ORIGINAL PAPER

Streptomyces albicerus sp. nov., a novel actinomycete isolated from the sediments of the Tailan River in Xinjiang, China

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Abstract

A novel actinomycete, designated TRM68295[T], was isolated from the sediments of the Tailan River, Xinjiang, northwest China. The study of the polyphasic approach showed that the characteristics of the strain were consistent with the genus *Streptomyces*. Phylogenetic analysis indicated that the strain had a high sequence similarity with *Streptomyces phaeochromogenes* ATCC 3338[T] (97.9%). The diagnostic diamino acid of cell walls was identified as LL-diaminopimelic acid. The whole cell sugars were identified as ribose, xylose, glucose and galactose. The major fatty acids were iso-$C_{14:0}$, iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{16:0}$, $C_{16:1}\omega9c$, $C_{16:0}$ and anteiso-$C_{17:0}$. The major menaquinones were MK-9 (H_{10}), MK-9 (H_6) and MK-9 (H_2). The polar lipids were composed of diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG), phosphatidylcholine (PC), phosphatidylinositol (PI) and phosphatidylinositol mannoside (PIM). The G+C content in the draft genome sequence of the strain was identified as 70.0 mol%. The average nucleotide identity (ANI) between strains TRM68295[T] and *S. phaeochromogenes* ATCC 3338[T] was 88.1%. Digital DNA-DNA hybridization (dDDH) value between strain TRM68295[T] and *S. phaeochromogenes* ATCC 3338[T] was 40.7%. The multilocus sequence analysis of five housekeeping genes (*atp*D, *gyr*B, *rec*A, *rpo*B, and *trp*B) indicated that the MLSA distances between the strain and similar species were greater than the threshold of 0.007. Based on the above studies, strain TRM68295[T] is considered as a novel species of the genus *Streptomyces*, for which the name *Streptomyces albicerus* sp. nov. is proposed. The type strain is TRM68295[T] (= CCTCC AA 2018085[T] = KCTC 49272[T]).

Keywords *Streptomyces albicerus* · *Streptomycetaceae* · Novel species · Polyphasic taxonomy

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Introduction

Waksman and Henrici first proposed *Streptomyces* in 1943. As of this writing, more than 850 species with valid names of *Streptomyces* have been published (https://www.bacterio.net/streptomyces.html) (Zhang et al. 2017). *Streptomyces* are aerobic Gram-positive bacteria with well-developed mycelia, which can produce a large number of conidia for reproduction. *Streptomyces* can produce a variety of secondary metabolites, such as antimicrobial drugs, antineoplastic drugs, enzyme inhibitory activities, herbicides, insecticides, antiparasitic agents, hypoglycemic agents (Deshpande et al. 1988). To find microorganisms that can produce new antibiotics, more attention focuses on the unexplored natural environments, such as deep sea (Tian et al. 2013), desert (Calasanz et al. 2013), polar (Encheva et al. 2013) and salt lake (Jose and Jebakumar 2012).

The Tailan River Basin is located in Wensu, Aksu District, Xinjiang. It originates from the Tuomuer Peak in the

southwestern Tianshan Mountains. The upper reaches are the Big Tailan River and the Small Tailan River. The two rivers are called Tailan River after merging in the area of 8 km before the mountain. The climate of the basin belongs to the continental temperate arid climate with properties of dry climate, abundant sunshine, windy sand, rare precipitation, large evaporation and large temperature difference between day and night. We sampled sediments of the Tailan River to isolate actinomycetes and analyze the diversity of actinomycetes. During the process, a novel species TRM68295[T] was isolated. This study determined the taxonomic status of the strain based on genotype, physiological and biochemical characteristics, and phylogeny.

Materials and methods

Strain isolation and culturing

Strain TRM68295[T] was isolated from the sediments of the Tailan River at Aksu, Xinjiang, northwest China (latitude 40° 71′; longitude 81° 16′). The strain was isolated by the spread plate method on glycerol–arginine medium which contained (g/l): arginine 2 g, glycerol 12 g, $MgSO_4$ 0.5 g, K_2HPO_4 1 g, agar 17 g, pH 7.5, supplemented with 100 µl of 50 mg $K_2Cr_2O_7$/ml in a 100 ml medium to reduce fungal contamination. The strain was isolated after culturing at 28 °C for 10 days. The strain was purified on Gauze's No. 1 medium at 28 °C. The strain was stored in 20% glycerol for a short term, and lyophilized in 20% skim milk powder for long-term storage. *Streptomyces phaeochromogenes* ATCC 3338[T] was purchased from American Type Culture Collection (ATCC). *Streptomyces ederensis* JCM 4958[T] was purchased from the Japan Collection of Microorganisms (JCM).

