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ORIGINAL PAPER

Nitratireductor luteus sp. nov. isolated from saline-alkali land

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Abstract The Gram-staining negative, oxidase and catalase negative strain KC-ST17^T, isolated from saline-alkali land, was characterized using a polyphasic approach to determine its taxonomic position. Using 16S rRNA gene sequence analysis, the highest similarity of strain KC-ST17^T was found with *Nitratireductor pacificus* CCTCC AB 209302^T (97.2%). Cells are aerobic, non-motile, and rod-shaped. The isolate was found to be able to grow in NaCl concentrations of 0–4.0%. The assembled genome of strain KC-ST17^T had a total length of 4.9 Mb with a G + C content of 62.7%. According to genome analysis, strain KC-ST17^T encodes genes involved in the reduction of nitrate to nitrite, which may play a role in the utilization of nitrogenous compounds from the soil as an immediate source of energy. Based on the phenotypic characteristics and phylogenetic analysis, strain KC-ST17^T was confirmed to represent a novel species in the *Nitratireductor* genus; thus, the name *Nitratireductor luteus* sp. nov. was proposed. The type strain of this species was KC-ST17^T (= KCTC 92119^T = MCCC 1K07309^T).

Keywords *Nitratireductor luteus* · KC-ST17^T · Saline-alkali land · 16S rRNA gene sequence analysis

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Introduction

The genus *Nitratireductor* was proposed by Labbé et al. (2004) and belongs to the family *Phyllobacteriaceae*, order *Rhizobiales*, class *Alphaproteobacteria*, and phylum '*Pseudomonadota*'. At the time of writing, the genus included ten validly published species with the correct name (https://lpsn.dsmz.de/genus/nitratireductor May 2022), and the type species was *Nitratireductor aquibiodomus* (Labbé et al. 2004). The type strains of this species have been isolated from various environmental habitats, including marine denitrification systems (Labbé et al. 2004), seaweed (Kang et al. 2009), black beach sand (Kim et al. 2009), deep-sea water (Lai et al. 2011), pyrene-degrading consortia (Lai et al. 2011), salt lakes (Yu et al. 2016) and estuaries (Ou et al. 2017), and diatom cultures (Jang et al. 2011). The bacteria of this genus are gram-negative, aerobic, rod-shaped or coccoid, with variable motility and nitrate-reducing abilities.

The major quinone is Q-10 and the genomic DNA G + C content is 56.7–63.0%.

In this study, we analyzed the characteristics of a novel species using a series of cultivation techniques and genetic manipulations (Ramasamy et al. 2014) including phenotype identification, housekeeping gene sequencing, phylogenetic analysis, genome sequencing and annotation, fatty acid methyl ester analysis, and antibiotic susceptibility test. We propose to establish this strain as a representative of a novel species of the genus *Nitratireductor*, with the name *Nitratireductor luteus* sp. nov.

Materials and methods

Isolation and culture conditions

Strain KC-ST17^T was originally isolated from saline-alkali land collected from the Akesu region (41°9′90″N, 80°30′80″E) in Xinjiang, China, in May 2021. Soil samples were suspended in sterile water and serially diluted. A 1:1000 dilution of the sample was cultivated on nutrient agar (NA) plates. The plates were incubated at 30 °C and checked for growth after 1–2 d. A single colony was picked and sub-cultured until it was pure. The pure strain was cultivated routinely on NA and NB media at 33 °C under aerobic conditions and then preserved at −80 °C in sterile 1.0% (w/v) saline supplemented with 15.0% (v/v) glycerol. *Nitratireductor pacificus* CCTCC AB209302^T was obtained from the China Center for Type Culture Collection (CCTCC). The reference strain was cultured under the same conditions as strain KC-ST17^T for comparative study.

