Sandaracinobacteroides hominis gen. nov., sp. nov., isolated from human skin

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Received: 22 January 2021 / Revised: 20 June 2021 / Accepted: 21 June 2021 / Published online: 24 July 2021
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Abstract
Strain SZY PN-1T, representing a novel Gram-negative, aerobic, non-motile, rod-shaped and yellow-pigmented bacterium, was isolated from a skin sample of a healthy Chinese male. Growth occurred at pH 6.0–8.0 (optimum, pH 7.0) and 10–37 ºC (optimum, 30 ºC) with 0–1.0% (w/v) NaCl in R2A agar. Comparative analysis of the 16S rRNA gene sequences revealed that strain SZY PN-1T shared high similarities with two invalid-published species, “Sandaracinobacter sibiricus” RB16-17 (97.1%) and “Sandaracinobacter neustonicus” JCM 30734 (96.6%), respectively. Phylogenetic analysis of 16S rRNA gene sequences together with protein-concatemer tree showed that SZY PN-1T formed a separate branch within the family Sphingosinicellaceae. The DNA G+C content of the strain SZY PN-1T was 65.0% (genome). The polar lipid profile included phosphatidylethanolamine, phosphatidylglycerol, two sphingoglycolipids, diphosphatidylglycerol, five unidentified glycolipids, and seven unidentified lipids. The predominant fatty acids (> 10.0%) were identified as C18:1ω7c and/or C18:1ω6c, C17:1ω6c, C16:1ω7c and/or C16:1ω6c. The major respiratory quinone was Q-10. Based on the phenotypic and genotypic features, a novel genus and species, Sandaracinobacteroides hominis gen. nov., sp. nov. is proposed, with type strain SZY PN-1T (= KCTC 82150T = NBRC 114675T).

Keywords Sandaracinobacteroides hominis gen. nov. · sp. nov. · Polyphasic taxonomy · Human skin

Introduction

The family Sphingosinicellaceae, which belongs to the order Sphingomonadales, class Alphaproteobacteria, and phylum Proteobacteria, was first proposed by Hördt et al. (2020). This family contains six members: Sphingosinicella (Maruyama et al. 2006) (the type genus), Pacificimonas (Liu et al. 2014), Polymorphobacter (Fukuda et al. 2014), Sandarakinorhabdus (Gich and Overmann 2006), Sphingoaurantiacus (Kim et al. 2016), and “Sandaracinobacter” (Yurkov et al. 1997). The ecologies of the family Sphingosinicellaceae spp. have been reported from environmental samples including varied lakes (Yurkov et al. 1997; Gich and Overmann 2006; Cai et al. 2018; Phurbu et al. 2020), seawater (Lee et al. 2020) and soil (Jia et al. 2015). In this study, we described a novel member of the family Sphingosinicellaceae, designated SZY PN-1T, which was isolated from a skin sample of a healthy Chinese male.
Materials and methods

Isolation and cultivation

Skin samples of the antecubital fossa for culture were obtained from healthy people by culture swabs (MRC, China) during an investigation for the diversity of skin microbiota in 2019 at Guangdong Provincial Hospital of Traditional Chinese Medicine, Guangzhou, PR China. The sampled cells were resuspended with a tube containing 2 mL of sterile saline solution, and then cultivated on BCYEα agar, R2A agar, and their modified medium at 28–32 °C under aerobic conditions. Single colonies were obtained by streaking onto fresh media several times.

A circular and yellow opaque colony, designed as SZY PN-1 T, was selected for taxonomic analysis due to a failure identification by matrix-assisted laser desorption ionization-time of flight mass spectrometry (MALDI-TOF MS) and low similarities of the 16S rRNA gene sequences compared with other species. The isolate was maintained as cells suspension in glycerol (30%, w/v) at –80 °C.

