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ORIGINAL PAPER

Roseihalotalea indica gen. nov., sp. nov., a halophilic Bacteroidetes from mesopelagic Southwest Indian Ocean with higher carbohydrate metabolic potential

Beihan Chen · Mingzhe Zhang · Dan Lin · Jianing Ye · Kai Tang

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Abstract The pink-colored and strictly aerobic bacterium strain, designated as TK19036^T, was isolated from mesopelagic layer of the Southwest Indian Ocean. This novel isolate can grow at 10–45 °C (optimum, 30 °C), pH 6.0–8.0 (optimum, pH 7.0), and 2–14% NaCl concentrations (w/v) (optimum, 6%). The predominant respiratory quinone was Menaquinone-7. Major polar lipid profiles contained two aminolipids, aminophospholipid, two glycolipids, phosphatidylethanolamine, and three unknown polar lipids. The preponderant cellular fatty acids were iso-$C_{15:0}$, $C_{16:1}$ $\omega5c$ and iso-$C_{17:0}$ 3-OH. Phylogenetic analyses based on 16S rRNA gene sequence uncovered that the strain TK19036^T pertained to the family *Catalinimonadaceae* under phylum *Bacteroidota*, and formed a distinct lineage with the closed species *Tunicatimonas pelagia* NBRC 107804^T. The up-to-bacteria-core gene phylogenetic trees also demonstrated a deep and novel branch formed by the strain TK19036^T within the family *Catalinimonadaceae*. Based on chemotaxonomic, phylogenetic and genomic features presented above, strain TK19036^T represents a novel species from a novel genus of the family *Catalinimonadaceae*, for which the name *Roseihalotalea indica* gen. nov. sp. nov. is proposed. The type strain is TK19036^T (=CGMCC 1.18940^T=NBRC 116371^T).

Keywords *Roseihalotalea indica* · Southwest Indian Ocean · Polyphasic taxonomic approach

Introduction

Bacteroidota, revised from *Bacteroidetes* (Oren and Garrity 2021), was proposed as a phylum of chemoheterotrophic bacteria that are rod-shaped and gram-stain-negative (Krieg et al. 2010). With extensive revision on the phylum, *Bacteroidota* was doubled in number in the last 13 years of research (Hudson and Egan 2022). However, the classification of *Bacteroidota* might still be unsatisfactory due to its high complexity (García-López et al. 2019). Being a

Beihan Chen and Mingzhe Zhang contributed equally to this work and should be considered co-first authors.

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B. Chen · M. Zhang · D. Lin · J. Ye · K. Tang (✉)
State Key Laboratory of Marine Environmental Science, College of Ocean and Earth Science, Fujian Key Laboratory of Marine Carbon Sequestration, Xiamen University, Xiamen, China
e-mail: tangkai@xmu.edu.cn

B. Chen
School of Oceanography, Shanghai Jiao Tong University, Shanghai, China

M. Zhang
School of Science, The Hong Kong University of Science and Technology, Hong Kong, China

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member of *Bacteroidota*, the family *Catalinimonadaceae* belonging to class *Cytophagia* and order *Cytophagales* was first proposed by Choi et al. (2013) after naming the type genus *Catalinimonas*. At the time of writing, *Catalinimonadaceae* was comprised of one validly published genus *Catalinimonas* with two species (Choi et al. 2013; Yoon et al. 2014). Strain TK19036^T, identified in this study, has been reported to encode a rich repertoire of carbohydrate-active enzymes (CAZymes), which may be useful for future biochemical or biotechnological studies (Chen et al. 2023). In this study, polyphasic taxonomic approaches will be used to identify a new strain of a novel genus *Roseihalotalea* within the family *Catalinimonadaceae*, with the type strain of *Roseihalotalea indica* TK19036^T.