Molecular analysis

Genomic DNA was isolated from a five-day-old NB liquid culture using a bacterial genomic DNA kit (Takara Bio, Shiga, Japan), following the manufacturer's instructions. The 16S rRNA gene was amplified using PCR with the forward primer 27F and reverse primer 1492R, as described previously (Liu et al. 2014). Purified PCR products were sequenced by BGI Co. Ltd (Qingdao, China) and resulted in a 1309 bp almost complete 16S rRNA gene sequence. The 16S rRNA gene sequence was compared with sequences from the NCBI database using BLAST analysis (http://www.ncbi.nlm.nih.gov/BLAST) (Altschul et al. 1990), as well as with sequences available in the EZTaxon database (www.ezbiocloud.net/) (Yoon et al. 2017). We performed phylogenetic analysis based on the available sequences. A phylogenetic tree was constructed using the neighbor-joining algorithm implemented in the software package MEGA (version 7.0) (Kumar et al. 2016). Phylogenetic trees were also generated using the maximum-likelihood and maximum-parsimony algorithms. Evolutionary distances were calculated using Kimura's 2-parameter method (Kimura et al. 1980), where gaps were completely deleted. Bootstrap analysis was performed with 1000 replications (bootstrap analysis; Felsenstein et al. 1985) to provide confidence estimates for tree topologies. Moreover, phylogenetic relationships based on nucleotide sequences were analyzed via UBCG (Na et al. 2018), and phylogenetic trees were constructed using FastTree (Price et al. 2010) with GTR + CAT parameters and IQTree (Trifinopoulos et al. 2016) with the GTR + F + I + G4 model and 1000 bootstrap replicates on the basis of 20 genomes.

Phenotypic characterization

To determine the morphological characteristics of the isolated strain, strain KC-ST17^T was cultured in modified NA medium at 33 °C for 48 h. The shape, size, gloss, edge, and color of the colonies on the plate were recorded. Light microscopy (E600; Nikon USA, Melville, NY, USA) and transmission electron microscopy (TEM; Jem-1200; JEOL) were used to observe the cell phenotypes. Motility was determined using the hanging-drop method and gliding motility was determined as described by Bowman (Bowman et al. 2000). Gram staining was performed as previously described by Smibert and Krieg (1994). Growth at different temperatures (10, 15, 20, 25, 30, 33, 35, 37, 40, 42, 45, and 50 °C) and pH (5.5–9.0, at increments of 0.5 pH units) was determined in NB. Growth in media with different NaCl concentrations was investigated on basal medium with various NaCl concentrations (0.5, 1.5, 2.0, 2.5, 3.0, 3.5, 4.5, and 6.5%, w/v) (Pridham and Gottlieb 1948). The growth range and optimal pH and NaCl concentrations were determined by measuring the optical density (OD) at 600 nm (Krist et al. 1998).

Oxidase activity was tested using an oxidase reagent kit (BioMérieux, Marcy l'Etoile, France), according to the manufacturer's instructions. Catalase activity was detected through bubble production using 3.0% (v/v) H_2O_2. The reduction of nitrate and hydrolysis of starch, casein, CM-cellulose, and Tween 40 and 80 were determined according to the methods described by Dong and Cai (Kanehisa et al. 2001). Growth under anaerobic (15% CO_2 and 85% N_2) condition was determined after incubation for 14 d in an anaerobic jar. Antibiotic susceptibility was investigated by the disc diffusion plate method (Bauer et al. 1966) using antibiotic discs on NA incubated for 7 d at 33 °C. Fourteen antibiotic discs were used (μg/disc, unless otherwise indicated): chloramphenicol (30), carbenicillin (100), penicillin (10), ceftriaxone (30), clarithromycin (15), erythromycin (15), tetracycline (30), gentamycin (10), tobramycin (10), vancomycin (30), streptomycin (10), lincomycin (2), streptomycin (10), and neomycin (30). Acid production from different carbon sources, assimilation of different substrates, and enzymatic activities of strain KC-ST17^T were investigated using API 50 CH, API 20 NE, and API ZYM kits (BioMérrieux) according to the manufacturer's instructions. The API 50 CH and 20 NE tests were performed after 24–48 h of incubation at 33 °C.

Chemotaxonomy

For cellular fatty acid analysis, strain KC-ST17^T was grown on NA plates at 33 °C for 48 h (at the late exponential stage of growth). Cellular fatty acid methyl esters (FAMEs) were obtained from cells by saponification, methylation, and extraction, following the MIDI protocol. Cellular FAMEs were separated using gas chromatography (GC) (6890) and identified and quantified using the Sherlock Microbial Identification System (MIDI-6890 with the database TSBA6). The isoprenoid quinone of strain KC-ST17^T was extracted from freeze-dried cell material using the two-stage method described by Tindall et al. (2007) and subsequently analyzed using HPLC (Hiraishi et al. 1996). Polar lipids were extracted using a chloroform/methanol system and analyzed using two-dimensional thin-layer chromatography, as described previously (Fang et al. 2017).