Morphological, cultural, physiological, and biochemical characteristics

To determine the culture characteristics, strain TRM68295[T] was cultured on ISP 1-7 medium (Shirling and Gottlieb 1966), Czapek's agar, Nutrient agar (Waksman 1967) and Gauze's No. 1 medium for 14 days at 28 °C. The colors of the substrate mycelium, aerial mycelium and soluble pigment were determined by the ISCC NBS color chart (Kelly 1964). Morphology properties were observed by light microscopy (Leica DM1000) and scanning electron microscopy (Thermo Apreo) using cultures grown on Gauze's No. 1 medium at 28 °C for 20 days. Different temperatures (4, 16, 20, 25, 28, 32, 37, 40, 45 and 50 °C), pH (pH 4.0–12.0, interval 1.0 pH unit) (Xu et al. 2005) and concentrations of NaCl (0–10%, interval 1%, w/v) for strain growth were examined on Gauze's No. 1 medium and were observed after at 28 °C for 14 days. The productions of peroxidase, urease,

esterase and catalase were tested using the method described by Gerhardt et al (1994). The uses of sole carbon source (0.5%, w/v), cellulose decomposition, starch hydrolysis, liquefaction of gelatin, milk peptonization and solidification, nitrate reduction and production of H_2S (Gordon 1974; Yokota et al. 1993) were studied.

Chemotaxonomy

Biomass used for studies was obtained by culture in liquid Gauze's No. 1 medium for 7 days in shake flasks at 28 °C. The cells collected by centrifugation were washed with distilled water, and then freeze-dried. Cell wall amino acids were determined by the method proposed by Staneck and Roberts (1974). The whole cell sugars were determined by the method proposed by Tang et al. (2009). Polar lipids were detected by two-dimensional TLC and identified by the method proposed by Minnikin et al. (1984). Menaquinones were extracted from freeze-dried biomass according to the method proposed by Collins et al. (1977), and analyzed by HPLC (Wang et al. 2011). Cellular fatty acids were extracted from the fresh cells according to the method proposed by Sasser (1990), and analyzed by GS chromatography using the Microbial Identification System (Sherlock version 6.1; MIDI database: RTSBA6).

Genome sequencing and phylogenetic analysis

The extraction of genomic DNA and PCR amplification of 16S rRNA sequence was performed by the method of Chun and Goodfellow (1995). The purified PCR product was cloned into the vector pMD18-T (Takara) and sent to Sangon for gene sequencing. The two sequences obtained by gene sequencing were spliced using SeqMan software. After using vecscreen (https://www.ncbi.nlm.nih.gov/tools/vecscreen/) to remove the vector sequences, an almost complete 16S rRNA gene sequence (1494 bp) was obtained. EzBioCloud (https://www.ezbiocloud.net/identify, Yoon et al. 2017) was used to calculate the 16S rRNA gene sequence similarity with other strains, and then the sequences of closely related strains were selected to construct the phylogenetic tree. The initial alignment was performed using clustal_x software (Thompson et al. 1997). The phylogenetic tree was constructed using the Neighbor-Joining (Saitou and Nei 1987), Maximum-Parsimony (Fitch 1971) and Maximum-Likelihood (Felsenstein 1981). The corresponding algorithms were realized using MEGA 7.0 (Kumar et al. 2016). The stability of the topology of the phylogenetic trees was evaluated by performing 1000 resamplings (Felsenstein 1985).