Sequencing and phylogenetic analysis of 16S rRNA gene

For phylogenetic characterization, DNA extraction, primers, as well as PCR amplification of the 16S rRNA gene were described previously (Li et al. 2007). The amplicon was purified using a PCR purification kit (Sangon Biotech, China). Then, the purified PCR product was cloned into Escherichia coli DH5α chemically competent cells using pMD™ 19-T vector and sequenced on a Sanger platform (Sangon Biotech, China). Then, the purified PCR product was cloned into Escherichia coli DH5α chemically competent cells using pMD™ 19-T vector and sequenced on a Sanger platform as described by Giovannoni (Giovannoni et al. 1991). The cloned 16S rRNA gene sequence of SZY PN-1 T was compared with other sequences on the EzBioCloud server (http://www.ezbiocloud.net) (Yoon et al. 2017) and the sequences of related species used for analysis were retrieved. The SZY PN-1 T strain sequence was aligned to those of related type strains using Clustal W (Larkin et al. 2007). Gaps at the 5’ and 3’ ends of the alignment were manually removed. Phylogenetic tree reconstructions were performed based on the neighbor-joining (NJ) (Saitou et al. 1987), maximum- likelihood (ML) (Felsenstein et al. 1981), and maximum- parsimony (MP) (Fitch et al. 1971) algorithms using MEGA X (Kumar et al. 2018). The evolutionary distance and topology of the phylogenetic trees were evaluated by Tamura-Nei model (Nei and Kumar 2000) and the bootstrap analysis based on 1000 replicates (Felsenstein 1985). Rhodospirillum rubrum ATCC 11170 T was used as an outgroup.

Genome sequences analysis

Whole-genome sequencing was performed for strain SZY PN-1 T using 100 bp paired-end sequencing method with the Illumina Hiseq 2000 platform. The raw data were filtered, and high-quality paired-end reads were assembled using the soapednovo version 2.04 (Yarza et al. 2014). The completeness and contamination of the assembled genome sequence was evaluated using Checkm (Abbas et al. 2014). For phylogenomic tree reconstruction, marker genes were extracted from 18 genomes available for the family Sphingosinicellaceae using AMPHORA2 (Parks et al. 2015). Sequences of the amino acid were aligned separately using MUSCLE (Wu and Scott 2012) and were checked to remove the poorly aligned regions via Gblocks (Castresana et al. 2000). Then, cleaned alignments were concatenated using perl script (https://github.com/nylander/catfasta2phylml). The protein-concatemer tree was generated using the RAxML method by applying the default parameter (Edgar 2004) and visualized using the online Tree of Life program version 4.2 (https://itol.embl.de) (Stamatakis 2014).

The genomic relatedness of strain SZY PN-1 T and the related type strains available in public databases was determined by several methods: average nucleotide identity (ANI), average amino acid identity (AAI), as well as the digital DNA–DNA hybridization (dDDH). ANIb and ANIm values were calculated by the online Riboco software (http://jspecies.ribohost.com/jspeciesws) (Richter et al. 2015). The AAI values were calculated using the CompareM software of the online server (https://github.com/dparks1134/CompareM). The dDDH analysis was also performed using the DSMZ Genome-to-Genome Distance Calculator (GGDC) version 2.1 (http://ggdc.dsmz.de/distcalc2.php) (Meier-Kolthoff et al. 2013).

Phenotypic and biochemical analysis

To determine the optimal growth conditions, strain SZY PN-1 T was cultured on R2A agar. BCYEα agar, Columbia blood agar, Haemophilus chocolate 2 agar, chocolate agar with PolyViteX (PVX agar), MacConkey agar and Mueller–Hinton agar (MH), CHAB agar (cysteine heart agar supplemented with 9% heated sheep red blood cells), tryptic soy agar (TSA), and lysogeny broth (LB) agar. The temperature for growth was evaluated on R2A medium at different temperatures (4, 10, 15, 20, 25, 28, 30, 32, 37, and 45 °C) for 5 days. For determining the growth of pH conditions (pH 5–11, prepared using the buffer system as described by Xu et al. (2005) and NaCl tolerance at
Chemotaxonomic analysis