Genome sequencing, annotation, and analysis

For genome sequencing, the DNA was prepared using a bacterial DNA isolation kit (Takara). The draft genome of strain KC-ST17^T was sequenced by MAGIGENE Biological Technology Co. Ltd. (Guangzhou, China) and assembled using hybrid assembly methods. Sequencing was carried out on an Illumina Hiseq Xten platform (Illumina Inc., San Diego, CA, USA) at Guangdong Magigene Biotechnology Co. LTD (Guangzhou, China) using the pair-end 150-bp sequencing protocol. Long reads were generated by SMRT sequencing using the Pacific Biosciences RS II sequencer (PacBio, Menlo Park, CA, USA) according to standard protocols. Low-quality reads were filtered using Mecat2 (https://github.com/xiaochuanle/MECAT2; Xiao et al. 2017) after sequencing and assembled using SMRT Link v5.1.0. The hybrid assembled genome was generated using Unicycler (https://github.com/rrwick/Unicycler; Wick et al., 2017). The assembled genome was polished by applying the arrow algorithm of the Genomic Consensus package (https://github.com/PacificBiosciences/GenomicConsensus).

Protein-encoding regions were identified using the Rapid Annotations in the Subsystem Technology (RAST) server (Aziz et al. 2008) and the Cluster of Orthologous Group of Proteins (COG) (Tatusov et al. 2003), and the genes were annotated using Koala (KEGG) (Kanehisa et al. 2016). Furthermore, the NCBI prokaryotic genome annotation pipeline server was used to identify the genes of strain KC-ST17^T (Angiuoli et al. 2008). The average nucleotide identity (ANI) (RodríguezR and Konstantinidis 2016) and in silico digital DNA:DNA hybridization (DDH) were calculated using JSpecies WS (http://jspecies.ribohost.com/jspeciesws/) and the GGDC method, with the recommended formula 2, available at the TYGS web service (Meier-Kolthof and Göker 2019). Gene clusters potentially involved in the production of secondary metabolites were determined using antiSMASH 4.0 (Blin et al. 2017).

Results and discussion

Phylogenic analysis

According to comparisons with the 16S rRNA full-length gene sequences (1501 bp) in the EzTaxon database, the highest levels of sequence similarity occurred with *N. pacificus* CCTCC AB209302^T (97.2%), *N. aquibiodomus* JCM 21793^T (96.9%), and *N. soli* ZZ-1^T (96.3%). The 16S rRNA gene-based phylogenetic trees suggest that strains SC-ST17^T and *N. pacificus* CCTCC AB209302^T form a distinct phyletic lineage within the *Nitratireductor* genus, and their relationship is shown in the neighbor-joining (NJ) phylogenetic tree (Fig. 1). Moreover, the overall topologies of the phylogenetic trees obtained with maximum likelihood (ML) and maximum parsimony (MP) were similar; therefore, it can be concluded that strain SC-ST17^T belongs to the genus *Nitratireductor*. Moreover, the phylogenetic analyses based on a more comprehensive data set of validly published name strains genomes is presented in Fig. 2, and similar conclusion was also obtained. Therefore, the low sequence similarity and phylogenetic position on the trees indicated that strain SC-ST17^T may represent a novel species in the genus *Nitratireductor*.

Phenotypic and biochemical characterization

The basic features of strain SC-ST17^T, including cell morphology, growth, and mechanism of cell division, are summarized in Table 1 and compared to those of *N. pacificus* CCTCC AB209302^T, *N. aquibiodomus* JCM 21793^T, and *N. soli* ZZ-1^T. The morphological features of SC-ST17^T cells harvested during the exponential growth phase were analyzed using TEM (Jem-1200; JEOL). Strain SC-ST17^T forms rod-shaped cells of approximately 0.3–0.4 µm width and 0.6–1.2 µm length (Fig. S1). The cell size and shape of strain SC-ST17^T are comparable to those of the known type species in the genus *Nitratireductor*. Cells of strain SC-ST17^T were Gram-staining negative, oxidase and catalase negative as typical for members of the genus *Nitratireductor*. Casein, starch, CM-cellulose, Tween 40 and 80 are negative.