The draft genome sequence of strain TRM68295[T] was sequenced using the Illumina platform. Velvet (Bankevich et al. 2012) software was used to assemble the sequencing

data of the strain. The completeness and contamination of the genome were evaluated by the software CheckM (Parks et al. 2015). The average depth of genome coverage was 137-fold. The assembled genome was predicted by prodigal (Hyatt et al. 2010). The software tRNAscan-SE (Lowe and Eddy 1997) was used to predict the tRNA in the genome, and the software Infernal1.1 (Nawrocki and Eddy 2013) was used to predict the rRNA in the genome based on the Rfam (Nawrocki et al. 2015) database. The putative biosynthetic gene clusters for secondary metabolites were identified using the AntiSMASH program, version 4.0 (Weber et al. 2015). The genome sequences of strain TRM68295[T] (accession no. VWMY00000000) and strain *S. phaeochromogenes* (accession no. LIQZ00000000) have been submitted to GenBank. The G+C content of strain TRM68295[T] was determined from the draft genome sequence by Average Nucleotide Identity (ANI) calculator (Yoon et al. 2017). The average nucleotide identity (ANI) was determined using the web-service (https://www.ezbiocloud.net/tools/ani) (Lee et al. 2015). The digital DNA–DNA hybridization (dDDH) values were calculated on the GGDC website using formula 2, originally described by Auch et al. (2010) and updated by Meier-Kolthoff et al (2013). Five housekeeping gene sequences of strain TRM68295[T] were obtained by PCR amplification. The housekeeping genes of closely related strains were downloaded from the website (https://199.133.98.43/cgi-bin/bigsdb/bigsdb.pl?db=public_ars_streptomyces_isolates&page=query). The phylogenetic tree was constructed using the Neighbor-Joining algorithm in MEGA 7.0 (Kumar et al. 2016). The MLSA distances were calculated using MEGA 7.0.

Results and discussion

After 14-day culture at 28 °C, the growth of strain TRM68295[T] on ten standard media, the colors of aerial mycelia and substrate mycelia were recorded (Table 1). The strain grew well on ISP 4, ISP 5, ISP 7, Gauze's No. 1 agar and Czapek's agar, and grew moderately on ISP 1, ISP 2, ISP 3, ISP 6 and nutrient agar medium. A soluble pigment (black) was produced on ISP 7 medium. The aerial mycelium was dense, cylindrical, with a smooth surface and no branches. The spore chain was helical. The spores were cylindrical, of which the surface was spiny (Supplementary Fig. 1). The strain could grow at 16–45 °C, pH 6.0–10.0 and 0–6% NaCl, and grow best at 2% (w/v) NaCl at 28 °C and pH 7.0. The strain was found to be positive for catalase, urease, gelatin liquefaction, milk peptonization and solidification, starch hydrolysis, nitrate reduction, cellulose decomposition, but negative for oxidase, melanin production, H_2S production. The strain could degrade Tweens 20, 40, 60 and 80.

Table 1 Characteristics of strain TRM68295[T] grown on various media at 28 °C for 14 days

Medium	Growth	Color of mycelia	
		Aerial	Substrate
ISP 1	Moderate	Brown	Brown
ISP 2	Moderate	Brown	Brown
ISP 3	Moderate	Brown	Brown
ISP 4	Good	Pale yellow	Pale yellow
ISP 5	Good	Pale yellow	Pale yellow
ISP 6	Moderate	Brown	Brown
ISP 7	Good	Pale yellow	Brown
Nutrient agar	Moderate	Brown	Brown
Gauze's No. 1 agar	Good	Pale yellow	Pale yellow
Czapek's agar	Good	Pale yellow	Pale yellow

The diagnostic diamino acid of cell wall was identified as LL-diaminopimelic acid. The whole cell sugars were found with ribose, xylose, glucose and galactose as main sugars. The polar lipids were composed of diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG), phosphatidylcholine (PC), phosphatidylinositol (PI) and phosphatidylinositol mannoside (PIM) (Supplementary Fig. 2). The menaquinones were identified as MK-9 (H_{10}), MK-9 (H_6) and MK-9 (H_2). The major fatty acids were identified (> 5%) as iso-$C_{14:0}$ (5.5%), iso-$C_{15:0}$ (11.2%), anteiso-$C_{15:0}$ (19.4%), iso-$C_{16:0}$ (21.0%), $C_{16:1}\omega9c$ (5.3%), $C_{16:0}$ (9.1%) and anteiso-$C_{17:0}$ (9.0%).

