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ORIGINAL PAPER

Streptomyces spiramenti sp. nov., isolated from a deep-sea microbial mat

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Abstract
Strain 5675061^T was isolated from a deep-sea microbial mat near hydrothermal vents within the Axial Seamount caldera on the Juan de Fuca Ridge (NE Pacific Ocean) and was taxonomically evaluated using a polyphasic approach. Morphological and chemotaxonomic properties are consistent with characteristics of the genus *Streptomyces*: aerobic Gram-stain-positive filaments that form spores, L,L-diaminopimelic acid in whole-cell hydrolysates, and *iso*-$C_{16:0}$ as the major fatty acid. Phylogenetic analysis, genomic, and biochemical comparisons show close evolutionary relatedness to *Streptomyces lonarensis* NCL716^T, *S. bohaiensis* 11A07^T, and *S. otsuchiensis* OTB305^T but genomic relatedness indices identify strain 5675061^T as a distinct species. Based on a polyphasic characterization, identifying differences in genomic and taxonomic data, strain 5675061^T represents a novel species, for which the name *Streptomyces spiramenti* sp. nov. is proposed. The type strain is 5675061^T (=LMG 31896^T = DSM 111793^T).

Keywords *Streptomyces* · Deep-sea · Hydrothermal vent · Marine

Introduction

The genus *Streptomyces* is the largest genus in the class *Actinobacteria*, with over 800 characterized species (https://lpsn.dsmz.de/genus/streptomyces), and was first described by Waksman and Henrici in 1943 (Waksman and Henrici 1943; Stackebrandt et al. 1997). *Streptomyces* strains are aerobic Gram-stain-positive filamentous bacteria with high DNA G + C contents of 69–78 mol% (Kämpfer 2015). Members of the *Streptomyces* genus are well-known producers of an array of desirable specialized metabolites, e.g., antibiotic,

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antiviral, cytotoxic, and immunosuppressive activities, the production of which is thought to facilitate *Streptomyces* colonization of many ecological niches (O'Brien and Wright 2011). Roughly two-thirds of all known antibiotics and various anticancer drugs are produced by actinobacteria, particularly *Streptomyces* species (Takahashi and Nakashima 2018; Khalifa et al. 2019). Recent work has focused on mining more than 3000 *Streptomyces* genome assemblies currently available in the NCBI repository for novel and cryptic gene clusters because individual strains may harbor 20–30 biosynthetic gene clusters (Lee et al. 2020; Nguyen et al. 2020). Similarly, *Streptomyces* strains have been recognized as producers of desirable extracellular enzymes for use in many industrial sectors, including bioconversion, bioremediation, and biofuel production (Kumar et al. 2020). While much research has focused on terrestrial *Streptomyces* species, it has been suggested that isolates from less-explored extreme environments may represent sources of novel biologically active compounds (Sivalingam et al. 2019). To that end, we isolated and characterized a *Streptomyces* species derived from a microbial mat growing near deep-sea hydrothermal vents. The results of a polyphasic approach characterizing strain 5675061^T support the classification of this isolate as a novel species, for which the name *Streptomyces spiramenti* sp. nov. is proposed.

Materials and methods

Strain 5675061^T was isolated from a microbial mat near hydrothermal vents within the Axial Seamount caldera on the Juan de Fuca Ridge in the NE Pacific Ocean. Deep-sea samples were collected on the 2011 New Millennium Observatory expedition in partnership with the NOAA Vents Program at Oregon State University and the NOAA Pacific Marine Environmental Laboratory. A microbial mat sample was obtained from the Axial Seamount (46.06°N, 130°W) at a depth of 2190 m using the ROV Jason II (aboard the R/V Thompson) with a custom-made syringe apparatus. This sample was collected from a diffuse venting area (seawater temperatures of 15–35 °C) because an analysis of species richness at hydrothermal vents indicated that diffuse venting zones support the highest amount of biomass and diversity, and that microbial diversity in most seafloor sediments is high (Fenical and Jensen 2006; Thornburg et al. 2010). Additionally, laboratory cultivation is most practical at temperatures of 10–40 °C. After collection, the sample was diluted 1:1000 in sterile Instant Ocean Sea Salt (36 g L^{-1}; Blacksburg, VA, USA) and spread on the surface of 1/10 Zobell marine agar plates (4 g L^{-1} Zobell marine broth 2216 (BD, Franklin Lakes, NJ, USA), 30 g L^{-1} Instant Ocean Sea Salt, 15 g L^{-1} agar, pH 8.3) with sterile cotton swabs. Following incubation at 28 °C for 2 weeks, colonies were purified on the same medium.

