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ORIGINAL PAPER

Shewanella shenzhenensis sp. nov., a novel Fe(III)-reducing bacterium with abundant possible cytochrome genes, isolated from mangrove sediment

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Abstract A facultative anaerobic bacterium, designated as A25^T, was isolated from a mangrove sediment sample collected in Shenzhen, China. Cells of strain A25^T were found to be Gram-staining negative, rod-shaped, flagella-harboring, and oxidase- and catalase-positive. The isolate was able to grow at 4–40 °C (optimum 28 °C) and pH 5.0–9.0 (optimum pH 6.0), and in 0–10% NaCl concentration (w/v) (optimum 1%). Strain A25^T was capable of reducing Fe(III) citrate under anaerobic conditions. The major fatty acids of this strain was $C_{16:1}\omega7c/C_{16:1}\omega6c$ (summed feature 3), $C_{17:1}\omega8c$ and iso-$C_{15:0}$. Results of phylogenetic analyses based on 16S rRNA gene sequences indicated that strain A25^T is affiliated with the genus *Shewanella*, showing the highest similarity to *Shewanella seohaensis* S7-3^T (98.4% similarity). The average nucleotide identity and digital DNA-DNA hybridization values between the genomes of strain A25^T and its closely related strains were ≤ 79.0% and ≤ 22.8%, respectively. Based on its phenotypic, phylogenetic properties and physiological and biochemical characteristics, strain A25^T (=JCM 34900^T = GDMCC 1.2731^T) was designated as the type strain of a novel species of the genus *Shewanella*, for which the name *Shewanella shenzhenensis* sp. nov. was proposed.

Keywords *Shewanella shenzhenensis* · Novel species · Polyphasic taxonomy · Reduction of Fe(III) citrate

Introduction

The genus *Shewanella*, belonging to the family *Shewanellaceae* within the order *Alteromonadales* of the class *Gammaproteobacteria*, was first described by MacDonell and Colwell (MacDonell and Colwell 1985). At the time of writing, this genus contains 76 species with validly published names (https://lpsn.dsmz.de/genus/shewanella). Members of the genus *Shewanella* have been isolated from diverse environments such as mangrove sediment (Zhang et al. 2021), seawater (Bae et al. 2020), brown algae (Kim et al. 2016), fish (Satomi et al. 2006), activated sludge (Xu et al. 2005), tidal flat sediment (Yoon et al. 2012) and Antarctic coastal areas (Bozal et al. 2002). The genus *Shewanella* compose a group of facultative anaerobic bacteria that are physiologically diverse, and the hallmark is the ability to utilize a diverse electron acceptors (e.g. Fe(III) and nitrate) in the absence of oxygen, which allows them to survive in

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diverse habitats (Wang et al. 2010). In light of their fascinating physiology, the genus *Shewanella* have several biotechnological uses, from bioremediation of chlorinated compounds and other environmental pollutants to energy-generating biocatalysis (Hau and Gralnick 2007).

Mangroves are highly productive ecosystems of tropical and subtropical coastlines which are of great interest for their ecological, sociological and economical roles (Holguin et al. 2001). In mangrove ecosystems, iron performs vital roles as it is an essential nutrient for pants and marine plankton, and the iron bioavailability is directly affected by microbial Fe(III) reduction in mangrove sediments (Queiroz et al. 2022). Up to date, several *Shewanella* strains have been isolated from the mangrove sediments, and with these isolates as type strains, a total of 5 *Shewanella* species have been established (Liu et al. 2015, 2021; Zhang et al. 2021). However, none of these species are reported to have the Fe(III) reduction capability.

In the present study, a bacterium of the genus *Shewanella*, designated A25^T, was isolated from a mangrove sediment sample, and was identified using polyphasic taxonomic approaches. As a result, a novel species *Shewanella shenzhenensis* sp. nov. is proposed using strain A25^T as the type strain. Since strain A25^T was capable of reducing Fe(III), the study of strain A25^T would have important implication for understanding the biogeochemical process of iron in mangrove ecosystem.

