Devosia litorisediminis sp. nov., isolated from a sand dune

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Abstract

A Gram-negative, aerobic, non-motile, and rod-shaped bacterial strain, designated BSSL-BM10^T, was isolated from a sand dune that was collected from the Yellow Sea, Republic of Korea. It was subjected to a polyphasic taxonomic study. 16S rRNA gene sequence analysis showed that strain BSSL-BM10^T fell phylogenetically within the radiation comprising type strains of *Devosia* species. The 16S rRNA gene sequence of strain BSSL-BM10^T shared sequence similarities of 98.2% with the type strain of *D. naphthalenivorans* and 93.5-97.7% with type strains of other *Devosia* species. ANI and dDDH values between strain BSSL-BM10^T and type strains of 18 *Devosia* species were 71.0-78.4% and 18.8-21.5%, respectively. The DNA G+C content of strain BSSL-BM10^T was 60.9% based on its genomic sequence data. Strain BSSL-BM10^T contained Q-10 as the predominant ubiquinone and 11-methyl $C_{18:1}$ *ω7c*, $C_{18:1}$ *ω7c*, summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), and $C_{16:0}$ as its major fatty acids. Major polar lipids of strain BSSL-BM10^T were phosphatidylglycerol and two unidentified glycolipids. Strain BSSL-BM10^T showed distinguished phenotypic properties with its phylogenetic and genetic distinctiveness separated from recognized *Devosia* species. Based on data presented in this study, strain BSSL-BM10^T should be placed in the genus *Devosia*. The name *Devosia litorisediminis* sp. nov. is proposed for strain BSSL-BM10^T (= KACC 21633^T = NBRC 115152^T).

Introduction

The genus *Devosia*, a member of the family *Devosiaceae* (Hördt et al. 2020) of the class *Alphaproteobacteria*, was proposed by Nakagawa et al. (1996) with transfer of "*Pseudomonas riboflavina*" to *Devosia riboflavina* (type species). The genus *Devosia* currently comprises 28 species with validly published names (https://lpsn.dsmz.de/genus/devosia; Parte 2018). Members of the genus *Devosia* are known to be Gram-negative, oval or rod-shaped, aerobic, and oxidase-positive with DNA G+C contents of 59-65 mol% and ubiquinone-10 (Q-10) or ubiquinone-11 (Q-11) as the predominant respiratory quinone (Jia et al. 2014; Quan et al. 2020; Yoon et al. 2007). Isolation sources of *Devosia* species include soils, hexachlorocyclohexan dumpsite, root nodule, alpine glacier cryoconite, surface of a medical leech, marine sediments, estuary environment, and seawater (Bautista et al. 2010; Galatis et al. 2013; Jia et al. 2014; Kumar et al. 2008; Lin et al. 2020; Park et al. 2016; Quan et al. 2020; Romanenko et al. 2013; Yoon et al. 2007; Zhang et al. 2012). Recently, in the course of screening novel bacteria from a sand dune close to the Yellow Sea of Republic of Korea, many bacterial isolates have been obtained followed by characterized taxonomically. One of these bacterial isolates, designated as BSSL-BM10^T, showed the closest affiliation to members of the genus *Devosia* from the result of 16S rRNA gene sequence comparison. In this study, strain BSSL-BM10^T is characterized further using a polyphasic characterization, combining phylogenetic analysis based on 16S rRNA gene sequences, genetic analyses based on genome data, and determinations of chemotaxonomic and other phenotypic properties.

Materials And Methods

Bacterial strains and culture conditions

A marine dune was collected from Boryeong (36°20’95“N, 126°53’80”E) close to the Yellow Sea of Republic of Korea. The sample (about 1-2 g) was serially diluted with 0.85% (w/v) saline solution and spread onto marine agar 2216 (MA; BD Difco). After incubation at 25 °C for 7 days, strain BSSL-BM10^T was isolated from the MA plate and speak onto trypticase soy agar (TSA; BD Bacto) at 30 °C. Cells of strain BSSL-BM10^T were suspended in a sterile solution containing 20% (w/v) glycerol and stored at –80 °C for long-term preservation. *Devosia naphthalenivorans* JCM 32509^T and *Devosia riboflavina* DSM 7230^T were obtained from the Japan Collection for Microorganisms (JCM; Japan) and Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ; Germany), respectively. Cells of strain BSSL-BM10^T and *D. riboflavina* DSM 7230^T obtained from culture grown for 3 days in trypticase soy broth (BD Bacto) at 30 °C were used to extract DNA and to analyze isoprenoid quinones and polar lipids. Cell masses for cellular fatty acid analysis were obtained under the following conditions: strain BSSL-BM10^T were harvested from TSA plates after cultivation for 3, 5, and 7 days at 30 ºC, and *D. naphthalenivorans* JCM 32509^T and *D. riboflavina* DSM 7230^T were harvested from MA and TSA plates, respectively, after cultivation for 5 days at 30 ºC.