The *Streptomyces bohaiensis* $11A07^T$ (DSM 42125) and *S. lonarensis* $NCL716^T$ (DSM 42084) type strains were provided by the Leibniz Institute DSMZ. Strains were routinely cultured at 28 °C in glucose seawater medium (4 g L^{-1} Zobell marine broth 2216, 5 g L^{-1} glucose, 36 g L^{-1} Instant Ocean Sea Salt, 2 g L^{-1} $NaNO_3$, 15 g L^{-1} agar, pH 8.0) and ISP2 supplemented with 0.1 M sodium phosphate buffer to pH 8.0 (hereafter buffered ISP2) (Shirling and Gottlieb 1966), solidified with 1.5% agar as needed, or shaken at 150 RPM for 3–7 days unless otherwise noted. Scanning electron micrographs of strain 5675061^T grown in buffered ISP2 for 2 or 7 days were taken on a JEOL JSM-6500F Field Emission Scanning Electron Microscope at the Mississippi State University Institute for Imaging and Analytical Technologies as previously described (Williams and Davies 1967). Strain properties were determined using ISP2, ISP3, ISP4, ISP5, ISP6, and ISP7 (Shirling and Gottlieb 1966), 1/10 Zobell marine agar, Czapek agar (Remel, Lenexa, KS, USA), nutrient agar (BD), potato dextrose agar (BD), and trypticase soy agar (BD), all prepared according to the manufacturer's instructions. Anaerobic growth was assessed on buffered ISP2 plates incubated at 28 °C for 2 weeks using the GasPak System according to the manufacturer's instructions (BD). The pH range supporting growth was determined with ISP2 medium adjusted to pH 5.0–11.0 in increments of 0.5 pH units with the following buffers: pH 5.0–6.0, citrate/Na_2HPO_4; pH 6.0–8.0, phosphate buffer; pH 9.0–11, glycine–NaOH buffer (McCauley et al. 2015). Media pH was adjusted prior to sterilization, verified after sterilization prior to inoculation, and verified again after incubation. The temperature range supporting growth was assessed on buffered ISP2 medium incubated from 0 to 45 °C in 5 °C increments, which were chosen to ensure that temperatures permissive for growth were bounded by non-permissive temperatures. Tolerance to NaCl was determined on buffered ISP2 medium supplemented with 0–10% NaCl in 1% increments.

Carbon source utilization and enzyme activity tests were carried out using the API 50 CH and API ZYM kits according to the manufacturer's instructions (BioMérieux, Marcy-l'Étoile, France). The ability to use amino acids as sole nitrogen sources (0.1% of L-alanine, L-glycine, L-histidine, L-lysine, L-methionine, L-phenylalanine, L-proline, and L-valine) was assessed as previously described (Williams et al. 1983). Gelatinase activity, casein degradation, and the hydrolysis of Tween 20, 40, 60, and 80 were conducted as previously described (Williams et al. 1983). Catalase activity was assessed with the addition of 3% H_2O_2 to colonies grown on buffered ISP2 medium, with the formation of bubbles interpreted as a positive result. Determination of oxidase activity was carried out with BD BBL DrySlide tests according to manufacturer's instructions (BD).

For all chemotaxonomic assessments, cells from strain 5675061^T were harvested during growth in buffered ISP2 at 28 °C. Cellular fatty acid, menaquinone, and polar lipid analyses were carried out at the Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures (Braunschweig, Germany), and the published profiles of related strains were used for comparison. The preparation of whole-cell hydrolysates and analysis of whole-cell sugars and diaminopimelic acid in the peptidoglycan were conducted as previously described and compared to purchased standards (Sigma-Aldrich, St. Louis, MO, USA) (Staneck and Roberts 1974).