Materials and methods

Isolation and culture conditions

Strain A25^T was isolated from a mangrove sediment sample in Futian district Shenzhen city (22° 30′–22° 32′ N, 113° 56′–114° 3′ E). In a sterile environment, mangrove sediment sample was diluted with physiological saline, and spread on LB agar containing (/L) 10.0 g peptone, 5.0 g NaCl, 1.0 g glucose, and 5.0 g yeast paste powder (pH 7.0 ± 0.2). After aerobic incubation at 30 °C for one week, the colonies were picked for bacterial purification by plate streaking on LB agar repeatedly. The resulting pure strain was maintained as aqueous glycerol suspensioin (50%; v/v) at − 80 °C and was then deposited in the Guangdong Microbial Culture Collection Center (GDMCC) and Japan Collection of Microorganisms (JCM).

Phylogeny analysis based on 16S rRNA gene sequences

Genomic DNA of strain A25^T was extracted using a DNA extraction Kit (Takara, Japan), and was used for sequencing of the 16S rRNA gene and the whole genome. The 16S rRNA gene was amplified by PCR using primers 27F and 1492R (Weisburg et al. 1991). The resulting PCR product was purified and cloned into the pMD19-T vector (Takara) and sequenced using Sanger sequencing. The 16S rRNA gene sequence obtained was subsequently compared with other type strains using the EzBiocloud platform (Yoon et al. 2017a, b). The 16S rRNA gene sequences of closely related species were subsequently aligned with strain A25^T by ClustalW algorithm of MEGA X (Kumar et al. 2018). Phylogenetic trees were reconstructed based on the mixmum-likelihood and neighbour-joining algorithms using MEGA X with *Psychrobium conchae* BJ-1^T as outgroup. For the neighbour-joining tree, the substitution model maximum composite likelihood method was chosen, and for the maximum-likelihood tree, the Tamura-Nei model was applied. The topology of the trees was evaluated by performing a bootstrap analysis based on 1000 replications.

Genome sequencing and analysis

For genome analyses of strain A25^T, the whole genomes were sequenced using Illumina Hiseq 2000 technology and were assembled by SOAPdenovo (Guangzhou Meige Biotechnology Co., Ltd.). The draft genome sequence of strain A25^T has been deposited in Genbank database under the accession numbers of JAKOGF000000000. Genome annotation was carried out using Rapid Annotation using Subsystem Technology (RAST) server (Aziz et al. 2008) and NCBI Prokaryotic Genome Annotation Pipeline (PGAP) (Tatusova et al. 2016). For functional classification, the predicted protein sequences were searched against the NCBI non-redundant database using BLASTP, and the outputs were imported into BLAST2GO V5.2.5 for GO term mapping (Conesa et al., 2005). The results of BLAST2GO were

submitted to the WEGO for GO classification (Ye et al., 2006). The predicted protein sequences were submitted to BlastKOALA for functional annotation based on KEFF orthology (KO), and the KO number were then submitted to KEGG Mapper to reconstruct the pathway (Kanehisa et al. 2016; Kanehisa 2017).

The relatedness between the genomic sequences of strain A25^T and type strains of *Shewanella* species was estimated based on the average nucleotide identity (ANI), and digital DNA–DNA hybridization (dDDH) using the ANI calculator in EzBioCloud platform (Yoon et al. 2017a, b) and Genome-to-Genome Distance Calculator (GGDC) version 2.1 (Meier-Kolthoff et al. 2013), respectively.

For genome phylogenetic analysis, the automated multi-locus species tree (autoMLST) online server was used to automatically identify house-keeping genes (Alanjary et al. 2019). The closely related type species of the new isolates and outgroup *Phenylobacterium zucineum* HLK1^T were selected to construct a high-resolution species tree. The final phylogenetic tree based on 100 core genes was reconstructed by MEGA X software using maximum-likelihood algorithm.