Materials and methods

Isolation and cultural conditions

Consistent with the methods in Chen et al. (2023), isolation of the strain TK19036^T was performed on the seawater sample collected from Southwest Indian Ocean (49°38' E, 37°46' S at a depth of 500 m; 13.27 °C; 35.25 psu and 7.56 mg/L dissolved oxygen) in 2019. Prior to isolation, the sample was temporarily preserved at 4 °C. The original isolation was achieved by spread-plate method on marine agar 2216E medium (Hopebio, China; HB8278). A reddish colony was picked up and incubated on the same agar medium at 28 °C under aerobic condition for a week. The colony was purified by repeated plate streaking. The purified culture subsequently grew in 2216E liquid medium (Hopebio, China; HB0132) at 28 °C for three days and then was cryopreserved at -80 °C, supplemented with 30% sterilized glycerol (v/v) to a final concentration of 15% (v/v).

16S rRNA gene phylogeny and genome features

The 16S rRNA gene sequence of the strain TK19036^T was amplified through polymerase chain reaction (PCR) with primers 27F (5'-AGAGTTTGATCCTGGCTCAG-3') and 1492R (5'-GGTTACCTTGTTACGACTT-3') (dos Santos et al. 2019). The complete 16S rRNA gene sequence was extracted by the tool ContEst16S (https://www.ezbiocloud.net/tools/contest16s) (Lee et al. 2017) and aligned via the online EzBioCloud database (https://www.ezbiocloud.net/). Based on the 16S rRNA gene sequence similarity, the top 3 highest similar strains, that are *Tunicatimonas pelagia* N5DB8-4^T (=NBRC 107804^T), *Porifericola rhodea* N5EA6-3A2B^T (=NBRC 107748^T) and *Catalinimonas niigatensis* A6F-52^T (=NBRC 109829^T), were selected as the reference strains (Chen et al. 2023). For the 16S rRNA gene sequence phylogenetic tree construction, sequences of related strains were downloaded from NCBI (https://www.ncbi.nlm.nih.gov/home/download/) using validly published accession numbers. The 16S rRNA gene phylogenetic trees were constructed by using Neighbor-joining (NJ), and maximum-likelihood (ML) with K2+G+I substitution model via MEGA version 7 (Kumar et al. 2016). Robustness and confidence of the tree topologies were verified by 1,000 bootstrap replicates (Felsenstein 1985; Pattengale et al. 2010). Sequencing, the annotation of protein-coding genes and the calculation of digital DNA-DNA hybridization (dDDH) and average nucleotide identity (ANI) of the whole genome sequences of the strain TK19036^T and the reference strains, were reported by Chen et al. (2023). The up-to-bacteria-core gene (UBCG) algorithms was used to build genomic phylogenic tree in Linux virtual system and RAxML and FastTree (Na et al. 2018; Price et al. 2010; Stamatakis 2014). All parameters were in default. All the assembled genome sequences used for analysis are available at the NCBI. The functional categories of the Cluster of Orthologous Groups (COGs) of predicted proteins were annotated by eggNOG-mapper v2 (http://eggnog-mapper.embl.de/) (Huerta-Cepas et al. 2019; Cantalapiedra et al. 2021). For each strain, gene counts per COG category were adjusted to relative counts using total predicted protein numbers. Subsequently, these relative counts were standardized within each COG category.

Physiology and chemotaxonomy

The Gram-staining test was performed by Chen et al. (2023). The hanging drop method was used to determine the motility (Bernardet et al. 2002). To evaluate anaerobic growth capabilities, strain TK19036^T was cultured on six marine agar 2216E