Cells are non-motile, grow at temperatures of 20–40 ℃, at a pH range of 6.5–9.0 and in 0–4.0% (w/v) NaCl. Optimal growth was observed at 30–33 ℃, 1.0% (w/v) NaCl and pH 7.0. Strain SC-ST17^T and *N. pacificus* CCTCC AB209302^T favour higher temperatures (40–42 ℃) than *N. aquibiodomus* JCM 21,793^T (37 °C) or *N. soli* ZZ-1^T (37 °C) (Table 1). With regard to pH range, strains SC-ST17^T, *N. pacificus* CCTCC AB209302^T, and *N. soli* ZZ-1^T are able to tolerate slightly alkaline growth conditions (pH 9.0–10.0), whereas *N. aquibiodomus* JCM 21,793^T require more neutral environments (pH 8.0). However, they all grow optimally under neutral conditions (pH 7.0–7.5). The NaCl concentration optimum of strain SC-ST17^T (1.0%) is approaching *N. soli* ZZ-1^T (1.0%); however, they all are slightly lower than *N. pacificus* CCTCC AB209302^T (3.0%) and *N. aquibiodomus* JCM 21793^T (2.5%). These differences

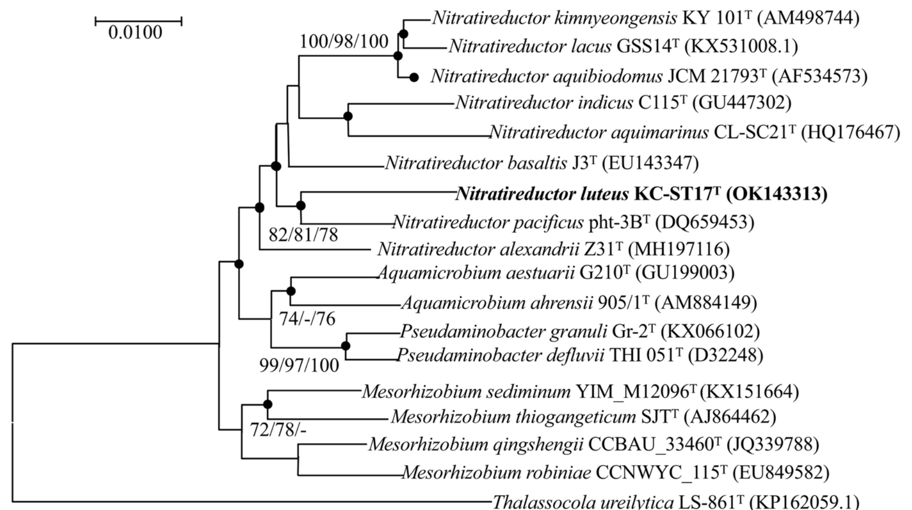

Fig. 1 Neighbour-joining phylogenetic tree based on full-length 16S rRNA gene sequence (1501 bp), showing the phylogenetic position of strain KC-ST17^T among members of the genus *Nitratireductor*. Numbers on nodes represent bootstrap values (NJ) based on 1000 replications. Only bootstrap values higher than 70.0% are marked on the branches. Filled circles indicate nodes also obtained in both maximum-likelihood and maximum-parsimony trees. Bar, 0.01 substitutions per nucleotide position