Phenotypic and chemotaxonomic characterization

Cell morphology was observed with a transmission electron microscope after cultivation on LB plate for 24 h. Clone morphology was observed after cultivation on LB agar for 48 h. The Gram reaction was determined by a Gram staining kit HB8278 (Qingdao Hope-Bio Technology Co., Ltd; China). Oxidase activity was determined using an oxidase reagent (BioMérieux), and catalase activity was determined by observing bubble production in 3% (v/v) hydrogen peroxide solution. Hydrolysis of Tween 20, Tween 40, Tween 80, starch and casein were performed on MA with a final concentration of 1% (w/v). The temperature range for growth was determined in the range 0–42 °C (at intervals of 0, 4, 10, 15, 20, 25, 28, 30, 37 and 42 °C). The pH range for growth was determined at pH 4.0–10.0 (at intervals of 1.0 pH unit). The tolerance for NaCl concentrations was determined with 0–12% (w/v) NaCl (with increments of 1.0%). The anaerobic growth was tested in mineral medium containing (L-1) 0.04 g $CaCl_2{\cdot}2H_2O$, 0.10 g $MgSO_4{\cdot}7H_2O$, 1.80 g $NaHCO_3$, 0.43 g Na_2CO_3, 0.42 g KH_2PO_4, 0.22 g K_2HPO_4, 0.20 g NH_4Cl, 0.38 g KCl, 10.0 ml vitamin stock solution and 10.0 ml mineral stock solution (Lovley and Phillips 1988) supplementary with lactate (10 mM) as electron donor and Fe(III) citrate (50 mM) or nitrate (20 mM) as electron acceptor; The optical density at 600 nm (OD_{600}) was measured to evaluate cell growth. Other physiological characteristics were characterized with the API 20NE systems (BioMérieux) according to the manufacturer's instructions. Disc diffusion was used to test the strain's sensitivity to antibiotics. The following antibiotics were tested: erythromycin (15 μg), neomycin (30 μg), penicillin (10 μg), kanamycin (30 μg), gentamicin (10 μg), carbenicillin (100 μg), clindamycin (2 μg), lincomycin (2 μg), polymixinB (300 iu), rifamipcin (5 μg), chloramphenicol (30 μg), ofloxacin (5 μg), norfloxacin (10 μg), and ciprofloxacin (5 μg). Sensitivity is assessed by determining the size of the diameter of the antibacterial ring.

For fatty acid profile analysis, cells of strain A25^T and its reference strains grown in LB medium to exponential growth phase were collected by centrifugation at 12,000 rpm at 4 °C, and freeze-dried using the vacuum freeze drying apparatus (Scientz-10 N, Ningbo, China). The fatty acids in whole cells were saponified, methylated and extracted according to the standard protocol of MIDI (Sherlock Microbial Identification System, version 6.0B). The fatty acids were analyzed with GC (Agilent Technologies 6850) and identified using the TSBA6.0 database of the Microbial Identification System.

Results and discussion

Phylogenetic analysis based on 16S rRNA gene and core genomes

The nearly complete 16S rRNA gene sequence of strain A25^T (1526 bp) was obtained. Sequence comparison showed that strain A25^T shared the highest 16S rRNA gene sequence similarity with *Shewanella seohaensis* S7-3^T (98.4% similarity) followed by *Shewanella decolorationis* S12^T (98.0% similarity). These values were below the threshold (98.7%) for species delineation (Chun et al., 2018). In the maximum-likelihood and neighbour-joining phylogenetic trees based on 16S rRNA gene sequences (Supplementary Fig. S1 and S2), strain A25^T fell within the clade of the genus *Shewanella* and formed

an internally independent branch with *S. seohaensis* S7-3^T and *S. decolorationis* S12^T. Above results suggested that strain A25^T represents a different species from known species of the genus *Shewanella*.

The genome sequence of strain A25^T was 4,821,510 bp with G+C content of 47.3 mol%. The results of dDDH and ANI analysis indicated that strain A25^T showed the highest dDDH and ANI values with *S. decolorationis* S12^T (22.8% for dDDH and 79.0% for ANI), which were lower than the standard cutoff value for species delineation (70% for dDDH and 95% for ANI) (Chun et al. 2018). As shown in phylogenetic tree based on core genomes (Fig. 1), strain A25^T was located in a cluster with *S. decolorationis* S12^T and was far from other type strains of the genus *Shewanella*. These results supported the proposal that this strain represented a novel species of the genus *Shewanella* (Fig. S1 and S2).