plates. These plates were incubated at 28 °C for a month: three of them were exposed to aerobic conditions, while the remaining three were placed in an anaerobic environment using anaerobic gas-producing bags (Hopebio, China; HBYY001). The temperature range for growth was determined at 4, 10, 15, 23.5, 25, 30, 35, 40, and 45 °C for a week, by incubating cells in 2216E liquid medium (Hopebio, China; HB0132). Salinity range for growth was determined between 0–15% NaCl concentration (w/v; in increments of 1%) in rich organic liquid medium (KCl 0.3 g, $MgSO_4 \cdot 7H_2O$ 0.5 g, $CaCl_2 \cdot 2H_2O$ 0.038 g, NH_4Cl 0.3 g, K_2HPO_4 0.3 g, yeast 1.0 g, tryptone 1.0 g, CH_3COONa 1.0 g and Milli-Q water 1 L) at 28 °C. The growth at different pH gradients (3.0–12.0, in a increment of 1.0) was observed in 2216E liquid medium for 4 days at 28 °C, with the pH adjusted using pH buffers (Na_2HPO_4/Citric Acid for pH 3.0–8.0, Glycine/NaOH for pH 9.0–10.0 and Na_2HPO_4/NaOH for pH 11.0–12.0). Catalase activity was tested using 3% H_2O_2 reagent (Xilong Science; 7722-84-1) with observation on bubble formation. Oxidase activity was determined using a commercial oxidase strip (Hopebio, China; BH2100) following the guidance of the manufacturer. The physiological and biochemical traits determination relied on API 20NE and API ZYM strips (bioMérieux) on bacterial suspension supplemented with 3.5% NaCl solution (w/v). The result interpretation followed the manufacturer's instruction.

The purified strain TK19036^T and reference strains were cultured in 2216E liquid medium at 28 °C (Hopebio, China; HB0132) for three days, reaching the exponential phase, at which point the colonies were harvested. Subsequently, cellular fatty acids were extracted and analyzed using the method proposed by Komagata and Suzuki (1988). Then cellular fatty acids were analyzed and identified through Microbial Identification System (MIDI, Sherlock v6.0) TSBA6 database. Polar lipids were extracted through a chloroform–methanol system and analyzed using two-dimensional thin-layer chromatography as the description of Minnikin et al. (1984). The major respiratory quinone of the strain TK19036^T was determined by High Performance Liquid Chromatography.

Results and discussion

Morphological and phenotypic analyses

The colonies formed by the strain TK19036^T are reddish-pink and about 0.5 cm in diameter on marine agar 2216E plates. Swimming motility was not observed. The differences in phenotypic properties between the strain TK19036^T and the related strains *T. pelagia* NBRC 107804^T, *P. rhodea* NBRC 107748^T, and *C. niigatensis* NBRC 109829^T, are listed in Table 1. Major properties like oxidase activities, growth conditions and results of API 20NE and API ZYM could provide clear discrimination between the strain TK19036^T and the reference strains (Table 1); especially, the negative result of acid phosphatase activity clearly differentiates this new isolate with its close phylogenetic neighbors.

16S rRNA gene sequence analysis

Comparative 16S rRNA gene sequence analysis on the strain TK19036^T revealed that, the sequence, with a full length of 1,520 bp, shares highest similarities with *T. pelagia* NBRC 107804^T of 94.3%, *P. rhodea* NBRC 107748^T of 90.7%, and *C. niigatensis* NBRC 109829^T of 90.6% (Chen et al. 2023). The 16S rRNA gene sequence similarities between the strain TK19036^T and the reference strains, which are lower than the threshold of genus differentiation (94.5%) but higher than that required for family delineation (86.5%), suggest a novel phylogenetic placement of the strain TK19036^T (Yarza et al. 2014). In the phylogenetic NJ and ML tree based on 16S rRNA gene sequences (Fig. 1, Fig. S1), strain TK19036^T clusters with the strain *T. pelagia* NBRC 107804^T and occupies a deep branch within the family *Catalinimonadaceae*. In contrast, strain TK19036^T exhibits a distinct phylogenetic placement from the strain *Imperialibacter roseus* P4^T in the family *Flammeovirgaceae* (16S rRNA gene sequence similarity: 86.4%) (Wang et al. 2013). Notably, two of the closely related strains, *T. pelagia* NBRC 107804^T and *P. rhodea* NBRC 107748^T, were primarily recognized as members of family *Flammeovirgaceae*, based on an array of subsequently corrected taxonomic classifications of *Bacteroidetes* (Yoon et al. 2011, 2012; García-López et al. 2019). The above conclusion was drawn before the family *Catalinimonadaceae*

