidentified polar lipids.

The type strain RS5-5^T (= KCTC 92277^T = GDMCC 1.3163^T) was isolated from a lake water sample collected from Sayram Lake, Xinjiang Uygur Autonomous Region, PR China. The genomic DNA G+C content of the type strain is 64.1%. The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequence and the genome sequence of strain RS5-5^T are OM267786 and JANKHH000000000, respectively.

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Author contributions MW and LX designed the experiments and guided the manuscript writing. MX and HD were responsible for the major experiments, data analysis and preparation of manuscripts. J-YW and WQ assisted in enzymatic experiments and determination of fatty acids and polar lipids experiment. All authors read and approved the manuscript.

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Data Availability All the data generated in this study have been included in this published article and its supplementary information files. The 16S rRNA gene and the whole-genome sequences of strain RS5-5^T have been deposited in the GenBank databases with the accession numbers OM267786 and JANKHH000000000 respectively.

Declarations

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

Bernardet JF, Nakagawa Y, Holmes B, Subcommittee on the taxonomy of flavobacterium and cytophaga-like bacteria of the international committee on systematics of prokaryotes (2002) Proposed minimal standards for describing new taxa of the family *Flavobacteriaceae* and emended description of the family. Int J Syst Evol Microbiol 52(3):1049–1070. https://doi.org/10.1099/00207713-52-3-1049

Chaumeil PA, Mussig AJ, Hugenholtz P, Parks DH (2022) GTDB-Tk v2: memory friendly classification with the genome taxonomy database. Bioinformatics 38(23):5315–5316. https://doi.org/10.1093/bioinformatics/btac672

Chun J, Oren A, Ventosa A, Christensen H, Arahal DR, da Costa MS, Rooney AP, Yi H, Xu XW, De Meyer S, Trujillo ME (2018) Proposed minimal standards for the use of genome data for the taxonomy of prokaryotes. Int J Syst Evol Microbiol 68(1):461–466. https://doi.org/10.1099/ijsem.0.002516

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17(6):368–376. https://doi.org/10.1007/BF01734359

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39(4):783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Feng XM, Mo YX, Han L, Nogi Y, Zhu YH, Lv J (2015) *Qipengyuania sediminis* gen. nov., sp. nov., a member of the family *Erythrobacteraceae* isolated from subterrestrial sediment. Int J Syst Evol Microbiol 65(10):3658–3665. https://doi.org/10.1099/ijsem.0.000472

Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. Syst Biol 20(4):406–416. https://doi.org/10.1093/sysbio/20.4.406

Goris J, Konstantinidis KT, Klappenbach JA, Coenye T, Vandamme P, Tiedje JM (2007) DNA–DNA hybridization values and their relationship to whole-genome sequence similarities. Int J Syst Evol Microbiol 57(1):81–91. https://doi.org/10.1099/ijs.0.64483-0

Kanehisa M, Sato Y, Morishima K (2016) BlastKOALA and GhostKOALA: KEGG tools for functional characterization of genome and metagenome sequences. J Mol Biol 428(4):726–731. https://doi.org/10.1016/j.jmb.2015.11.006

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol 16:111–120. https://doi.org/10.1007/BF01731581

Konstantinidis KT, Tiedje JM (2005) Towards a genome-based taxonomy for prokaryotes. J Bacteriol 187(18):6258–6264. https://doi.org/10.1128/-JB.187.18.6258-6264.2005

Kristyanto S, Lee SD, Kim J (2017) Porphyrobacter algicida sp. nov., an algalytic bacterium isolated from seawater. Int J Syst Evol Microbiol 67(11):4526–4533. https://doi.org/10.1099/ijsem.-0.002324

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35(6):1547. https://doi.org/10.1093/molbev/msy096

Lee SD (2019) *Altererythrobacter lutipelagi* sp. nov., isolated from a tidal mudflat, and emended description of the genus *Altererythrobacter*. Int J Syst Evol Microbiol 69(7):1980–1985. https://doi.org/10.1099/ijsem.0.003414

Leifson E (1963) Determination of carbohydrate metabolism of marine bacteria. J Bacteriol 85(5):1183–1184. https://doi.org/10.1128/jb.85.5.1183-1184.1963

Meier-Kolthoff JP, Carbasse JS, Peinado-Olarte RL, Göker M (2022) TYGS and LPSN: a database tandem for fast and reliable genome-based classification and nomenclature of prokaryotes. Nucleic Acids Res 50(1):D801–D807. https://doi.org/10.1093/nar/gkab902