According to the EzBioCloud analysis, the 16S rRNA gene sequence of strain TRM68295[T] (GenBank accession no. MK795696) had high similarity with members of the genus *Streptomyces*, and the closest phylogenetic neighbor was *S. phaeochromogenes* ATCC 3338[T] (97.9%). The phylogenetic tree constructed from the 16S rRNA gene sequences by the Neighbor-Joining method showed that strain TRM68295[T] formed a distinct clade (Fig. 1), which was also recovered in the Maximum-Parsimony and Maximum-Likelihood trees (Supplementary Figs. 3, 4). The draft genome sequence consists of 307 contigs and 200 scaffolds covering a total sequence length of 10,359,585 bp, with an N50 contig size of 82,685 bp and an N50 scaffold size of 138,999 bp. The completeness and contamination of the genome were 99.5% and 0.6%, respectively. The number of rRNAs and tRNAs predicted by genome was 5 and 68, respectively. The draft genome contains 47 putative biosynthetic gene clusters capable of producing various secondary metabolites, including polyketides, non-ribosomal peptides, terpenes, lanthipeptides, siderophores, ectoine, bacteriocins, lassopeptides, melanin and thiopeptide, which suggested that strain TRM68295[T] had the potential to produce novel antimicrobial compounds or their analogues.
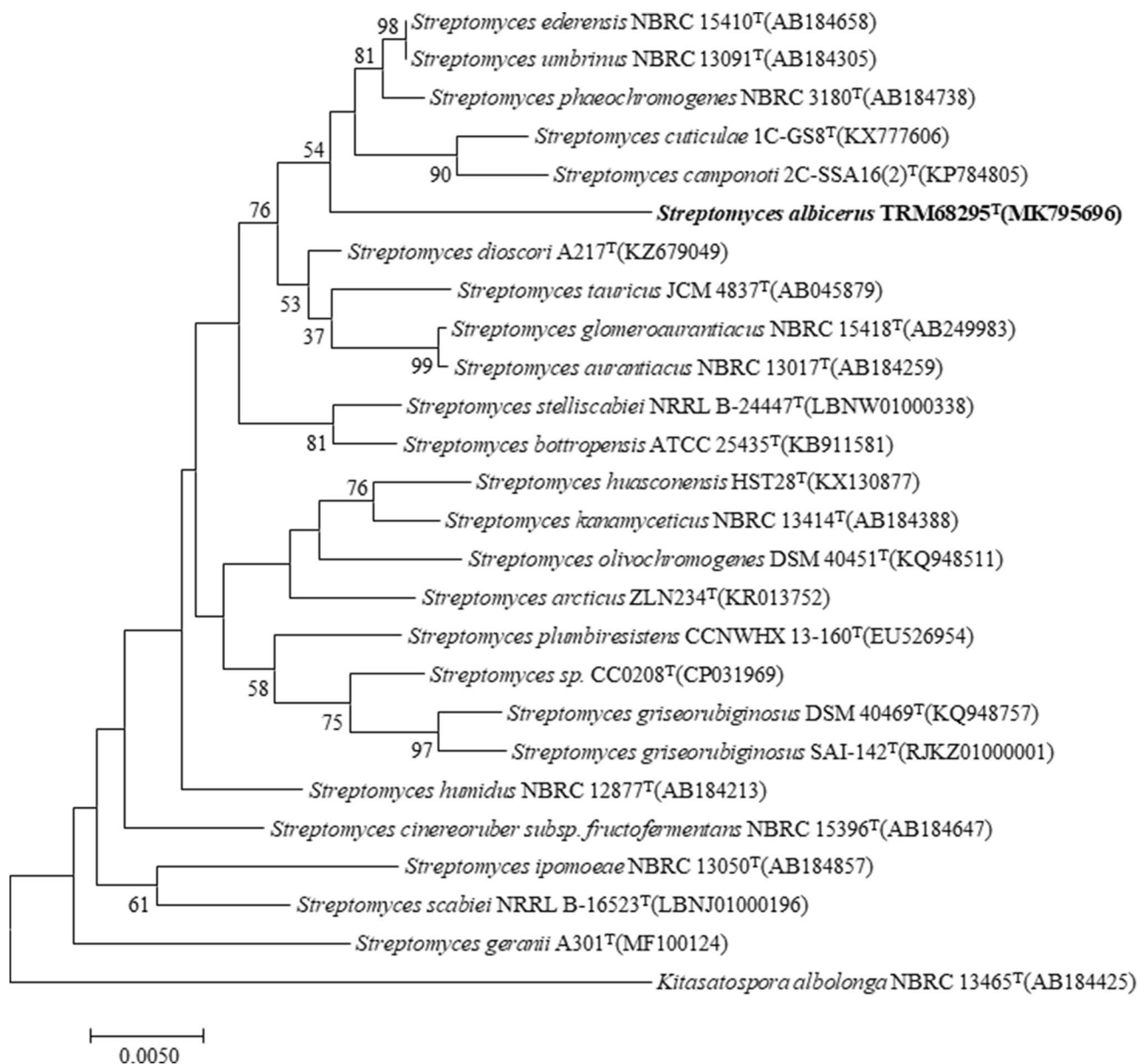
Fig. 1 Neighbor-joining tree based on 16S rRNA gene sequences, illustrating the positions of strain TRM68295[T] among related type strains. Numbers at nodes are percentage bootstrap values based on 1000 resampled datasets; only values above 50% are indicated. Bar, 0.005 substitutions per nucleotide position