Genomic DNA was isolated from strain 5675061^T via phenol chloroform extraction and used in a PCR with the primers 8F (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492R (5′-TACGGYTACCTTGTTACGACTT-3′) to amplify a fragment of the 16S rRNA gene (Sambrook 2001; Aebischer et al. 2006). The product was purified with the Wizard SV Gel and PCR Clean-up System (Promega, Madison, WI) and sequenced by Sanger sequencing in the Biotechnology Center at Southern Oregon University using the same primers. The 16S rRNA gene sequences of strain 5675061^T and related strains were aligned using the MUSCLE algorithm (Edgar 2004), and a neighbor joining phylogenetic tree was generated using the MEGA11 software package (Tamura et al. 2021).

The genome of strain 5675061^T, those of related *Streptomyces* species, and that of an outgroup (*Kitasatospora setae* LM-6054^T) were annotated using Prokka (version 1.14.5) (Seemann 2014). The resulting genome annotations were used as inputs to identify conserved single-copy core genes using PhyloPhlAN (version 3.0.51) (Asnicar et al. 2020). Phylogenomic inference was performed using IQ-TREE (version 2.1.4-beta) with an aligned, trimmed, and concatenated multiple-sequence alignment produced by PhyloPhlAN representing 363 conserved single-copy core genes and 86,632 characters (Minh et al. 2020). Of these, 68,530 characters were deemed parsimony-informative sites by IQ-TREE. The best model for inference was tested in IQ-TREE using the "-m TESTONLY" parameter. The best-fit model for amino acid substitution (Q.pfam + F + G4) was used, and 1000 Ultrarapid Bootstrap replicates were performed during the analysis.

DNA–DNA hybridization (isDDH) was conducted in silico using GGDC 2.1 with the default parameters (Meier-Kolthoff et al. 2013). ANIb analysis was run on JSpeciesWS with default parameters to calculate the pairwise average nucleotide identities (ANI) between closely related genomes used for phenotypic comparison (Richter et al. 2015).

Results and discussion

Strain 5675061^T exhibited phenotypic and chemotaxonomic characteristics consistent with the genus *Streptomyces*. Strain 5675061^T produced Gram-stain-positive filaments (Fig. S1) in white, smooth, raised, translucent colonies with entire margins and a dry powdery appearance that grew aerobically. Strain 5675061^T produced white spores on all tested media and grew well on all media except Czapek agar (Table S2). The spores grew in rectiflexibiles chains with smooth spore surfaces, which is a similar arrangement and surface to the related *Streptomyces* strain used for comparison below (Table 1, Fig. S1). White mycelia were observed following growth on ISP3, ISP4, ISP5, ISP6, ISP7, and 1/10 Zobell marine agar, while beige, brown, gray, and yellow mycelia were observed following growth on potato dextrose agar, ISP2, nutrient agar, and trypticase soy agar, respectively. A brown diffusible pigment was apparent following growth on ISP7. Strain 5675061^T grew in 0–5% NaCl, at 5–40 °C but not at 0 °C or 45 °C, and in pH 6.0–10.0, with optimal growth observed in 1–3% NaCl, at 25–35 °C, and pH 7.0–8.5. Notable characteristics that differentiate strain 5675061^T from closely related *Streptomyces* species are provided in Table 1.

In biochemical assessments, strain 5675061^T was positive for catalase, oxidase, acid phosphatase, alkaline phosphatase, α-chymotrypsin, cystine arylamidase, esterase (C4), esterase lipase (C8), α-glucosidase, β-glucosidase, α-mannosidase, and naphthol ASBI phosphohydrolase. Strain 5675061^T also hydrolyzes Tween 20, 40, 60, and 80, degrades casein, and utilizes amidon, amygdalin, D-cellobiose, D-fructose, D-galactose, D-glucose, D-lactose, D-maltose, D-mannitol, D-mannose, D-melezitose, D-ribose, D-saccharose, D-sorbitol, D-trehalose, D-turanose, esculin, gentiobiose, glycerol, L-rhamnose, L-sorbose, methyl-α-D-mannopyranoside, *N*-acetylglucosamine, potassium gluconate, and potassium 5-ketogluconate as carbon sources, and is negative for gelatinase. Strain 5675061^T can utilize L-alanine, L-glycine, L-histidine, L-lysine, L-methionine, L-phenylalanine, L-proline, and L-valine as sole nitrogen sources. The enzyme activity profile for strain 5675061^T and complete carbon source utilization profile for strain 5675061 ^{T}, *S. bohaiensis* 11A07^T, and *S. lonarensis* NCL716^T are presented in Tables S3 & S4 in the Supplementary Material.

