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ORIGINAL PAPER

Streptomyces deserti sp. nov., isolated from hyper-arid Atacama Desert soil

Rakesh Santhanam · Chinyere K. Okoro · Xiaoying Rong · Ying Huang · Alan T. Bull · Barbara A. Andrews · Juan A. Asenjo · Hang-Yeon Weon · Michael Goodfellow

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Abstract The taxonomic position of a *Streptomyces* strain isolated from a hyper-arid desert soil was established using a polyphasic approach. The organism had chemical and morphological properties typical of the genus *Streptomyces* and formed a phyletic line at the periphery of the *Streptomyces coeruleorubidus* subcluster in the 16S rRNA gene tree. DNA:DNA relatedness values between the isolate and its nearest phylogenetic neighbours, *Streptomyces lomondensis* NRRL 3252^T and *Streptomyces lusitanus* NRRL B-12501^T were 42.5 (±0.48)% and 25.0 (±1.78)%, respectively. The isolate was readily distinguished from these organisms using a combination of morphological and phenotypic properties. On the basis of these results, it is proposed that isolate C63^T (CGMCC 4.6997^T, = KACC 15425^T) be classified as the type strain of *Streptomyces deserti* sp. nov.

Keywords Actinomycetes · *Streptomyces* · Atacama Desert

The GenBank accession number for the 16S rRNA gene sequence of *Streptomyces deserti* C63^T is HE577172.

R. Santhanam · C. K. Okoro · A. T. Bull · M. Goodfellow (✉)
School of Biology, Newcastle University, Newcastle upon Tyne NE1 7RU, UK
e-mail: m.goodfellow@ncl.ac.uk

X. Rong · Y. Huang
State Key Laboratory of Microbial Resources, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China

A. T. Bull
Department of Biosciences, University of Kent, Canterbury CT2 7NJ, UK

B. A. Andrews · J. A. Asenjo
Department of Chemical Engineering and Biotechnology, University of Chile, Beauchef 850, Santiago, Chile

H.-Y. Weon
Korean Agricultural Culture Collection, Agricultural Microbiology Team, National Academy of Agricultural Science, Rural Development Administration, Suwon 441-707, Republic of Korea

Introduction

Unusual and underexplored habitats, such as those found in desert and marine ecosystems, are rich sources of novel filamentous actinomycetes some of which have a capacity to produce interesting new natural products, notably antibiotics (Goodfellow and Fiedler 2010; Mao et al. 2011). One of the least explored biomes is the Atacama Desert in northwest Chile where conditions have been considered to be too extreme for any sort of life due to low concentrations of organic compounds, high salinity, the presence of inorganic oxidants and high levels of UV radiation. Nevertheless, novel actinomycetes belonging to the genera *Amycolatopsis, Lechevalieria* and *Streptomyces* have been isolated from this hyper-arid environment (Okoro et al.

2009, 2010), with two *Streptomyces* strains shown to produce new natural products, the atacamycins (Nachtigall et al. 2011) and chaxamycins (Rateb et al. 2011).

The genus *Streptomyces* is a unique source of novel antibiotics (Goodfellow and Fiedler 2010) and encompasses, by far, the largest number of published bacterial species, nearly 600 (Euzéby 2011). The subgeneric classification of the genus is complex but has been clarified by the application of genotypic and phenotypic methods (Kumar and Goodfellow 2010; Labeda et al. 2011). In their comprehensive phylogenetic study, Labeda and colleagues assigned *Streptomyces* species to over 120 statistically-supported 16S rRNA gene clades, as well as to unsupported and single membered clades, and found that many of their taxa were consistent with results from earlier morphological and numerical taxonomic studies. However, it was apparent that insufficient variation was present in the gene sequences of the species to support relationships between many of the individual clades, notably between small and single membered clade. Nevertheless, Labeda et al. (2011) concluded that 16S rRNA sequence and phenotypic data, notably morphological features such as spore colour, spore arrangement and spore surface ornamentation, provide a reliable way of assigning new species to the genus. *Streptomyces* species are a predominant component of soils across the world but, to date, none have been described from Atacama Desert soils.