The G+C content in the draft genome sequence of strain TRM68295[T] was identified as 70.0 mol%. The average nucleotide identity (ANI) value of strains TRM68295[T] and *S. phaeochromogenes* ATCC 3338[T] was 88.1%. The average nucleotide identity value is significantly lower than the widely accepted threshold for describing prokaryote species (95–96%; Kim et al. 2014). The dDDH value of strain TRM68295[T] and its closest strain *S. phaeochromogenes* ATCC 3338[T] was 40.7%, which is significantly lower than 70% of the species defined threshold (Richter et al. 2016; Wayne et al. 1987). The MLSA phylogenetic analysis showed *Streptomyces dioscori* (MLSA distance = 0.049), *Streptomyces cinereoruber subsp. fructofermentans* (MLSA distance = 0.051), *Streptomyces tauricus* (MLSA distance = 0.053) and *S. phaeochromogenes* (MLSA distance = 0.056) as the nearest neighbors (Fig. 2). The MLSA distance was much larger than the threshold for species classification (> 0.007) (Rong and Huang 2012). The characteristics differentiating between strain TRM68295[T] and closely related strains are shown in Tables 2 and 3. Based on the above studies, strain TRM68295[T] is considered a novel species of the genus *Streptomyces*, for which the name
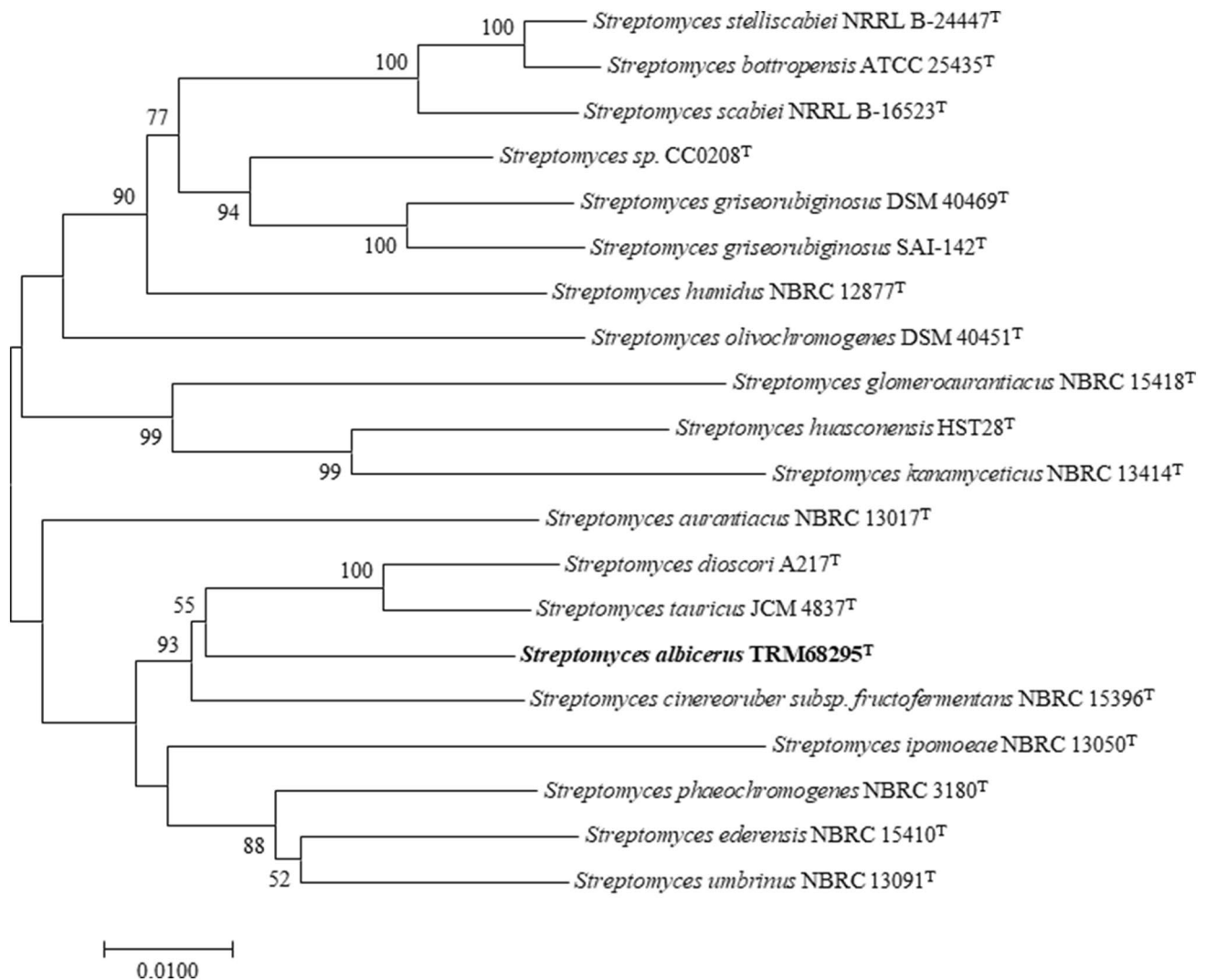
Fig. 2 Neighbour-joining tree based on concatenated partial sequences of five housekeeping genes (*atp*D, *gyr*B, *rec*A, *rpo*B and *trp*B) shows the position of strain TRM68295^T amongst its phyloge-netic neighbours. Only bootstrap values above 50% (percentages of 1000 replications) are indicated. Bar, 0.01 substitutions per nucleotide position