Analysis of the 16S rRNA gene sequence placed strain 5675061^T within the genus *Streptomyces* and in a cluster with *S. bohaiensis* 11A07^T, *S. lonarensis* NCL716^T, and *S. otsuchiensis* OTB305^T (Fig. S2). Comparison of the strain 5675061^T 16S rRNA sequence indicates 99.63% identity with *S. lonarensis* NCL716^T, 99.49% with *S. bohaiensis*

Table 1 Characteristics that differentiate strain 5675061^T from related *Streptomyces* type strains

Characteristic	Strain 5675061^T	*S. lonarensis* NCL716^T	*S. bohaiensis* 11A07^T	*S. otsuchiensis* OTB305^T
Morphology of:				
Spore chains	Rectiflexibiles	Rectus–Flexibilis	Straight or rectiflexibiles	Rectiflexibiles
Spore surface	Smooth	Smooth	Smooth	Smooth
NaCl concentration range for growth (%)	0–5	0–6	0–11	1–6
Growth temperature (°C)	5–40	28–30	15–40	15–37
pH range	6.0–10.0	8.0–10.0	6.0–10.0	7.0–10.0
Enzymes activity				
Lipase (C14)	−	−	+	W
Leucine arylamidase	−	+	+	+
Valine arylamidase	−	−	+	W
α-Chymotrypsin	+	−	+	−
α-Fucosidase	−	−	+	−
Carbon sources				
D-Arabinose	−	+	+	N/A
L-Arabinose	−	+	−	+
L-Xylose	−	+	−	+
D-Fructose	+	+	−	+
D-Fucose	−	+	+	N/A
Potassium 5-ketogluconate	+	−	−	N/A
Whole-cell sugars	Gal, Glu, Man	Glu, Man, Rib	Gal, Glu, Man, Rib, Xyl	Glu
Predominant menaquinones (> 10%)	MK-9($H_{4,6,8}$)	MK-9($H_{4,6}$)	MK-9($H_{2,4,6}$)	MK-9($H_{4,6,8}$)
Diagnostic phospholipids	DPG, GL, PE, PGL, PL	DPG, PE, PG, PI	DPG, PE, PI, PIM, PL	DPG, PE, PI, PL
Major fatty acids (> 10%)	*i*-$C_{16:0}$	*i*-$C_{16:0}$, $C_{17:1}$	$C_{18:0}$, *i*-$C_{16:0}$, *ai*-$C_{17:0}$, 10-m-$C_{18:0}$	*i*-$C_{16:0}$, $C_{16:0}$, $C_{16:1}\omega 7c$
DNA G+C content (%)	73.3	73.8	73.8	72.8

S. lonarensis NCL716^T data for characteristics, enzyme activity, carbon sources, and DNA G+C content (%) collected/verified here and from Sharma et al. (Sharma et al. 2016); *S. bohaiensis* 11A07^T characteristics, enzyme activity, carbon sources, and DNA G+C content (%) collected/verified here and from Pan et al. (Pan et al. 2015); *S. otsuchiensis* OTB305^T from Terahara et al. (Terahara et al. 2019). For *S. otsuchiensis* OTB305^T, differences in test conditions from those used here may result in differences in test outcomes

+ positive, − negative, *NA* not available, *ai anteiso*, *DPG* diphosphatidylglycerol, *Gal* galactose, *GL* glycolipid, *Glu* glucose, *i iso*, *m* methyl, *Man* mannose, *PE* phosphatidylethanolamine, *PG* phosphatidylglycerol, *PGL* phosphoglycolipid, *PI* phosphatidylinositol, *PIM* phosphatidylinositol mannoside, *PL* phospholipids, *Rib* ribose, *Xyl* xylose, *w* weakly positive