The present study was designed to establish the taxonomic status of a *Streptomyces* strain, designated C63^T, which was isolated from a hyper-arid Atacama Desert soil and found to form a distinct clade in the *Streptomyces* 16S rRNA gene tree together with a second strain from the same habitat, isolate C39, which had an identical sequence (Okoro et al. 2009). A polyphasic study showed that isolate C63^T belonged to a new *Streptomyces* species, *Streptomyces deserti* sp. nov.

Materials and methods

Organisms, maintenance and culture conditions

Strain C63^T was isolated on raffinose-histidine agar (Vickers et al. 1984) after incubation at 28°C for 14 days following inoculation with a suspension of soil taken from the Salar de Atacama in the Atacama Desert (Okoro et al. 2009). The isolate and the type strains of *S. lomondensis* and *S. lusitanus* were maintained on modified Bennett's agar (Jones 1949) slopes and as suspensions of hyphal fragments and spores in 20% v/v glycerol at −20°C. Biomass for the chemotaxonomic and molecular systematic studies on isolate C63^T was scraped from 14 day-old modified Bennett's agar plates and washed twice in distilled water; biomass for the chemotaxonomic analysis was freeze dried and that for the molecular systematic work stored at −20°C.

Chemotaxonomy and morphology

The isolate was examined for chemotaxonomic and morphological properties considered to be typical of the genus *Streptomyces* (Williams et al. 1989; Manfio et al. 1995). The arrangements of hyphae and spore chains were observed on oatmeal agar (ISP medium 3; Shirling and Gottlieb 1966) after 14 days at 28°C, using the coverslip technique of Kawato and Shinobu (1959). Spore chain arrangement and spore surface ornamentation were observed by scanning gold-coated dehydrated specimens taken from the oatmeal agar plate and examined using a scanning electron microscope (Cambridge Stereoscan 240 instrument), as described by O'Donnell et al. (1993). Cultural characteristics were determined using standard ISP media (Table 1) after 14 days at 28°C. The procedure described by Hasegawa et al. (1983) was used to detect diaminopimelic acid isomers while menaquinones were extracted and purified after Collins (1985), and then examined by high pressure liquid chromatography (Minnikin et al. 1984). For quantitative analysis of fatty acids, strain C63^T was grown on GYM broth for 3 days at 25°C. The cellular fatty acids were extracted, methylated, separated by gas chromatography (model 6890; Hewlett Packard), according to the protocol of the Sherlock Microbial Identification System (MIDI; Sasser 1990). The fatty acid methyl esters were identified and quantified by using the ACTIN1 database (version 6.10) of the MIDI.

Phylogeny

Genomic DNA was extracted from strain C63^T purified using modifications of the method of Chun and Goodfellow (1995). Washed cells were suspended

Table 1 Growth and cultural characteristics of strain C63^T on standard agar media after incubation for 14 days at 28°C

Media	Growth	Substrate mycelium colour	Aerial mycelium colour	Diffusible pigment
Glycerol-asparagine agar (ISP 5)	+++	Light cream	Cream	None
Inorganic salts-starch agar (ISP 4)	+++	Brownish white	White	None
Oatmeal agar (ISP 3)	+++	Light olive green	White	None
Peptone-yeast extract-iron agar (ISP 6)	++	Brown	Whitish grey	Dark brown
Tryptone-yeast extract agar (ISP 1)	+++	Light yellowish brown	Brownish white	None
Tyrosine agar (ISP 7)	+	Dark brown	Brown	Brown
Yeast extract-malt extract agar (ISP 2)	++	Light yellowish brown	White	Brown

+++ abundant, ++ moderate, + poor growth

in 2 ml STE buffer (75 mM NaCl, 25 mM Tris-HCl, 25 mM EDTA, pH 8.0) which contained 2 mg lysozyme ml^{-1} (Sigma); the suspensions were incubated for 2–8 h at 37°C, lysed completely by adding 0.2 ml 20% (w/v) SDS and incubated at 55°C for 1–2 h with periodic mixing by inversion; after being extracted with phenol/chloroform and precipitated with ethanol, the total crude DNA preparations were gently agitated with a thin rod and rinsed twice with 70% ethanol. The crude DNA preparations were dissolved in 0.5 ml TE (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) and treated with RNase A and proteinase K. After being extracted with phenol/chloroform until the interfaces were clean, pure DNA was precipitated with an equal volume of isopropyl alcohol and rinsed twice with 70% ethanol, dried and dissolved in distilled water. The purity and concentration of the prepared DNA solutions were measured with a Beckman model DU-800 spectrophotometer. Solutions with an $A260/A280$ ratio at 1.7–1.9 were used for 16S rRNA PCR and DNA–DNA hybridization.