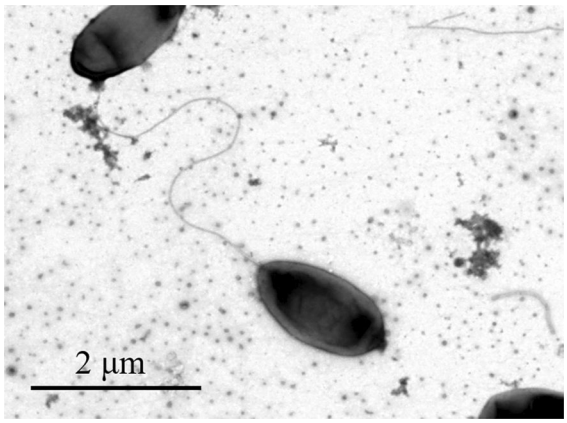

Fig. 2 Transmission electron microscopy image of new isolated strain

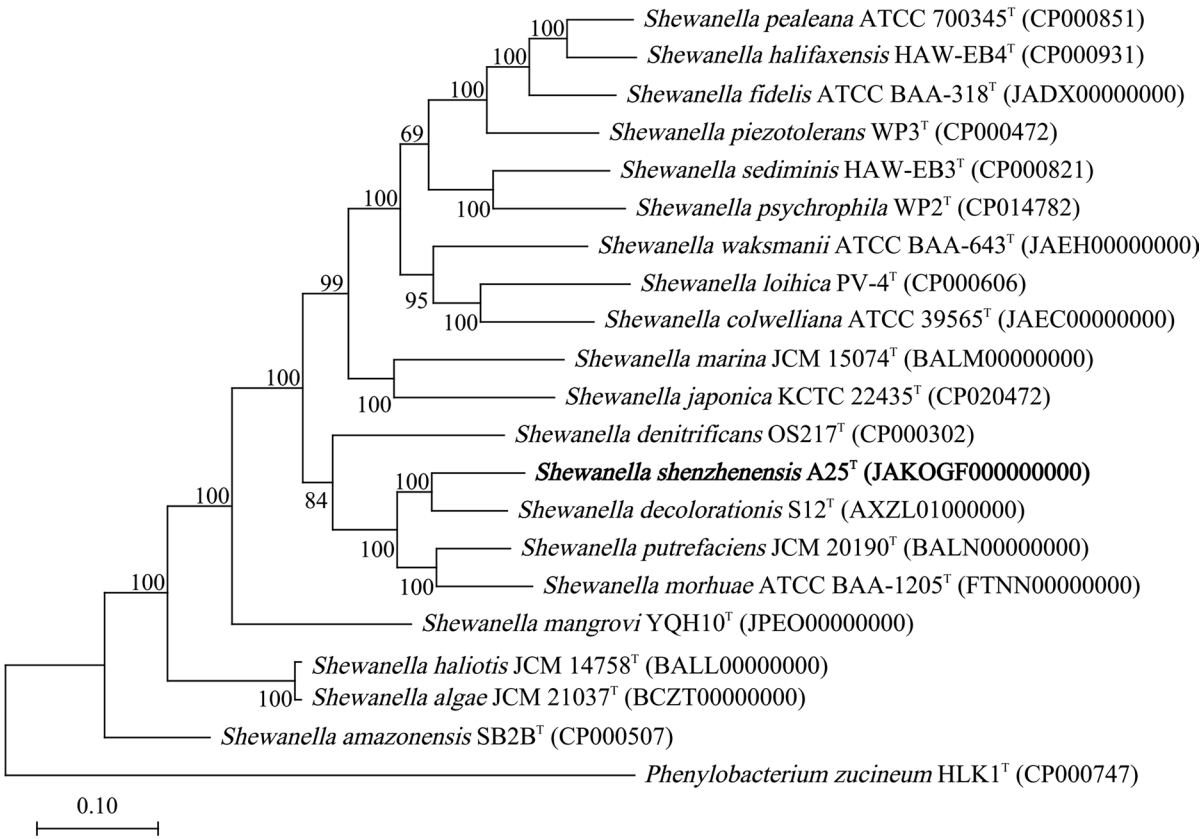

Fig. 1 Phylogenetic tree based on the core genomes showing the position of strain A25^T and related type species of family *Shewanella*ceae. *Phenylobacterium zucineum* HLK1^T was selected as outgroup. Numbers at branch refer to bootstrap values based on 1000 replicates and only values above 50% were given at nodes. Bar, 0.10 substitutions per nucleotide position

Phenotypic characteristics

Colonies of strain A25^T were 1–2 mm in diameter, pink, circular and smooth. Cells were observed to be Gram-staining-negative and facultative anaerobic. Under electron microscope (Fig. 2), the cells were rod-shaped, 1.7–2.1 μm in length, and 0.5–0.6 μm in diameter and a polar flagellum was detected.