11A07^T, and 99.05% with *S. otsuchiensis* OTB305^T, which are all above the 98.65% identity threshold for members of the same species (Kim et al. 2014). Sequencing the genomes of strain 5675061^T, *S. bohaiensis* 11A07^T, *S. lonarensis* NCL716^T, and *S. otsuchiensis* OTB305^T revealed their G+C contents to be 73.3%, 73.8%, 73.8%, and 72.8%, respectively, which are within the expected range for the genus *Streptomyces* (Kämpfer 2015; Terahara et al. 2019; Loughran et al. 2020). Preparation of a phylogenomic tree to interrogate the relationships of these strains further, resulted in clustering of strain 5675061^T with *S. bohaiensis* 11A07^T, *S. lonarensis* NCL716^T, and *S. otsuchiensis* OTB305^T (Fig. 1). Genomic similarity was assessed with average nucleotide identity (ANI) and in silico DNA–DNA hybridization (isDDH) comparisons. ANI values ranged from 81.1 to 88.8% between strain 5675061^T and the related strains used for comparison, which fall below the 95–96% cutoff for species delineation (Table 2) (Richter et al. 2015; Jain et al. 2018). The isDDH values ranged from 25.1 to 36.2% between strain 5675061^T and the related strains used for comparison, which fall well below the 70% cutoff for species delineation (Goris et al. 2007). Despite the high degree of similarity among the 16S rRNA sequences, the ANI and isDDH comparisons with related strains are well below accepted cutoffs and support strain 5675061^T as a novel species. In both phylogenetic and genome-based assessments, *S. lonarensis* NCL716^T was most closely related to strain 5675061^T. Based on their phylogenomic grouping and genomic relatedness, *S. bohaiensis* 11A07^T, *S. lonarensis* NCL716^T, and *S. otsuchiensis* OTB305^T were the most closely related type strains and served as the basis of comparison throughout this study.