The almost complete 16S rRNA gene sequence of the isolate [1,440 nucleotides (nt)] was aligned with corresponding sequences of the most closely related *Streptomyces* type strains drawn from the EzTaxon database (Chun et al. 2007). The sequences were aligned using CLUSTAL W (Thompson et al. 1994) and phylogenetic trees generated using the maximum-parsimony (Fitch 1971), minimum-evolution (Rzhetsky and Nei 1992) and neighbour-joining (Saitou and Nei 1987) tree-making algorithms from the MEGA 4 package (Tamura et al. 2007). The Jukes and Cantor (1969) model was used to derive an evolutionary distance matrix for the neighbour-joining data. The resultant tree topologies were evaluated by a bootstrap analysis (Felsenstein 1985) of the neighbour-joining data based on 1,000 resequences using MEGA 4 software (Tamura et al. 2007).

DNA:DNA pairing

DNA:DNA relatedness studies were performed, in duplicate, between strain C63^T and the type strains of *S. lomondensis* and *S. lusitanus* using the optical reassociation method (De Ley et al. 1970) and a reassociation temperature of 85°C.

Phenotypic tests

Isolate C63^T and the type strains of *S. lomondensis* and *S. lusitanus* were examined for a broad range of phenotypic properties using media and methods described by Williams et al. (1983); the isolate was examined for additional tests drawn from those used by Williams and his colleagues.

Results and discussion

The chemotaxonomic and morphological features shown by isolate C63^T were consistent with its classification in the genus *Streptomyces* (Williams et al. 1989; Manfio et al. 1995). The isolate formed an extensively branched substrate mycelium which supported aerial hyphae that differentiated into smooth surfaced spores carried in straight chains and open loops (Fig. 1). Major amounts of LL-diaminopimelic acid were present in whole-organism hydrolysates; hexa- and octa-hydrogenated menaquinones with nine isoprene units were present in a ratio of 3:7;

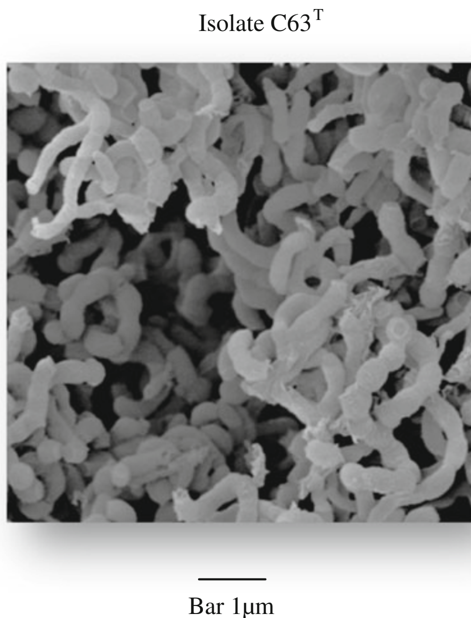

Fig. 1 Scanning electron micrograph of isolate C63^T on oatmeal agar after 14 days at 28°C showing spores in straight chains and open loops

and iso-$C_{15:0}$ (11.6%), anteiso-$C_{15:0}$ (16.9%), iso-$C_{16:0}$ (10.3%), iso-$C_{17:0}$ (5.8%) and anteiso-$C_{17:0}$ (10.8%) were the predominant fatty acids. The strain grew well on most of the ISP media exhibiting a range of aerial spore mass and substrate mycelial pigments (Table 1).