Table 1 Morphological and phenotypic profiles of the strain TK19036^T and the reference strains. Strains: 1, strain TK19036^T; 2, *T. pelagia* NBRC 107804^T; 3, *P. rhodea* NBRC 107748^T; 4, *C. niigatensis* NBRC 109829^T. Symbols: -, negative; +, positive; w, weakly positive; nc, not collected

Characteristics	1	2*	3†	4‡
Isolation source	Sea water	Sea anemone	Marine sponge	Blackish lake sediment
Colony color	Reddish-pink	Reddish-pink	Reddish-pink	Reddish-pink
Gram-staining	-ξ	-	-	-
Cell size (μm)	0.7–0.8 × 3.3–6.0ξ	0.3–0.5 × 15–30	0.4–0.5 × 20–25	0.5–0.7 × 3–4
Catalase activity	+	+	+	+
Oxidase activity	+	-	-	+
Strictly aerobic	+	+	+	+
Polar lipids	AL, APL, PE, GL, UL	nc	nc	PE, UPL, UL
Growth range (optimal)				
Temperature (°C)	10–45 (30)	20–37 (25–30)	15–37 (20–30)	20–40 (28)
NaCl (%, w/v)	2–14 (6)	0–8 (nc)	0–10 (nc)	0–4 (nc)
pH	6–8 (7)	6–10 (7)	6–9 (7)	6–8 (7)
API ZYM				
Trypsin	+	+	+	w
Acid phosphatase	-	+	+	+
β-galactosidase	+	-	w	+
β-glucuronidase	+	-	+	+
α-glucosidase	-	-	-	+
N-acetyl-*β*-glucosaminidase	+	-	+	+
β-fucosidase	+	+	w	+
API 20NE				
Nitrate reduction	-	-	-	+
Glucose fermentation	+	-	-	+

AL, aminolipid; *APL*, aminophopholipid; *PE*, phosphatidylethanolamine; *GL*, glycolipid; *UL*, unidentified polar lipid; *UPL*, unidentified phospholipid

Citations: ξ(Chen et al. 2023); *(Yoon et al. 2012); †(Yoon et al. 2011); ‡(Yoon et al. 2014)

Positive results shared among the four strains in API tests: API ZYM-esterase (C4), esterase lipase (C8), lipase (C14), valine arylamidase, cystine arylamidase, chymotrypsin, naphthol-AS-BI-phosphohydrolase, *α*-galactosidase, *β*-glucosidase and *α*-mannosidase; API 20NE-esculin hydrolysis, gelatin hydrolysis and 4-nitrophenyl-*β*-D-galactopyranoside

Negative results shared among the four strains in API tests: API ZYM-alkaline phosphatase and leucine-arylamidase; API 20NE-indole production, arginine dihydrolase and urease

was proposed (Choi et al. 2013). However, with more strains discovered, our study demonstrates that the strains TK19036^T, *T. pelagia* NBRC 107804^T and *P. rhodea* NBRC 107748^T exhibit a closer phylogenetic relationship with the family *Catalinimonadaceae* than the family *Flammeovirgaceae* (Fig. 1, Fig. S1).

Genome analysis

The whole genome sequence size of the strain TK19036^T reaches 8.20 Mb. As reported by Chen et al. (2023), the ANI and average amino acid identity (AAI) values between the genomes of the strain TK19036^T and reference strains are less than the threshold of distinguishing genus (ANI: 95%; AAI: 65–72%) (Barco et al. 2020; Konstantinidis and Tiedje 2007). Additionally, the UBCG tree, based on 92 core genes, confirmed the deduction made from the phylogeny of the 16S rRNA gene sequence and phylogenetic analysis, indicating the affiliation of the strain TK19036^T with the family *Catalinimonadaceae* (Fig. S2). Combined with the results of genome analysis and other genomic features (Tabel 1 in Chen et al. 2023), it is strongly