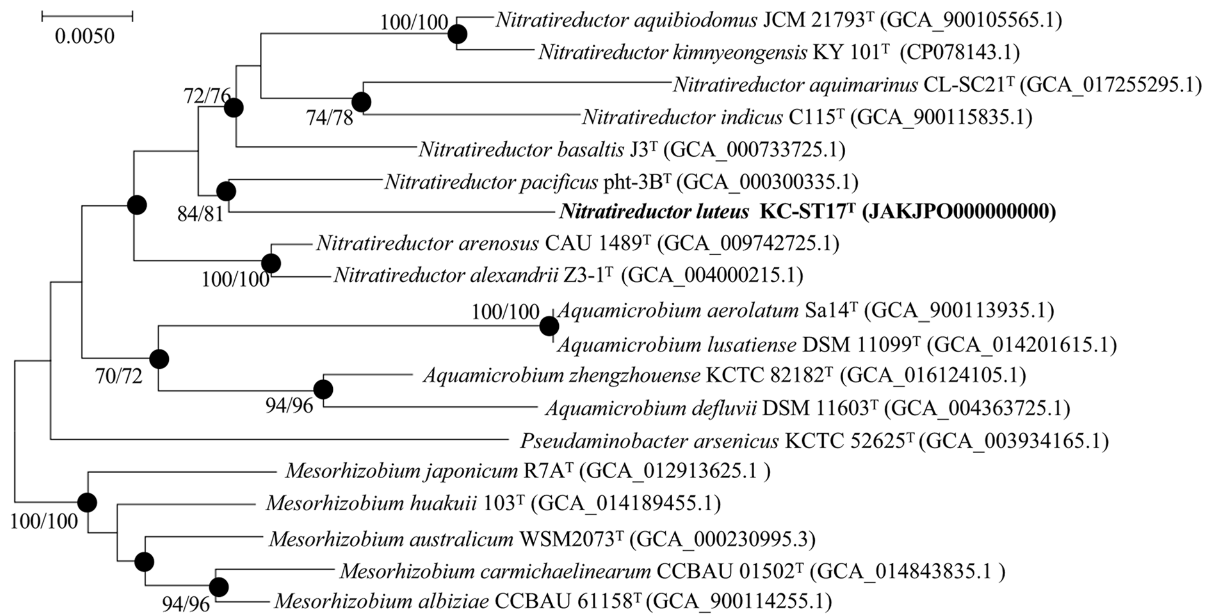

Fig. 2 The phylogenetic trees based on based on nucleotide sequences from 20 genomes of related strains showed the taxonomic position of strain KC-ST17^T. Filled circles indicate nodes overlapping on trees reconstructed using FastTree and IQTree algorithms. Numbers on nodes represent bootstrap values (FastTree/IQTree) based on 1000 replications. Bootstrap values (> 70.0%) based on 1000 replicates are shown at branch nodes. Bar, 0.005 substitutions per nucleotide position

likely reflect the different natural habitats in which the strains were isolated. *N. pacificus* CCTCC AB209302^T was isolated from enriched sediment from the Pacific Ocean, whereas *N. aquibiodomus* JCM 21793^T was isolated from the marine denitrification system, explaining the preference for NaCl concentrations. In contrast, strains SC-ST17^T and *N. soli* ZZ-1^T were isolated from soil. Meanwhile, it is also an important point to distinguish strain SC-ST17^T from the closest neighbour *N. pacificus* CCTCC AB209302^T.

Chemotaxonomic characteristics

The predominant cellular fatty acids in strain SC-ST17^T are summed feature 8 ($C_{18:1}\omega 7c$ and/or $C_{18:1}\omega 6c$, 55.3%) and $C_{19:0}$ $\omega 8c$ cyclo (17.3%). The fatty acid profile is similar to that of *N. pacificus* CCTCC AB209302^T, which is in accordance with the description of the *Nitratireductor* genus. However, the ratios of the different components are different. The complete fatty acid compositions are shown in Table S3. The only respiratory quinone in the strain SC-ST17^T is Q-10. Strain SC-ST17^T exhibits a complex polar lipid profile consisting of diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), one phospholipid (PL), and one uncharacterized lipids (L) as the dominant elements. In comparison, *N. pacificus* CCTCC AB209302^T differed from strain SC-ST17^T by different contents of one phospholipid (PL) and an unidentified lipid (L2) (Fig. S2). Overall, it could be distinguished from on the basis of the chemotaxonomic characteristics of the new specie that distinguished it from the closely related species in the genus *Nitratireductor*.