Comparison of the almost complete 16S rRNA gene sequence of isolate C63^T with the corresponding sequences of phylogenetically related *Streptomyces* strains showed that it formed a distinct branch at the periphery of the *Streptomyces coeruleorubidus* 16S rRNA gene sequence subcluster, an association which was supported by all of the tree-making algorithms and by a 63% bootstrap value (Fig. 2). The previous close relationship with isolate C39, which had an identical sequence over 1,300 nucleotides (Okoro et al. 2009), was not supported by the near full length sequence data. Instead, the isolate was most closely related to the type strain of *Streptomyces lusitanus*; the two strains shared a similarity of 99.1%, a value which corresponded to 14 differences from 1,440 nucleotides. It was also closely related to the type strain of *Streptomyces lomondensis*; these organisms had a 16S rRNA gene sequence similarity of 98.9%, a value equivalent to 15 differences from 1,440 nucleotides. However, the phylogenetic position of the isolate is likely to change as new species are assigned to what is an unstable part of the *Streptomyces* 16S rRNA gene tree (Labeda et al. 2011).

DNA hybridization data showed that the isolate shared DNA:DNA relatedness values of 42.2 (±0.48)% and 25.0 (±1.78) % with the type strains of *S. lomondensis* and *S. lusitanus*, respectively; these values are well below the 70% cut-off point recommended for the delineation of prokaryotic species

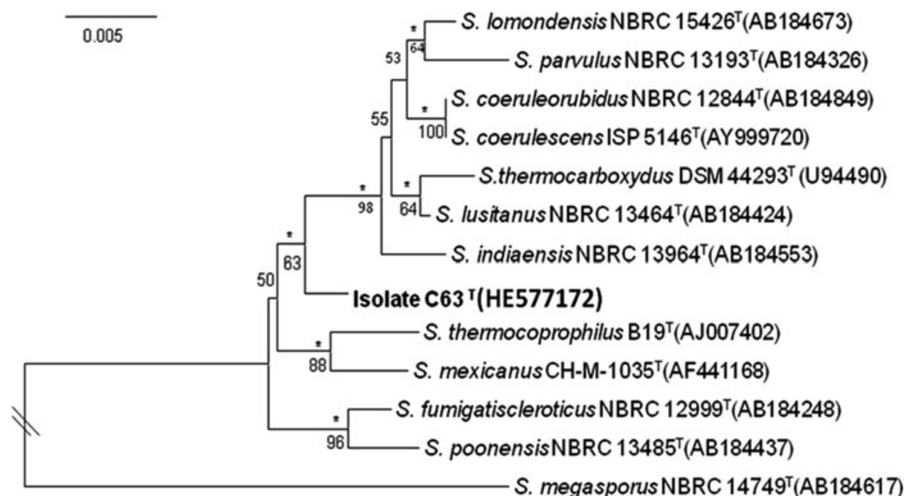

Fig. 2 Neighbour-joining tree based on nearly complete 16S rRNA gene sequences (1,440 nt) showing relationships between isolate C63^T and closely related *Streptomyces* species. *Asterisks* indicate branches of the tree that were also found using the maximum-parsimony and minimum-evolution tree-making algorithms. Numbers at the nodes are percentage bootstrap values based on 1,000 resampled datasets, only values above 50% are given. *Bar* 0.005 substitutions per nucleotide position

Table 2 Phenotypic properties which distinguish isolate C63^T from the type strains of *S. lomondensis* and *S. lusitanus*