Strain A25^T was able to grow under the temperature range of at 4–40 °C (optimum 28 °C) and pH 5.0–9.0 (optimum pH 6.0), and in 0–10% NaCl (w/v). The optimal pH for growth of strain A25^T was lower than that of its reference strains *S. seohaensis* S7-3^T (optimal pH 7–8) and *S. decolorationis* S12^T (optimal pH 7) (Table 1), but such low optimal pH was common for some *Shewanella* species such as *Shewanella mangrovi* (optimal pH 6) and *Shewanella yunxiaonensis* (optimal pH 5) which were sourced from mangrove sediments (Liu et al. 2015, 2021). Strain A25^T could hydrolyze Tween 20, Tween 40, Tween 80 and gelatin but not casein and starch. Activities of oxidase and catalase were found to be positive. Nitrate cannot be reduced under anaerobic conditions. In API 20NE test, activities of β-glucosidase and urease, reduction of nitrate, and utilization of D-glucose, L-arabinose, *N*-acetyl-glucosamine, maltose, gluconate, adipic acid and malic acid were positive, but activities of arginine dihydrolase and β-galactosidase, production of indole, production of acid from glucose, and utilization of D-mannose, mannitol, capric acid, citrate and phenylacetic acid were negative. Strain A25^T was susceptible to neomycin, penicillin, kanamycin, gentamicin, clindamycin, lincomycin, rifamipcin, erythromycin, chloramphenicol, polymixinB, ofloxacin, norfloxacin, and ciprofloxacin, but resistant to carbenicillin. The physiological properties differentiated strain A25^T from its closest neighbours were listed in Table 1.

Chemotaxonomic analysis

The whole-cell fatty acid profile of strain A25^T contained the major cellular fatty acids (> 10%) of $C_{16:1}\omega7c/C_{16:1}\omega6c$ (summed feature 3) (19.3%), $C_{17:1}\omega8c$ (17.2%) and iso-$C_{15:0}$ (14.4%), which was the same pattern found in the two reference strains (*S. seohaensis* S7-3^T and *S. decolorationis* S12^T) (Table S1) and several type strains of other *Shewanella* species (Cha et al. 2020; Verma et al. 2011).

Capacity of Fe(III) reduction

Under anaerobic conditions, strain A25^T was capable of reducing about 50 mM of Fe(III) citrate with lactate as the sole electron donor within 5 days, and the Fe(III) reduction could support the cell growth of strain A25^T (Supplementary Fig. S3). It has been reported that members of the genus *Shewanella* such as *S. decolorationis* S12^T (relative of strain A25^T) and *Shewanella oneidensis* MR-1 (well-studied model of

Table1 Differential characteristics of strain A25 and related type species

Characteristics	1	2	3
Cell size (μm)	0.5–0.6 × 1.7–2.1	0.6–1.0 × 1.0–3.0	0.6–1.0 × 1.0–4.0
Color	Pink	Transparent light brown	Pink
DNA G + C content (mol%)	47.3	51.8	49.3
Optimal temperature (°C)	28	30	25
Optimal pH	6	7–8	8
Optimal NaCl (%)	1	2	2
β-glucosidase	+	−	−
Hydrolysis of			
Casein	−	+	+
Aesculin	+	−	−
Utilization of			
L-Arabinose	+	−	+
N-acetyl-D-glucosamine	+	−	+

1, *S. shenzhenensis* A25^T; 2, *S. seohaensis* S7-3^T; 3, *S. decolorationis* S12^T. +, positive; -, negative

Fe(III) reduction of the genus *Shewanella*) have the ability of iron reduction which play important roles in the global iron and carbon cycle (Fu et al. 2016; Li et al. 2012). Although there are more than 20 *Shewanella* species which are capable of reducing Fe(III), none of them were obtained from mangrove sediments. Therefore, strain A25^T might represent the first mangrove-sourced *Shewanella* species capable of reducing Fe(III).

Genomic features

A total of 4885 genes were predicted in the genomes of strains A25^T including 4723 protein-coding genes, 108 RNA genes (24 rRNA genes, 79 tRNA genes and 5 ncRNA genes) and 54 pseudogenes. The GO analysis indicated that these genes were assigned to a wide range of functional categories with three main categories: biological process, molecular function and cellular components (Supplementary Fig. S4). The majority of GO terms were assigned to the biological process in which the top five subgroups were metabolic process, cellular process, single-organism process, localization and biological regulation.