The fatty acid profiles, polar lipids, and respiratory quinones of strain SZY PN-1<sup>T</sup> were analyzed in this study. The cellular fatty acid profiles were determined for SZY PN-1<sup>T</sup> and reference strains grown on R2A plates incubated at 30 °C for 72 h. Cellular fatty acid methyl ester profiles were prepared and analyzed according to the standard protocol of the Microbial Identification System (Sherlock version 6.2; MIDI database: TSBA6) using a gas chromatograph (7890B, Agilent). Polar lipids of strain SZY PN-1<sup>T</sup> were extracted, separated by two-dimensional thin-layer chromatography on Silica gel 60 plates (Merck; Germany) and further analyzed according to the methods as previously described (Minnikin et al. 1979; Collins and Jones 1980). Respiratory quinones were extracted, purified, and analyzed using high-performance liquid chromatography (HPLC) (Kroppenstedt et al. 1982) following the process of Collins et al. (1977). The Bacteriochlorophyll α (BChl α) and carotenoid pigment analysis were performed using the middle-late logarithmic phase as described by Saga et al. (2005). Then, the cells were washed with NaCl-saturated and the pigments were extracted with acetone/methanol (7:2, v/v). The absorption spectrum of the cell extractive at 200–900 nm was analyzed by using GenS™ (Biotek).

**Results and discussion**

**16S rRNA gene sequence and phylogenetic characterization**

Comparison of the 16S rRNA gene sequence of SZY PN-1<sup>T</sup> (1409 bp) with those of other species showed that the most similar sequence was that of strain “Sandaracinobacter sibiricus” RB16-17 (97.1% similarity), followed by strain “Sandaracinobacter neustonicus” JCM 30734 (96.6% similarity; Lee et al. 2020) and other type strains with less than 94.2% similarity within the family Sphingosinicellaceae, which were lower than the threshold (98.65%) for bacterial species demarcation (Kim et al. 2014). The maximum-likelihood tree based on 16S rRNA gene sequences demonstrated that strain SZY PN-1<sup>T</sup> formed a monophyletic clade and clustered closer to the genus “Sandaracinobacter” (Fig. 1). A similar result was obtained when using the neighbor-joining and maximum-parsimony algorithms (Fig. S1–2, available in the online version of this article).

**Genome sequence and phylogenetic characterization**

The genomic size of the strain SZY PN-1<sup>T</sup> was 3.53 Mbp and the DNA G+C content was 65.0%. The protein-concatemer tree based on 29 marker genes indicated that the novel strain SZY PN-1<sup>T</sup> clustered within the genus “Sandaracinobacter”, forming a clade with the strain “S. neustonicus” JCM 30734 (Fig. 2). The threshold limits (95.0–96.0% ANI, 95% AAI and 70% dDDH) for delineation of bacterial species were considered as recommended (Chun et al. 2018; Thompson et al. 2013). The results confirmed that strain SZY PN-1<sup>T</sup> represented a novel genomic species within the family Sphingosinicellaceae, with ANI values ≤ 85.0%, AAI values ≤ 76.0%, and dDDH values ≤ 21.1%. The detailed characteristics of the genomes of the strain SZY PN-1<sup>T</sup> and other type strains within the family Sphingosinicellaceae are listed in Table S1.

**Morphological, physiological, and biochemical characterization**

Strain SZY PN-1<sup>T</sup> showed good growth on R2A agar and BCYEagar; weak growth on Columbia blood agar, MH agar, TSA, and LB agar; but not on Haemophilus chocolate 2 agar, chocolate agar with PolyViteX (PVX agar, Bio-caring, China), CHAB agar and MacConkey agar (Bio-caring, China). After incubation on R2A at 30 °C for 72 h, the colonies were 1–2 mm in diameter, circular, convex, a little hard and yellow colored. Strains were able to grow at
10–37 °C (optimum, 30 °C), pH 6.0–8.0 (optimum, pH 7.0) and in the presence of up to 1.0% (w/v) NaCl with optimum at non-additional NaCl on R2A. Cell of strain SZY PN-1 T was observed to be Gram-negative, aerobic, non-spore-forming and non-motile. The strain was enhanced by the presence of 5% CO2. Transmission electron microscopy image showed that the strain was a rod, 0.71–0.97 µm long and 0.53–0.63 µm wide without flagella, as shown in Fig. S3.