Genome analysis

The complete genome size of strain SC-ST17^T was 4,886,370 bp with DNA G+C content of 62.7%, which was consistent with the G+C content of the genus *Nitratireductor*. Similar genome features were observed for the closest neighbor *N. pacificus* CCTCC AB209302^T (genome size 4,611,341 bp and G+C content 62.1%). The genome of strain SC-ST17^T has a larger size than majority of the existing-sequenced

Table 1 Physiological and chemotaxonomic properties of strain KC-ST17^T compared with the closely related species of the genus *Nitratireductor*. Strains: 1, KC-ST17^T; 2, *N. pacificus* CCTCC AB209302^T; 3, *N. aquibiodomus* JCM 21793^T (data from Labbe´ et al., 2004); 4, *N. soli* ZZ-1^T (data from Chen et al., 2015). Data were obtained in the present study unless indicated. +, Positive; w, Weakly positive; −, Negative

Characteristics	1	2	3	4
Cell dimensions (μm)				
Width	0.3–0.5	0.8–0.9	1.0	0.4–0.5
Length	0.6–1.2	1.4–1.5	2.0–3.0	1.2–2.7
Motility	−	+	+	+
Oxidase	−	+	+	−
Catalase	−	+	+	+
Temp. for growth (°C)				
Range	20–40	10–41	25–37	15–37
Optimum	30–33	25–30	28	25–30
NaCl for growth (%, w/v)				
Range	0–4	0–7.0	0–5.0	0–8.0
Optimum	1.0	3.0	1.0	0.5
pH for growth				
Range	6.5–9.0	6.0–9.0	6.5–9.0	6.0–10.0
Optimum	7.0	7.0	7.0	7.5
API ZYM				
Lipase (C14)	+	+	w	w
Valine arylamidase	w	+	+	+
Trypsin	−	+	+	w
Cystine arylamidase	−	−	+	−
α-Chymotrypsin	−	−	+	+
API 20NE assay:				
d-Maltose	+	+	+	−
β-Galactosidase	−	w	+	w
d-Mannose	w	−	+	−
Maltose	w	+	+	+
DNA G+C content (%)	62.7	62.1	61.4	64.1
Genome size (Mb)	4.9	4.5	4.5	5.1
Genomic genes	4867	4297	4026	4866

strains, indicating substantial strain-to-strain variation. Annotation of the genome of strain SC-ST17^T consisted of 4867 predicted protein-coding genes and 48 tRNAs, by contrast, *N. pacificus* CCTCC AB209302^T possessed 4297 predicted protein-coding genes and 48 tRNAs. The genomic properties of strain SC-ST17^T and other type strains within the genus *Nitratireductor* are summarized in Table S1. The average nucleotide identity (ANI) and in silico digital DDH (dDDH) values between strain SC-ST17^T and strain *N. pacificus* MCCC 1A01024^T were 76.2% and 33.8% (using GBDP distance formula 2), respectively. The ANI and dDDH values between strain SC-ST17^T and other related species of the genus *Nitratireductor* were below the recommended thresholds of 95–96% and 70.0%, species demarcation (Ciufo et al. 2018; Meier-Kolthof and Göker 2019) (Table S2).

Based on the genomes of strain SC-ST17^T and closely related species, we analyzed the number of putative carbohydrate-active enzymes and gene clusters putatively involved in the synthesis of secondary metabolites. These numbers can provide a first impression of the metabolic capabilities of the strain, for example, in competitive environments, in which complex polysaccharides (e.g., derived from macroscopic phototrophs) function as a major source of carbon and energy. The observed number of 124 putative carbohydrate-active enzymes of strain SC-ST17^T is in the middle range to higher than that of its relatives, which harbor between 87 and more than 150 such enzymes. Strain SC-ST17^T has the second largest genome of the four compared strains and is the strain with the second-lowest number of carbohydrate-active enzymes.

Although the difference in the genome size of strains SC-ST17^T and *N. pacificus* CCTCC AB209302^T was only approximately 0.28 Mb, the number of carbohydrate-active enzymes was nearly 1.2-fold different in a direct comparison of these two species. The number of proteins belonging to such classes is more likely a reflection of the complexity of the isolated environment, and perhaps, there is a certain correlation with the size of the genome. Meanwhile, the number of gene clusters putatively involved in the production of secondary metabolites was clearly correlated with genome size. Strain *N. soli* ZZ-1^T had both the largest genome and the highest number of predicted clusters among the four strains.