Streptomyces albicerus sp. nov. is proposed. The type strain is TRM68295^T (=CCTCC AA 2018085^T =KCTC 49272^T).

Description of *Streptomyces albicerus* sp. nov.

Streptomyces albicerus (al.bi'cer.us L. masc. adj. *albicerus*, Pale yellow, because of the pale yellow aerial hyphae of the strain).

Gram-positive, aerobic actinomycetes. The aerial mycelium is dense, cylindrical, and the surface is smooth. The spore chain is spiral, and the spore surface is spiny. Grow well on ISP 4, ISP 5, ISP 7, Gauze's No. 1 medium and Czapek's agar; grow moderately on ISP 1, ISP 2, ISP 3, ISP 6 and Nutrient agar medium. Soluble pigment (black) is produced on ISP 7 medium. The strain can grow at 16–45 °C, pH 6.0–10.0 and 0–6% NaCl, and grow best at 2% (w/v) NaCl at 28 °C and pH 7.0. Maltose, D-trehalose, xylose, raffinose, D-galactose, chitosan, L-sorbose, lactose, D-cellobiose, glucose, L-fucose, sucrose, xylan, Inositol, D-ribose, L-arabinose, D-fructose, starch or L-rhamnose are utilized. Melezitose, D-Salicin and xylitol are not utilized. Positive for catalase, urease, gelatin liquefaction, milk peptonization and solidification, starch hydrolysis, nitrate reduction, cellulose decomposition, degradations of Tweens 20,40, 60 and 80, whereas negative for oxidase, melanin production, production of H_2S; contains LL-diaminopimelic as diagnostic amino acid of the peptidoglycan and ribose, xylose, glucose and galactose in whole cell hydrolysates. The polar lipids contain diphosphatidylglycerol (DPG), phosphatidylethanolamine (PE), phosphatidylglycerol (PG), phosphatidylcholine (PC), phosphatidylinositol (PI) and phosphatidylinositol mannoside (PIM). The