A comparison of the physiological and biochemical characteristics between strain SZY PN-1 T and related genera is shown in the phylogenetic trees below.

Fig. 1 Maximum-likelihood tree of 16S rRNA gene sequences, showing relationships between strain SZY PN-1 T and related taxa. Bootstrap values > 50% based on 1000 replications are shown at branch nodes. Rhodospirillum rubrum ATCC 11170 T was used as an outgroup. Bar, 0.02 substitutions per nucleotide position

Fig. 2 Phylogenomic tree showing the relationship of strain SZY PN-1 T and closely related taxa. The phylogenetic relationship of the related genomes was determined with the concatenated alignment of 29 marker genes (frr, infC, nasA, pgk, pyrG, rplA, rplB, rplC, rplD, rplE, rplF, rplK, rplL, rplM, rplN, rplP, rpsL, rpsT, rpoA, rpsB, rpsC, rpsE, rpsL, rpsJ, rpsK, rpsM, rpsS, smpB, tuf) present in 12 genomes. Bootstrap values (> 50%) are given at the nodes. The genome of Rhodospirillum rubrum ATCC 11170 T (CP000230) was used as an outgroup. Bar, 0.1 substitution per nucleotide position

Sandaracino bacteroides hominis SZY PN-1 T (MW135304)

Sandarakinorhabdus limnophila DSM 17366 T (ATVO01000004)

Sandarakinorhabdus cyanobacteriorum LMG 30294 T (MG519281)

Rhodospirillum rubrum ATCC 11170 T (D30778)
shown in Table 1. Detailed physiological and biochemical characteristics of strain SZY PN-1T determining clear differences from P. fuscus CGMCC 1.12714T and closely related “Sandaracinobacter” species are summarized in Table S2. Other results without differences carried out by commercial test kits (API 20NE, API ZYM and API 50CH) are shown in Table S3.

**Chemotaxonomic characteristics**

Summed feature 8 (C\(_{18:1}\) ω7c and/or C\(_{18:1}\) ω6c; 41.8%), C\(_{17:1}\) ω6c (12.5%), and summed feature 3 (C\(_{16:1}\) ω7c and/or C\(_{16:1}\) ω6c; 10.9%) were the predominant cellular fatty acids (> 10.0%) in SZY PN-1T, in agreement with those of “S. neutostionicus” JCM 30734. Detailed fatty acid compositions are shown in Table 2. Polar lipids of strain SZY PN-1T contained phosphatidylethanolamine (PE), phosphatidylglycerol (PG), and sphingoglycolipids (SGLs) as major polar lipids (Fig. S5). Diphosphatidylglycerol (DPG), unidentified glycolipids (GLs), and unidentified lipids (Ls) were also present as minor polar lipids. The respiratory quinones comprised Q-10 (92.2%) and Q-11 (7.8%), whereas Q-11 was absent in other members of the genera within the family Sphingosinicellaceae. Moreover, strain SZY PN-1T lacked Q-9, which was found to present in the strain of “S. sibiricus” RB16-17. The absorption spectrum of pigments extracted from the cells showed two peaks at 452 and 478 nm (Fig. S4), indicating the presence of carotenoids. No peaks were detected above 600 nm, which showed that BChl α was absent in the strain SZY PN-1T.

**Taxonomic conclusion**

Based on the phenotypic and genotypic features, strain SZY PN-1T was observed to be a novel member of the family Sphingosinicellaceae. Although sharing the highest 16S rRNA gene sequence similarities, closely phylogenetic distance, similar physiological, cellular fatty acid, and polar lipid characteristics with the genus “Sandaracinobacter”, strain SZY PN-1T should be classified as a novel species of a new genus in the family Sphingosinicellaceae. The major issue is that the genus “Sandaracinobacter” is now considered as an illegitimate name, for the type strain of the type species is not available from any public collections. Therefore, we proposed Sandaracinobacteroides hominis gen. nov., sp. nov., which is resembling the genus “Sandaracinobacter”.