Characteristic	Isolate C63^T	*S. lomondensis* NRRL 3252^T	*S. lusitanus* NRRL B-12501^T
Spore chain morphology	Straight/open loops	Open loops/spiral	Open loops/spiral
Spore surface ornamentation	Smooth	Warty to spiny	Spiny
Biochemical tests			
Allantoin hydrolysis	–	–	+
Nitrate reduction	+	+	–
Hydrogen sulphide production	–	–	+
Degradation tests			
Adenine	+	+	–
Cellulose	–	+	+
DNA	+	+	–
RNA	+	+	–
Xanthine	–	+	+
Xylan	–	+	+
Growth on sole carbon sources at 1%, w/v			
Amygdalin	+	+	–
L-Arabinose	+	+	–
D-Arabitol	–	+	+
Arbutin	+	+	–
Inulin	–	+	–
Lactose	–	+	+
D-Maltose	–	+	+
D-Melezitose	–	–	+
α-Methyl-D-glucoside	+	+	–
D-Raffinose	+	+	–
Salicin	–	+	+
D-Sorbitol	+	–	–
D-Sucrose	–	+	–
D-Xylose	–	+	+
Growth on sole nitrogen sources at 1%, w/v			
L-Aminobutyric acid	+	+	–
L-Isoleucine	–	+	–
DL-Methionine	–	+	–
DL-*nor*leucine	–	+	–
L-*nor*valine	–	+	–
L-Ornithine	+	–	+
L-Tryptophan	–	+	–
L-Valine	–	+	+
Growth in the presence of NaCl (7%, w/v)	–	+	+

(Wayne et al. 1987). The DNA G+C content of the isolate was 72.4%.

Isolate C63^T carries spores in straight chains and open loops (Fig. 1) and can thereby be distinguished from strains in and around the *S. coeruleorubidus* subclade, all of which produce spiral spore chains (Labeda et al. 2011); it can be readily separated from the type strains of *S. lomondensis* and *S. lusitanus* as it

forms smooth spores, as opposed to the warty to spiny, and spiny spores produced by these organisms, respectively. It can also be distinguished from its two closest phylogenetic neighbours using a combination of phenotypic tests (Table 2). Thus, unlike the latter it uses sorbitol, but not D-arabitol, inulin, lactose, maltose, salicin or xylose as sole carbon sources nor does it degrade cellulose, xanthine or xylan or grow in the presences of 7% (w/v) NaCl. The additional tests carried out on isolate C63^T are given in the species description.

Minimal standards for the delineation of *Streptomyces* species need to be based on a judicious selection of genotypic and phenotypic data (Manfio et al. 1995; Kumar and Goodfellow 2010). Isolate C63^T was readily distinguished from its nearest phylogenetic neighbours, the type strains of *S. lomondensis* and *S. lusitanus,* on the basis of 16S rRNA sequence, DNA:DNA pairing, morphological and phenotypic data. It is, therefore, proposed that this organism be recognised as a new species, *S. deserti* sp. nov.

Description of *S. deserti* sp. nov

S. deserti (de'ser.ti. L. gen. n. *deserti*, of a desert, pertaining to the Atacama Desert of northwest Chile, the source of soil from which the strain was isolated).

Aerobic, gram-positive, non- acid-alcohol-fast actinomycete which forms an extensively branched substrate mycelium that bears aerial hyphae which differentiate into straight chains and open loops of smooth surfaced spores (0.9 –0.7 µm). Melanin pigments are formed on peptone-yeast extract-iron and tyrosine agars. Growth occurs from 10 to 35°C, between pH 4 and 11 and in the presence of 4% (w/v) NaCl. Aesculin and arbutin are hydrolysed, casein, chitin, gelatin, guanine, hypoxanthine, keratin, RNA, starch, L-tyrosine, Tweens 40 and 80 and uric acid are degraded, but not elastin or Tween 20. D-fructose, D-galactose, D-glucose, glycerol, glycogen, D-mannitol, D-mannose, *meso*-inositol, and D-trehalose are used as sole carbon sources for energy and growth (at 1%, w/v), but not L-arabitol, butane 1,4 diol, dextran, dulcitol, *meso*-erythritol, methanol, propanol, salicin, L-sorbose or xylitol (at 1%, w/v or 1%, v/v). Similarly, sodium citrate and sodium pyruvate are used as sole carbon sources at 0.1%, w/v. L-alanine, L-glycine, L-histidine, L-phenylalanine, L-proline, L-serine and L-threonine are used as sole nitrogen sources. Additional phenotypic properties are cited in the text and in Tables 1 and 2. Chemotaxonomic properties are typical of the genus.

The type strain, C63^T (CGMCC 4.6997^T = KACC 15425^T) was isolated from soil taken from the Salar de Atacama in the Atacama Desert. The species description is based on a single strain and hence serves as a description of the type strain.

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