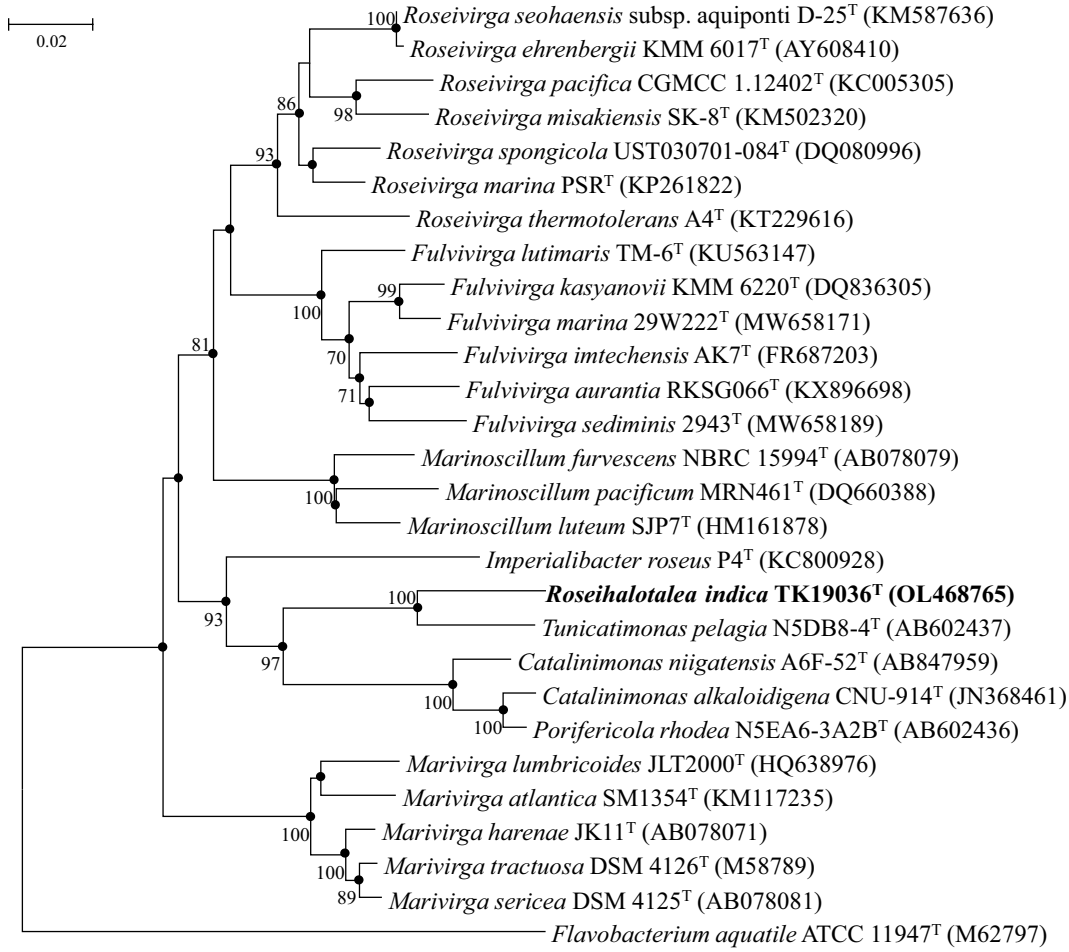


Fig. 1 Neighbour-joining (NJ) tree based on 16S rRNA gene sequences of the strain TK19036^T and reference strains with close 16S rRNA gene sequence similarities. Values are supported by 1000 bootstrap replicates. *Bar*, 0.02 substitution rate units. Filled circles indicate branches shared in both NJ and ML trees

implied that the strain TK19036^T could be classified as the type strain of a novel species in a new genus within the family *Catalinimonadaceae*.