**Description of Sandaracinobacteroides gen. nov.**

Sandaracinobacteroides (San.da-ra.ci.no.bac.te.ro’i.des. N.L. masc. n. Sandaracinobacter, a (not validly published) genus name; Gr. adj. suff. -oides, resembling; N.L. neut. n. Sandaracinobacteroides, a genus resembling Sandaracinobacter).
Sandalacinobacteroides hominis

The DNA G+C content is 65.0%. The type species is

\[ \text{phosphatidylglycerol} \]

The major respiratory quinone is Q-10.

Cells are Gram-negative, aerobic and rod-shaped, being 0.71–0.97 µm long and 0.53–0.63 µm wide without flagella. Growth occurs from 10 to 37 °C (optimal at 30 °C). Cells absorb at 430–490 nm, because of the presence of carotenoids. In the API ZYM, API 20NE, and API 50CH strips, it is positive for alkaline phosphatase, esterase (C4), leucine arylamidase, trypsin, acidic phosphatase, naphthol-AS-BI-phosphophydrolase, and α-glucosidase, and weakly positive for esterase lipase (C8), α-chymotrypsin, hydrolysis of ascucl, β-galactosidase, assimilation of glucose and maltose, and esculin ferric citrate. The major cellular fatty acids are Summed feature 8 (C₁₈:₁ ω₇c and/or C₁₈:₁ ω₆c), C₁₇:₁ ω₆c and summed feature 3 (C₁₆:₁ ω₇c and/or C₁₆:₁ ω₆c). The polar lipids are composed of phosphatidylethanolamine, phosphatidylylglycerol, two sphingoglycolipids, diphosthatidyglycerol, five unidentified glycolipids, and seven unidentified lipids. The major respiratory quinone is Q-10, whereas Q-11 is present in smaller amounts. The DNA G+C content of the type strain is 65.0%.

The type strain SZY PN-1\(^T\) (KCTC 82150\(^T\) = NBRC 114675\(^T\)) was isolated from a skin sample of a Chinese male. The GenBank accession number for the 16S rRNA gene sequence of the strain SZY PN-1\(^T\) is MW135304. The GenBank/EMBL/DDBJ/PIR accession number for the Whole Genome Shotgun projects of the strain SZY PN-1\(^T\) is JADCUC00000000.

**Supplementary Information** The online version contains supplementary material available at [https://doi.org/10.1007/s00203-021-02454-9](https://doi.org/10.1007/s00203-021-02454-9).

**Acknowledgements** This research was supported by Guangdong Provincial Key Laboratory of Chinese Medicine for Prevention and Treatment of Refractory Chronic Diseases (2018B030322012) and National Natural Science Foundation of China (31972856).

**Author contributions** YL and CC designed the research and project outline. PHQ, HML, JHF, SL, LD and YZM performed isolation, deposition, and identification. PHQ, HML and JHF analyzed the data. PHQ, HML and WJL drafted the manuscript. All authors read and approved the final manuscript.

**Declarations**

**Conflict of interest** All the authors have declared that there are no conflicts of interest.

**Ethical approval** All experiments involving human subjects were carried out according to the institutional review board protocols approved by the Medical Ethics Committee of Guangdong Provincial Hospital of Chinese Medicine in China (BE2019-165). Informed consent was obtained from all subjects.
References

Abbas MM, Malluhi QM, Balakrishnan P (2014) Assessment of de novo assemblers for draft genomes: a case study with fungal genomes. BMC Genomics 15:S10

Aslanzadeh J (2006) Biochemical profile-based microbial identification systems. In: Tang YW, Stratton CW (eds) Advanced techniques in diagnostic microbiology. Springer, New York, pp 87–121

Cai H, Cui H, Zeng Y, An M, Jiang H (2018) Sandarakinorhabdus cyanobacterium sp. nov., a novel bacterium isolated from cyanobacterial aggregates in a eutrophic lake. Int J Syst Evol Microbiol 68:730–735

Castricena J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol 17:540–552

Chun J, Oren A, Ventosa A, Christensen H, Arahal DR, da Costa MS, Rooney AP, Yi H, Xu XW, De Meyer S, Trujillo ME (2018) Proposed minimal standards for the use of genome data for the taxonomy of prokaryotes. Int J Syst Evol Microbiol 68:461–466