Strain SC-ST17^T can convert nitrate to nitrite but cannot reduce nitrite to nitrogen. The genome of strain SC-ST17^T is also predicted to have genes involved in the reduction of nitrate to nitrite, potentially enabling strain SC-ST17^T to utilize nitrogenous compounds from the soil as an immediate source of energy. The genome sequence of strain SC-ST17^T and its curated annotation are important assets for better understanding its interaction with crops and other organisms in the soil environment, and will open up new opportunities in the functional analysis of this

species in the global biogeochemical nitrogen cycle (Gu et al. 2013).

Conclusion

Taken together, strain SC-ST17^T could be distinguished from the closely related type strains by several phenotypic characteristics (morphological and chemotaxonomic markers), especially with regard to optimum temperature, genome size, and DNA G + C content. The 16S rRNA gene sequence similarities to the closely related taxa and overall genome-related indices (ANI and dDDH) also indicate its distance from other species. These differences support the results of the phylogenetic inference and justify the delineation of strain SC-ST17^T from previously described species in the genus *Nitratireductor*. Thus, we propose assigning the strain to a novel species of a novel genus, for which the name *Nitratireductor luteus* sp. nov. is proposed. The GenBank accession numbers of the 16S rRNA gene and genome sequences of strain SC-ST17^T are OK143313 and JAKJPO000000000, respectively.

Description of *Nitratireductor Luteus* sp. nov.

Cells are gram-negative, aerobic, non-motile, rod-shaped, 0.3–0.4 µm in width, and 0.6–1.2 µm in length. Colonies on NA plates are circular, convex, smooth, pale-pigmented, and approximately 0.6–1.0 mm in diameter after 48 h at 33 °C. Growth occurs at 20–40 °C (optimum 30–33 °C), at pH 6.5–9.0 (optimum pH 7.0), and in the presence of 0–4.0% (w/v) NaCl (optimum 1.0%). The strain reduces nitrate to nitrite but does not produce nitrogen. It is catalase and oxidase-negative, negative for H_2S production, indole production, gelatinase, Voges–Proskauer reaction, ONPG test, and Simmons citrate utilization. It does not hydrolyse starch, casein, CM-cellulose, Tween 40, and Tween 80. Acid is produced from d-ribose, l-sorbose, esculin ferric citrate, d-turanose, and d-tagatose, but not from glycogen, glucose, d-fucose, l-arbaitol, potassium 5-ketogluconate, d-raffinose, and d-ribose. The cells were positive for alkaline phosphatase, esterase (C4), esterase lipase (C8, weakly), leucine arylamidase, valine arylamidase (weakly), α-glucosidase (weakly), and N-acetyl-β-glucosaminidase (weakly). The tests for lipase (C14), trypsin, cystine arylamidase, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, β-glucosidase, α-mannosidase, and α-fucosidase were negative. The API 20 NE utilizes adipic acid (weakly), maltose, d-glucose, d-mannose (weakly), *n*-acetylglucosamine, and trisodium citrate, but not maltose, d-mannitol, l-arabinose, malic acid, phenylacetic acid, or potassium gluconate. Q-10 is the sole respiratory quinone. The major cellular fatty acids are summed feature 8 ($C_{18:1}\omega7c$ and/or $C_{18:1}\omega6c$) and $C_{19:0}$ $\omega8c$ cyclo. The major polar lipids are diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), one phospholipid (PL), and one uncharacterized lipid (L) as the dominant elements.

The type strain SC-ST17^T (= KCTC 92,119^T = MCCC 1K07309^T) was isolated from saline-alkali land. The G + C content of the genomic DNA of strain SC-ST17^T is 62.7%.

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Author contributions XPY wrote the manuscript and analysed the cultivation data. LYZ and XWW performed the genomic and phylogenetic analysis. JPD and PBL isolated the strain and performed the initial cultivation and strain deposition. ZFW contributed to text preparation and revised the manuscript. ZHT took the samples. YQX corrected and reviewed the draft. All authors read and approved the final version of the manuscript.

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Data availability The genome and 16S rRNA gene sequence are available from GenBank under the accession numbers provided in the manuscript.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval This article does not contain any studies with animals performed by any of the authors.

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