In the genome of strain TK19036^T, aside from [S] Function unknown (1113 genes), the most represented COG functional category was [G] Carbohydrate transport and metabolism (435 genes) (Fig. 2A). Compared to the phylogenetically related strains, gene counts for category [G] in the genome of strain TK19036^T were relatively higher (Fig. 2B). Consistent with the rich repertoire of CAZymes (Chen et al. 2023), this finding indicates that strain TK19036^T may have greater capabilities for carbohydrate transport and metabolism.

Chemotaxonomic characteristics

The major fatty acids of strains TK19036^T (> 10% of the total) are iso-$C_{15:0}$ (39.7%), $C_{16:1}$ *ω5c* (25.6%) and iso-$C_{17:0}$ 3-OH (14.5%) (Table S1). Compared to the three reference strains, the top three major fatty acids are shared, except for the largest fatty acid for *T. pelagia* NBRC 107804^T. Unlike the reference strains, the branched anteiso-$C_{15:0}$ and hydroxyl iso-$C_{16:0}$ 3-OH was not detected in the strain TK19036^T. Profiles of the fatty acids indicated the novel evolutionary status of the strain TK19036^T. There are nine polar lipids detected, including two aminolipids (AL1-2), aminophospholipid (APL), two glycolipids

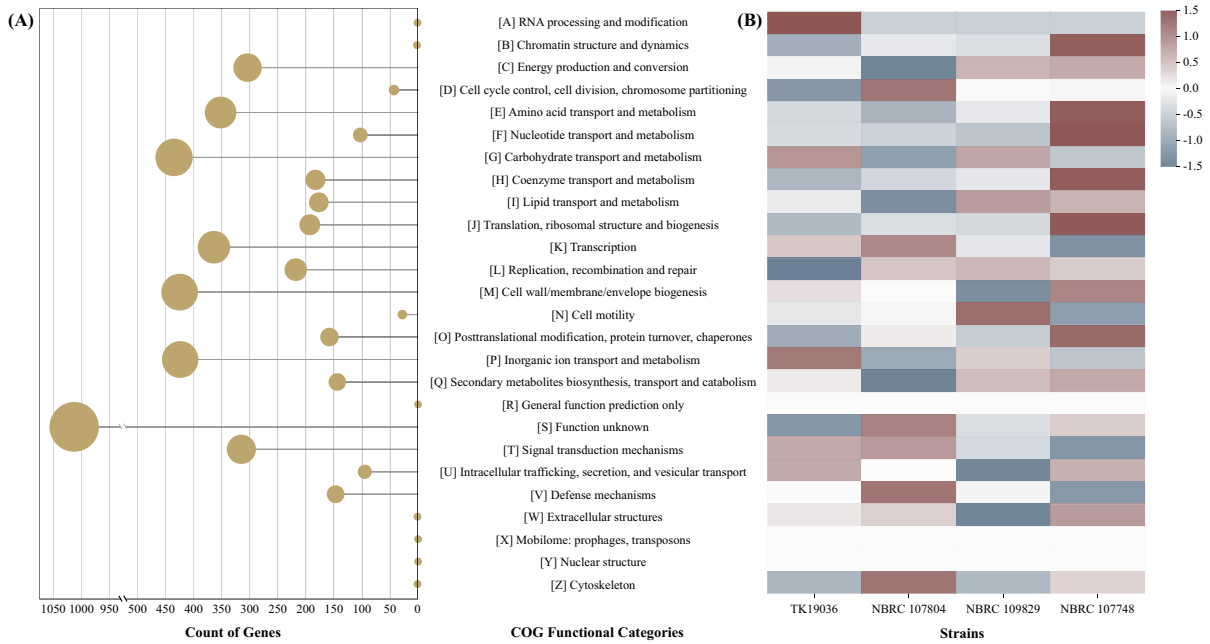


Fig. 2 **A** Counts of genes based on the 26 COG functional categories of the isolate TK19036^T. The length of the lollipop sticks and the diameter of the circles indicate gene counts for each COG category. **B** Heatmap of the standardized relative gene counts for each COG functional category of the isolate TK19036^T and related strains

(GL1-2), phosphatidylethanolamine (PE), three unidentified polar lipids (UL1-3) (Fig. S3). Phosohatidylethanolamine is the only polar lipid shared by the strain TK19036^T and *C. niigatensis* NBRC 109829^T (Table 1) (Yoon et al. 2014). The major respiratory quinone was identified as Menaquinone-7, providing evidence for the similarities between the strain TK19036^T and reference strains (Costa et al. 2011; Hiraishi 1988; Yoon et al. 2011, 2012, 2014).