Collins MD, Jones D (1980) Lipids in the classification and identification of coryneform bacteria containing peptidoglycan based on 2,4-diaminobutyric acid. J Appl Bacteriol 48:459–470

Collins MD, Pirouz T, Goodfellow M, Minnikin DE (1977) Distribution of menaquinones in actinomycetes and corynebacteria. J Gen Microbiol 100:221–223

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32:1792–1797

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17:368–376

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791

Fitch WM (1971) Toward defining the course of evolution: minimum change for a specific tree topology. Syst Biol 20:406–416

Fukuda W, Chino Y, Araki S, Kondo Y, Imanaka H, Kanai T, Atomi H, Imanaka T (2014) Polymorphobacter multimanifer gen. nov., sp. nov., a polymorphic bacterium isolated from Antarctic white rock. Int J Syst Evol Microbiol 64:2034–2040

Gich F, Overmann J (2006) Sandarakinorhabdus limnophila gen. nov., sp. nov., a novel bacteriochlorophyll α-containing, obligately aerobic bacterium isolated from freshwater lakes. Int J Syst Evol Microbiol 56:847–854

Giovannoni SJ (1991) The polymerase chain reaction. In: Stackebrandt E, Goodfellow M (eds) Modern microbiological methods: nucleic acids techniques in bacterial systematics. Wiley, New York, pp 177–203

Hansen GH, Sørheim R (1991) Improved method for phenotypic characterization of marine bacteria. J Microbiol Methods 13:231–241

Hördt A, López MG, Meier-Kolthoff JP, Schleuning M, Weinhold LM, Tindall BJ, Gronow S, Kyrpides NC, Woyke T, Göker M (2020) Analysis of 1000+ type-strain genomes substantially improves characterization of marine bacteria. J Microbiol Methods 177–203

Huson DH, Imelfort M, Skennerton CT, Hugenholtz P, Tyson GW (2012) DNAbarcoding: a tool for species delimitation and ecological studies of planktonic metazoans. PLoS ONE 7:e4698–4703

Kroppenstedt RM (1982) Separation of bacterial menaquinones by HPLC using reverse phase (RP18) and a silver loaded ion exchange as stationary phases. J Liq Chromatogr 5:2359–2367

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547–1549

Kumar MA, Blackshields G, Brown NP, Chenna R, Mcgrettigan PA (2007) Clustal W and Clustal X version 2.0. Bioinformatics 23:2947–2948

Lee I, Jang GI, Cho Y, Yoon SI, Pham HM, Nguyen AV, Lee YM, Park H, Rhee TS, Kim SH, Hwang CY (2020) Sandaracineobacter neustonicus sp. nov., isolated from the sea surface micro-layer in the Southwestern Pacific Ocean, and emended description of the genus Sandaracinobacter. Int J Syst Evol Microbiol 70:4698–4703

Lee P, Mu J, Huang H, Luo P, Zhang Q, Ji XH, Liu ZL, Zhang YQ, Xiao Q, Li J, Liang Y, Peng C (2016) Georgenia actinobacterium sp. nov., a novel bacteriochlorophyll c-containing, obligately aerobic bacterium isolated from Antarctic white rock. Int J Syst Evol Microbiol 64:346–351

Lee I, Jang GI, Cho Y, Yoon SI, Pham HM, Nguyen AV, Lee YM, Park H, Rhee TS, Kim SH, Hwang CY (2020) Sandaracineobacter neustonicus sp. nov., isolated from the sea surface micro-layer in the Southwestern Pacific Ocean, and emended description of the genus Sandaracinobacter. Int J Syst Evol Microbiol 70:4698–4703

Liu K, Li S, Jiao N, Tang K (2014) Pacificamonas flava gen. nov., sp. nov., a novel member of the family Sphingomonadaceae isolated from the Southeastern Pacific. Curr Microbiol 69:96–101

Logan NA, Vos PD (2009) The genus Bacillus. In: Vos PD, Garrity GM, Jones D, Krieg ND, Ludwig W, Rainey FA, Schleifer KH, Whitman WB (eds) Bergeys manual of systematic bacteriology, vol 3, 2nd edn. Springer, New York, p 62