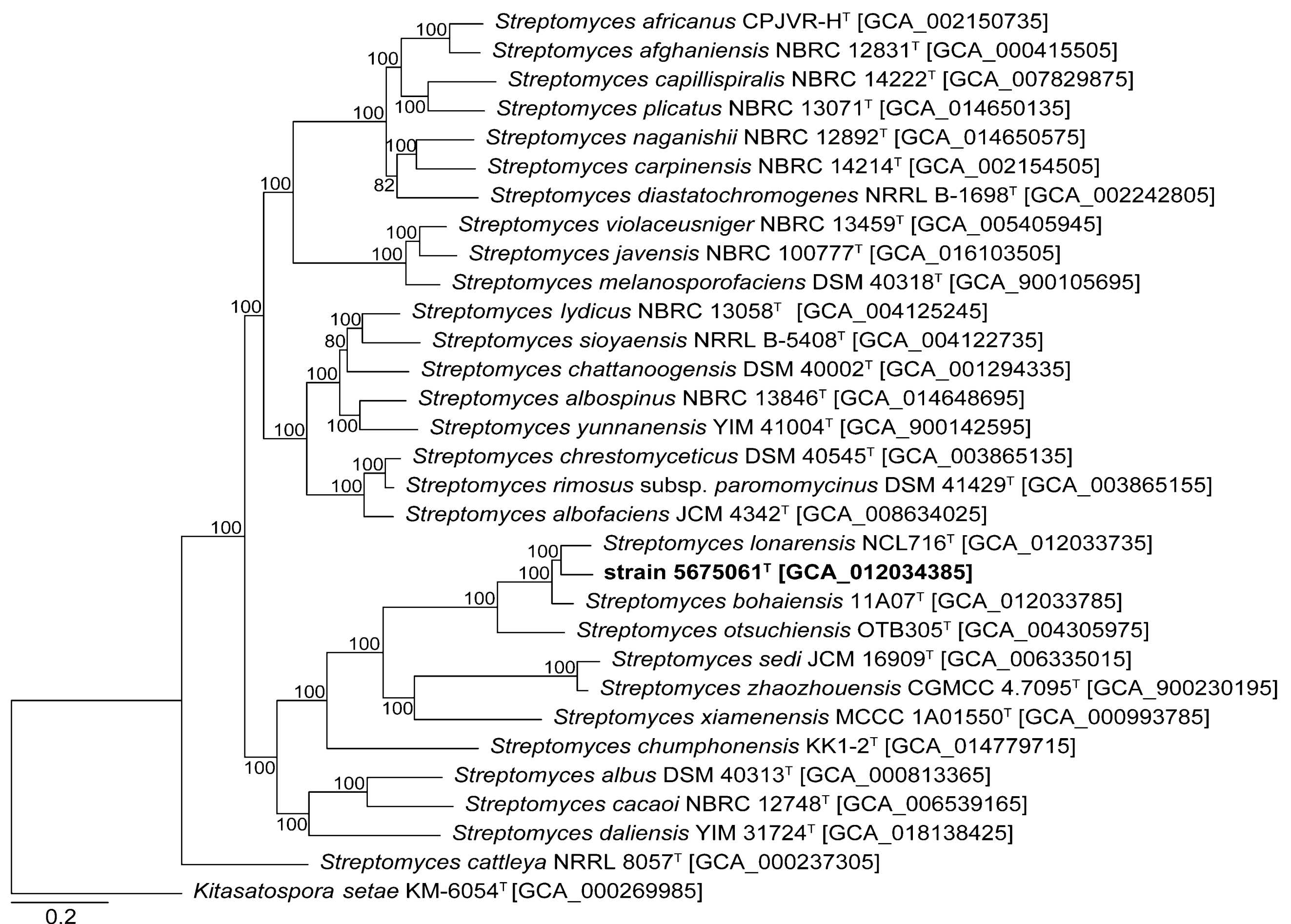

Fig. 1 A maximum likelihood phylogenomic tree was constructed using 363 conserved core genes (86,632 characters) shared between related *Streptomyces* species and the outgroup, *Kitasatospora setae* LM-6054^T. Ultrafast bootstrap values based on 1000 replicates are indicated at branch nodes. Accession numbers of genomes are shown in parentheses and are listed in Table S1. Bar, number of amino acid substitutions per site

Table 2 ANI and isDDH values (%) measured via pairwise comparison are presented above and below the midline, respectively, between related *Streptomyces* species

	1	2	3	4
1		87.9	88.8	81.1
2	34.6		89.4	81.2
3	36.2	38.1		81.0
4	25.1	25.5	25.0	

Strains: 1, strain 5675061^T; 2, *S. bohaiensis* 11A07^T; 3, *S. lonarensis* NCL716^T; 4, *S. otsuchiensis* OTB305^T

Whole-cell hydrolysates from strain 5675061^T contained L,L-diaminopimelic acid, glucose, galactose, and mannose (Table 1). The respiratory quinones detected were MK-9(H_8) (41%), MK-9(H_6) (33%), MK-9(H_4) (18%), MK-9(H_{10}) (4%), and MK-9(H_2) (4%). The polar lipids detected were diphosphatidylglycerol, phosphatidylethanolamine, phosphoglycolipid, three glycolipids, and six phospholipids (Fig. S3). The single major cellular fatty acid detected (> 10%) was *iso*-$C_{16:0}$ (Table S5), which is notably different from the related strains used as comparator species that all have at least two major fatty acids.

Strain 5675061^T may be differentiated from phylogenetically related strains by its ability to utilize potassium 5-ketogluconate and lack of leucine arylamidase activity. Strain 5675061 ^{T} differs from the most closely related strain, *S. lonarensis* NCL716^T, in α-chymotrypsin, cystine arylamidase, α-glucosidase, and α-mannosidase activities, and the utilization of 29 different sugars including D- and L-arabinose, L-xylose, and D-fucose. The preceding summary of characteristics and genomic analyses support the inclusion of strain 5675061^T in the genus *Streptomyces* and demonstrate that it exists as a distinct and novel species, for which the name *Streptomyces spiramenti* sp. nov. is proposed.

Description of *Streptomyces spiramenti* sp. nov.