Taxonomic conclusion

Combining the phylogenetic, phylogenomic, phenotypic and chemotaxonomic properties, strain TK19036^T, that was isolated from Southwest Indian Ocean seawater, represents a novel species from a novel genus under the family *Catalinimonadaceae*, for which the name *Roseihalotalea indica* gen. nov., sp. nov. is proposed.

Description of *Roseihalotalea* gen. nov.

Roseihalotalea (ro.se.i.ha.lo.ta'le.a L. masc. adj. *roseus*, rose-colored, pink; Gr. masc. n. *hals (gen. halos)*, salt; L. fem. n. *talea*, a long rod; N.L. fem. n. *Roseihalotalea*, a long rod, pink-colored and halophilic bacteria).

Cells are Gram-stain-negative, long-rod-shaped and strictly aerobic. The major fatty acids (> 10%) are iso-$C_{15:0}$, $C_{16:1}$ *ω5c* and iso-$C_{17:0}$ 3-OH. The major polar lipids are two aminolipids, aminophospholipid, two glycolipids, phosphatidylethanolamine, three unidentified polar lipids. The major respiratory quinone is Menaquinone-7. The type species is *Roseihalotalea indica*.

Description of *Roseihalotalea indica* gen. nov., sp. nov.

Roseihalotalea indica (in'di.ca. L. fem. adj. *indica*, Indian, isolated from the Indian Ocean).

Cells are Gram-stain-negative, long-rod-shaped, none-swimming motile, 0.7–0.8 μm in width and 3.3–6.0 μm in length. Colonies are reddish-pink-colored and about 0.5 cm in diameter on marine agar 2216E plates (Chen et al. 2023). Positive for oxidase and catalase. Growth is observed at 10–45 °C (optimum, 30 °C), pH 6.0–8.0 (optimum, pH 7.0), and 2–14% NaCl concentrations (w/v) (optimum, 6%).

Esterase (C4), esterase lipase (C8), lipase (C14), valine arylamidase, cystine arylaminase, trypase, chymotrypsinalpha, Naphthol-AS-BI-phosphohydrolase, α-galactosidase, β-galactosidase, β-glucuronidase, β-glucuronidase, β-glucosidase, β-glucosidase, α-mannosidase, β-fucosidase and 4-nitrophenyl-β-D-galactopyranoside activities are present, while alkaline phosphatase, acid phosphatase and α-glucosidase are absent. Negative for nitrate and nitrite reduction. Positive for gelatin and esculin hydrolyze activities and glucose fermentation.

The type strain is TK19036^T (=CGMCC 1.18940^T=NBRC 116371^T), which was isolated from mesopelagic seawater of the Southwest Indian Ocean. The whole genome size of the type strain is 8.20 Mb, with a GC content of 45.2% (Chen et al. 2023). The GenBank/EMBL/DDBJ accession number for the full-length 16S rRNA gene sequence and the whole genome shotgun sequence of the strain TK19036^T are OL468765 and CP120682, respectively (Chen et al. 2023).

Author contributions B.C., M.Z. and J.Y. designed and performed the experiments. B.C. and M.Z. analyzed the data. M.Z., B.C., D.L. and K.T. wrote the manuscript. B.C., D.L. and M.Z. revised the manuscript. All authors read and approved the final manuscript.

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Data availability All the data generated or analyzed during this study are included in this published article and its supplementary information files and fully available to the public.

Declarations

Competing interests The authors declare no competing interests.

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

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