Maruyama T, Park HD, Ozawa TY, Sumino T, Hamana K, Hiraishi A, Kato K (2006) Sphingosinicella microcystinivorans gen. nov., sp. nov., a microcystin-degrading bacterium. Int J Syst Evol Microbiol 56:85–89

Meier-Kolthoff JP, Auch AF, Klenk HP, Göker M (2013) Genome sequence-based species delimitation with confidence intervals and improved distance functions. BMC Bioinformatics 14:60

Minnikin DE, Collins MD, Goodfellow M (1979) Fatty acid and polar lipid composition in the classification of Cellulomonas, Oerskovia and related taxa. J Appl Bacteriol 47:87–95

Nei M, Kumar S (2000) Molecular evolution and phylogenetics. Oxford University Press, New York

Parks DH, Imelfort M, Skennerton CT, Hugenholtz P, Tyson GW (2015) CheckM: assessing the quality of microbial genomes recovered from isolates, single cells, and metagenomes. Genome Res 25:1043–1055

Phurbu D, Liu ZX, Liu HC, Lhamo Y, Yangzom P, Li AH, Zhou YG (2020) Polymorphobacter arshaanensis sp. nov., containing the photosynthetic gene puFML, isolated from a volcanic lake. Int J Syst Evol Microbiol 70:1093–1098

Richter M, Rosselló-Móra R, Oliver Glöckner F, Peplies J (2015) JSpeciesWS: a web server for prokaryotic species circumscription based on pairwise genome comparison. Bioinformatics 32:929–931

Saga Y, Osumi S, Higuchi H, Tamiaki H (2005) Bacteriochlorophyll c homolog composition in green sulfur photosynthetic bacterium Chlorobium vibrioforme dependent on the concentration of sodium sulfide in liquid cultures. Photosynth Res 86:123–130

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406–425

Smibert RM, Krieg NR (1994) Phenotypic characterization. In: Gerhardt P, Murray RGE, Wood WA et al (eds) Methods for general and molecular bacteriology. American Society for Microbiology, Washington, pp 607–654
Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313
Thompson CC, Chimetto L, Edwards RA, Swings J, Stackebrandt E, Thompson FL (2013) Microbial genomic taxonomy. BMC Genomics 14:913
Wu M, Scott AJ (2012) Phylogenomic analysis of bacterial and archaeal sequences with AMPHORA2. Bioinformatics 28:1033–1034
Xing T, Liu Y, Wang N, Xu B, Shen L, Liu K, Gu Z, Guo B, Zhou Y, Liu H (2017) Polymorphobacter glacialis sp. nov., isolated from ice core. Int J Syst Evol Microbiol 67:617–620
Xu P, Li WJ, Tang SK, Zhang YQ, Chen GZ, Chen HH, Xu LH, Jiang CL (2005) Naxibacter alkalitolerans gen. nov., sp. nov., a novel member of the family ‘Oxalobacteraceae’ isolated from China. Int J Syst Evol Microbiol 55:1149–1153
Yarza P, Yilmaz P, Glöckner FO, Ludwig W, Schleifer KH, Whitman WB, Euzéby J, Amann R, Rosselló-Móra R (2014) Uniting the classification of cultured and uncultured bacteria and archaea using 16S rRNA gene sequences. Nat Rev Microbiol 12:635–645
Yoon SH, Ha SM, Kwon S, Lim J, Kim Y, Seo H, Chun J (2017) Introducing EzBioCloud: a taxonomically united database of 16S rRNA gene sequences and whole-genome assemblies. Int J Syst Evol Microbiol 67:1613–1617
Yurkov V, Stackebrandt E, Buss O, Vermeglio A, Gorlenko V, Beatty JT (1997) Reorganization of the genus Erythromicrobium: description of Erythromicrobium sibiricum as Sandaracinobacter sibiricus gen. nov., sp. nov., and of Erythromicrobium ursincola as Erythromonas ursincola gen. nov., sp. nov. Int J Syst Bacteriol 47:1172–1178

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