Table 2 Characteristics differentiating strain TRM68295[T] from closely related members of the genus *Streptomyces*

Characteristic	1	2	3	4	5
Spore surface	Spiny	Smooth	Smooth	Smooth	Smooth
Spore chain morphology	Spiral	Straight	Spiral	Straight	Straight
Grown on sole carbon sources (0.5%, w/v)					
Maltose	+	+	+	−	+
Xylose	+	+	−	+	+
Sucrose	+	+	+	−	+
D-Ribose	+	−	+	+	+
L-Arabinose	+	+	−	+	+
D-Fructose	+	+	−	−	+
L-Rhamnose	+	+	−	+	+
Gelatin liquefaction	+	−	−	−	−
Hydrolysis of starch	+	+	+	−	+
Reduction of nitrate	+	+	−	−	+
Decomposition of cellulose	+	−	−	−	−
Hydrolysis of Tween 20	+	+	−	−	+
Production of H2S	−	−	−	+	−
Temperature range for growth (°C)	16–45	4–40	15–37	10–37	4–40
pH range for growth	6–10	6–11	5–10	6–11	5–10
NaCl concentration for growth (%, w/v)	0–6	0–3	0–3	0–6	0–5

Strains: 1, TRM68295[T]; 2, *Streptomyces phaeochromogenes* ATCC 3338[T]; 3, *Streptomyces cuticulae* 1C-GS8[T] (Piao et al. 2017); 4, *Streptomyces dioscori* A217[T] (Wang et al. 2018); 5, *Streptomyces ederensis* JCM 4958[T]

+ Positive, − negative

Table 3 Cellular fatty acid profiles of strain TRM68295[T] and closely related species

Fatty acids	1	2	3	4	5
Iso-$C_{14:0}$	5.5	5.5	TR	7.9	TR
$C_{15:0}$	TR	5.1	14.9	15.9	ND
Iso-$C_{15:0}$	11.2	10.9	ND	ND	TR
Anteiso-$C_{15:0}$	19.4	16.6	ND	20.4	20.4
$C_{16:0}$	9.1	12.2	27.3	36.4	TR
Iso-$C_{16:0}$	21.0	19.9	30.5	ND	7.8
$C_{16:1}\omega 7c$	ND	ND	8.9	5.1	ND
$C_{16:1}\omega 9c$	5.3	7.0	ND	ND	6.8
Iso-$C_{16:1}$ H	TR	TR	ND	ND	5.3
Anteiso-$C_{17:0}$	9.0	TR	6.0	TR	21.2
Anteiso-$C_{17:1}$C	TR	TR	ND	ND	13.0

Strains: 1, TRM68295[T]; 2, *Streptomyces phaeochromogenes* ATCC 3338[T]; 3, *Streptomyces cuticulae* 1C-GS8[T] (Piao et al. 2017); 4, *Streptomyces dioscori* A217[T] (Wang et al. 2018); 5, *Streptomyces ederensis* JCM 4958[T]

TR (<5%), *ND* not detected

menaquinone system contains MK-9 (H$_{10}$), MK-9 (H$_6$) and MK-9 (H$_2$). The major fatty acids are iso-$C_{14:0}$, iso-$C_{15:0}$, anteiso-$C_{15:0}$, iso-$C_{16:0}$, $C_{16:1}\omega 9c$, $C_{16:0}$, anteiso-$C_{17:0}$.

The G+C content in the draft genome sequence of strain TRM68295[T] is 70.0 mol%.

The type strain is TRM68295[T] (= CCTCC AA 2018085[T] = KCTC 49272[T]), isolated from sediment samples of the Tailan River at Aksu, Xinjiang, northwest China. The GenBank accession number of 16S rRNA gene sequence is MK795696. The GenBank accession number for the whole genome sequence is VWMY00000000.

Compliance with ethical standards

Conflict of interest The authors state that there is no conflict of interest.

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