Minnikin DE, Odonnell AG, Goodfellow M, Alderson G, Athalye M, Schaal A, Parlett JH (1984) An integrated procedure for the extraction of bacterial isoprenoid quinones and polar lipids. J Microbiol Methods 2(5):233–241. https://doi.org/10.1016/0167-7012(84)90018-6

Overbeek R, Olson R, Pusch GD, Olsen GJ, Davis JJ, Disz T, Edwards RA, Gerdes S, Parrello B, Shukla M, Vonstein V, Wattam AR, Xia F, Stevens R (2014) The SEED and the rapid annotation of microbial genomes using Subsystems Technology (RAST). Nucleic Acids Res 42(Database issue):D206–D214. https://doi.org/10.1093/nar/gkt1226

Parks DH, Chuvochina M, Rinke C, Mussig AJ, Chaumeil PA, Hugenholtz P (2022) GTDB: an ongoing census of bacterial and archaeal diversity through a phylogenetically consistent, rank normalized and complete genome-based taxonomy. Nucleic Acids Res 50(1):D785–D794. https://doi.org/10.1093/nar/gkab776

Richter M, Rosselló-Móra R (2009) Shifting the genomic gold standard for the prokaryotic species definition. Proc Natl Acad Sci 106(45):19126–19131. https://doi.org/10.1073/pnas.0906412106

Rodriguez-R LM, Konstantinidis KT (2016) The enveomics collection: a toolbox for specialized analyses of microbial genomes and metagenomes. PeerJ Preprints 4:e1900v1. https://doi.org/10.7287/peerj.preprints.1900v1

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4(4):406–425. https://doi.org/10.1093/oxfordjournals.molbev.a040454

Shi W, Sun Q, Fan G, Hideaki S, Moriya O, Itoh T, Zhou Y, Cai M, Kim SG, Lee JS, Sedlacek I, Arahal DR, Lucena T, Kawasaki H, Evtushenko L, Weir BS, Alexander S, Dénes D, Tanasupawat S, Eurwilaichitr L, Ma J (2021) gcType: a high-quality type strain genome database for microbial phylogenetic and functional research. Nucleic Acids Res 49(1):D694–D705. https://doi.org/10.1093/nar/gkaa957

Stackebrandt E, Goebel BM (1994) Taxonomic note: a place for DNA-DNA reassociation and 16S rRNA sequence analysis in the present species definition in bacteriology. Int J Syst Evol Microbiol 44(4):846–849. https://doi.org/10.1099/00207713-44-4-846

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res 22(22):4673–4680. https://doi.org/10.1093/nar/22.22.4673

Tindall BJ (1990) Lipid composition of halobacterium lacusprofundi. FEMS Microbiol Lett 1–3:199–202. https://doi.org/10.1016/0378-1097(90)90282-U

Xamxidin M, Wu YH, Jian SL, Zhou YD, Wang CS, Tohty D, Xu XW (2016) *Aquaticitalea lipolytica* gen. nov., sp. nov., isolated from Antarctic seawater. Int J Syst Evol Microbiol. https://doi.org/10.1099/ijsem.0.001101

Xu XW, Wu YH, Zhou Z, Wang CS, Zhou YG, Zhang HB, Wang Y, Wu M (2007) *Halomonas saccharevitans* sp. nov., *Halomonas arcis* sp. nov. and *Halomonas subterranea* sp. nov., halophilic bacteria isolated from hypersaline environments of China. Int J Syst Evol Microbiol 57(7):1619–1624. https://doi.org/10.1099/ijs.0.65022-0

Xu L, Sun C, Fang C, Oren A, Xu XW (2020) Genomic-based taxonomic classification of the family *Erythrobacteraceae*. Int J Syst Evol Microbiol 70(8):4470–4495. https://doi.org/10.1099/-ijsem.-0.004293

Yoon JH, Kang SJ, Lee MH, Oh HW, Oh TK (2006) *Porphyrobacter dokdonensis* sp. nov., isolated from sea water. Int J Syst Evol Microbiol 56(5):1079–1083. https://doi.org/10.1099/ijs.0.63840-0

Yoon BJ, Lee DH, Oh DC (2013) *Erythrobacter jejuensis* sp. nov., isolated from seawater. Int J Syst Evol Microbiol 63(4):1421–1426. https://doi.org/10.1099/ijs.0.038349-0