Streptomyces spiramenti sp. nov. (spi.ra.ment'i L. gen. n. spiramenti, meaning vent; referring to the deep-sea vent location from which the strain was isolated).

Aerobic Gram-stain-positive actinobacterium with branched filaments. Rectiflexibiles spore chains are observed, and the spore surface is smooth. Aerial mycelia are white. Substrate mycelia appear white following growth on ISP3, ISP4, ISP5, ISP6, ISP7, and 1/10 Zobell marine agar. Beige, brown, gray, and yellow mycelia are observed following growth on potato dextrose agar, ISP2, nutrient agar, and trypticase soy agar, respectively. Brown diffusible pigment is observed on ISP7. Growth occurs at 5–40 °C, pH 6.0–10.0, and with 0–5% NaCl, with optimal growth at 25–35 °C, pH 7.0–8.5, and 1–3% NaCl. Tween 20, 40, 60, and 80 are hydrolyzed, casein is degraded, and positive for oxidase and catalase. Positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), cystine arylamidase, α-chymotrypsin, acid phosphatase, naphthol ASBI phosphohydrolase, α-glucosidase, β-glucosidase, and α-mannosidase. Negative for gelatinase, lipase (C14), leucine arylamidase, valine arylamidase, trypsin, α-galactosidase, β-galactosidase, β-glucuronidase, *N*-acetyl-β-glycosaminidase, and α-fucosidase. Utilized carbon sources include glycerol, D-ribose, D-galactose, D-glucose, D-fructose, D-mannose, L-sorbose, L-rhamnose, D-mannitol, D-sorbitol, methyl-α-D-mannopyranoside, *N*-acetylglucosamine, amygdalin, esculin, D-cellobiose, D-maltose, D-lactose, D-saccharose, D-trehalose, D-melezitose, amidon, gentiobiose, D-turanose, potassium gluconate, and potassium 5-ketogluconate; but not erythritol, D-arabinose, L-arabinose, D-xylose, L-xylose, D-adonitol, methyl-β-D-xylopyranoside, dulcitol, inositol, methyl-α-D-glucopyranoside, arbutin, salicin, D-melibiose, inulin, D-raffinose, glycogen, xylitol, D-lyxose, D-tagatose, D-fucose, L-fucose, D-arabitol, L-arabitol, or potassium 2-ketogluconate. L-Alanine, L-glycine, L-histidine, L-lysine, L-methionine, L-phenylalanine, L-proline, and L-valine are utilized as sole nitrogen sources.

Cell wall contains L,L-diaminopimelic acid. Galactose, glucose, and ribose are whole-cell sugars. The predominant menaquinones are MK-9(H_4), MK-9(H_6), and MK-9(H_8). The major fatty acid is *iso*-$C_{16:0}$. The polar lipids consist of diphosphatidylglycerol, phosphatidylethanolamine, phosphoglycolipid, three glycolipids, and six phospholipids. The G + C content of the genome is 73.3%.

The type strain, 5675061^T (= LMG 31896^T = DSM 111793^T), was isolated from a microbial mat collected near hydrothermal vents within the Axial Seamount caldera on the Juan de Fuca Ridge in the NE Pacific Ocean (46.06°N, 130°W).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-022-03326-6.

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Author contributions KLMP and PV conceived of the study and all authors contributed to its design. Material preparation, experimentation, data collection, and analysis were performed by RML, Caitlin MD, JR-VS, EAM, OBV, DAG, GM, MJK, DKO, OSR, BU, JHS, and MOG. The first draft of the manuscript was written by PV and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The 16S rRNA gene sequence for strain 5675061^T was deposited in DDBJ/ENA/GenBank under the accession number OP470020. The main datasets analyzed in this work are the genomes of strain 5675061^T, *S. bohaiensis* 11A07^T, *S. lonarensis* NCL716^T, and *S. otsuchiensis* OTB305^T, which are deposited in DDBJ/ENA/GenBank under the accession numbers JAAVJB010000000, JAAVJC010000000, JAAVJD010000000, and BHZI01000000, respectively. The remaining genomes used in this work are listed in Table S1.

Declarations

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

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