Mangrove habitats are subjected to stressors such as high salinity, hypoxia and strong tidal flows (Soldan et al. 2019), and the bacteria in mangrove sediments have evolved several stress response mechanisms to adapt to such conditions (Liu et al. 2021). In the genome of strain A25^T, there are 12 genes associated with antioxidant activity (Supplementary Fig. S4) which confer the stress tolerance ability to bacteria, 4 associated with potassium ion homeostasis which are involved in osmoregulation and pH homeostasis (MacGilvary et al. 2019). These genes might be essential for survival of strain A25^T in mangrove sediment, because they are crucial for detecting and responding to perturbations caused by environmental stress. The homologous genes of such stress-associated genes had been ever been reported in other *Shewanell*a species including *Shewanella avicenniae*, *Shewanella sedimentimangrovi* and *Shewanella yunxiaonensis* which were sourced from mangrove sediments (Liu et al. 2021).

Strain A25^T was detected to be positive for nitrate reduction under aerobic conditions, and thereby the genes responsible for nitrate reduction were analyzed using KEGG. Results showed that there is a complete pathway of dissimilatory nitrate reduction in the A25^T genome, which could mediate the reduction of nitrate to ammonia. In detail, the genes associated with dissimilatory nitrate reduction include *napAB* (L9G16_05415, L9G16_05420, L9G16_13485 and L9G16_13490), *nirBD* (L9G16_06820 and L9G16_06825) and *nrfAH* (L9G16_04630, L9G16_07330).

As reported, cytochromes are key components for Fe(III) reduction of *Shewanella* members (Shi et al. 2009). To explore the Fe(III) reduction mechanism of strain A25^T, the cytochrome genes in A25^T genome were analyzed. Results showed that the A25^T genome contains 60 cytochrome encoding genes among which most have homologous genes in the genomes of strain MR-1 and strain S12^T and 3 (MCH1933042, MCH1933053 and MCH1932204) are unique in the genome of strain A25^T (Table S2). In addition, homologous genes (MCH1928961, MCH1928962 and MCH1928963) of the *mtrABC* gene cluster which is known in strain MR-1 are also detected in the genome of strain A25^T. In a word, the abundant cytochrome genes might be responsible for Fe(III) reduction ability of strain A25^T.

Taxonomic conclusion

In sum, phylogenetic analysis based on the 16S rRNA genes and the genomes, the phenotypic characteristics, and the fatty acid profile supported the classification of strain A25^T as a member of the genus *Shewanella*, and suggested that the new isolate represents a novel species of the genus *Shewanella*, for which the name *Shewanella shenzhenensis* sp. nov. is proposed.

Description of *Shewanella shenzhenensis* sp. nov.

Shewanella shenzhenensis (shen.zhen.en'sis. N.L. fem. adj. *shenzhenensis*, referring to Shenzhen, the city where the type strain was isolated).

Cells are Gram-strain-negative, facultative aerobic and rod-shaped, with 1.7–2.1 μm long and 0.5–0.6 μm wide. Colonies are 1–2 mm in diameter, pink, circular and smooth after incubation on LB agar for 2 days. Bacteria growth occurs in the range of 4–40 °C (optimum 28 °C), pH 5.0–9.0 (optimum pH 6.0) and 0–10% (w/v) NaCl (optimum 1%). Nitrate can be reduced under aerobic conditions but not

under anaerobic conditions. Anaerobic growth occurs using Fe(III) citrate as electron acceptor and lactate as electron donor. Cells are positive for oxidase, catalase and hydrolysis of Tween 20, Tween 40, Tween 80 and gelatin, but negative for production of indole and hydrolysis of starch and casein. The predominant cellular fatty acids (> 5%) contain summed feature 3, C17:1ω8c, iso-$C_{15:0}$, and $C_{16:0}$. The G + C content of genomic DNA of the type strain is 47.3 mol%.

The type strain A25^T (= JCM 34900^T = GDMCC 1.2731^T) is isolated from a mangrove sediment in Futian district, Shenzhen, China. The 16S rRNA gene sequence and the whole genome sequence of the type strain are available from GenBank with accession number MZ477861 and JAKOGF000000000, respectively.

Author contribution GQY drafted the manuscript. XYZ and SJY performed isolation, deposition and identifications. XYZ performed the genome analysis. LZ designed all the experiments and revised the manuscript.

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Data availability All data generated or analyzed during this study are included in this published article, its supplementary information file and GenBank/EMBL/DDBJ. The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene and the genome sequences of strain A25^T are MZ477861 and JAKOGF000000000, respectively. Supplementary file including Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, transmission electron microscopy image strain A25^T, and reduction of Fe(III) citrate is available with the online version of this paper.

Declarations

Competing interests The authors declare no competing interests.

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

Ethical approval This study does not describe any experimental work related to human.

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