Sequencing and phylogenetic analysis of 16S rRNA gene

Chromosomal DNA extraction was performed using a Wizard Genomic DNA isolation kit (Promega) according to the manufacturer’s instruction. The 16S rRNA gene amplification was performed as described previously (Yoon et al. 1997) using PCR in which 9F (5’-GAGTTTGATCCTGGCTCAG-3’) and 1512R (5’-ACGGTTACCTTGTTACGACTT-3’) were used. Sequencing of the 16S rRNA gene followed by phylogenetic analysis were carried out as described by Yoon et al. (2003). Similarity between 16S rRNA gene sequences was calculated from alignment obtained using Clustal W program.

Genomic analysis

A TruSeq DNA LT Sample Prep kit (Illumina) was used to prepare a library for genomic sequencing. The library was sequenced using Illumina MiSeq platform. Sequencing data were assembled with SPAdes (Bankevich et al. 2012). Contamination of genome sequence was assessed using ContEst16S (Lee et al. 2017). Library construction and sequencing were performed by Chunlab Inc. (Republic of Korea). The ANI value based on BLAST+ was calculated using JSpecies WS (http://jspecies.ribohost.com/jspeciesws/; Richter et al. 2015) or OrthoANI (Yoon et al. 2017) in EZBioCloud. The dDDH value was estimated using TYGS (https://tygs.dsmz.de/user_requests/new) with BLAST+ in which the recommended formula 2 (Meier-Kolthoff et al. 2013) was used. Phylogenetic tree was constructed based on genomic sequences using previous methods (Lefort et al. 2015; Meier-Kolthoff et al. 2013) described in the TYGS. Intergenomic distances inferred under the algorithm 'trimming' and distance formula d_5 (Meier-Kolthoff et al. 2013) and 100 distance replicates were calculated each. The resulting distances were used to infer a balanced minimum evolution tree with branch support via FASTME 2.1.6.1 including SPR postprocessing (Lefort et al. 2015).

Chemotaxonomic characterization

Extraction and analysis of isoprenoid quinones were performed as described by Komagata and Suzuki (1987) and Park et al. (2014), respectively. Fatty acid analysis was performed as described by Park et al. (2014) using the standard MIDI protocol (Sherlock Microbial Identification System, version 6.2B), GC (Hewlett Packard 6890), and TSBA6 database of the Microbial Identification System (Sasser 1990). Extraction of polar lipids were carried out according to procedures described by Minnikin et al. (1984). They were separated by two-dimensional TLC using the solvent systems as described by Embley and Wait (1994). The TLC plates were sprayed with various reagents as described by Park et al. (2014) and individual polar lipids were visualized followed by identified with heating at 150 ºC for 3min.

Morphological, cultural, physiological and biochemical characterization

Cell morphology, Gram reaction, anaerobic growth, pH range for growth, growth at various concentrations of NaCl, hydrolysis of gelatin and urea and susceptibility to antibiotics were investigated as described by Park et al. (2014). For transmission electron microscopy (JEM1010; JEOL), cells were negatively stained with 1% (w/v) phosphotungstic acid and air-dried. Grids were then examined. Growths at 4, 10, 20, 25, 28, 30, 35, 37, and 40 °C on MA were measured to estimate the optimal temperature and temperature range for its growth. Nitrate reduction and hydrolysis of aesculin or Tween 80 were investigated as described previously (Lányí 1987) using artificial seawater (Bruns et al. 2001) for the preparation of the media. Hydrolysis of other substrates was tested as described by Barrow and Feltham (1993) with the modification that MA was used. Activities of catalase and oxidase were determined as described by Lányí (1987). Utilization of various substrates (each 0.2%) for growth was investigated as described by Kämpfer et al. (1991). Other biochemical and physiological properties were determined using API ZYM and API 20NE systems (bioMérieux; France). Enzyme activities by the API ZYM system were determined after incubation at 30 ºC for 8 h. Other physiological and biochemical properties by the API 20NE system were determined after incubation at 30 ºC for 2 days.

Results And Discussion

Phylogenetic analysis based on 16S rRNA gene sequence

The 16S rRNA gene sequence of strain BSSL-BM10^T determined in this study had a continuous stretch of 1421 nucleotides, corresponding to positions 28-1491 (95%) of the *Escherichia coli* 16S rRNA sequence. Phylogenetic trees using three different algorithms (neighbour-joining, maximum-likelihood and maximum-parsimony) showed that strain BSSL-BM10^T formed an independent lineage within the clade comprising type strains of *Devosia* species (Fig. 1; Figs. S1 and S2). Strain BSSL-BM10^T shared the highest 16S rRNA gene sequence similarities (98.2%) with *D. naphthalenivorans* CM5-1^T. It also shared 93.5-97.7% 16S rRNA gene sequence similarities with type strains of other *Devosia* species. These sequence similarities indicated that strain BSSL-BM10^T might be a species different from recognized

Devosia species according to the threshold value (98.7%) recommended for delineation of a bacterial species by Chun et al. (2018).

Genomic Features

The genome size of strain BSSL-BM10^T obtained from the assembly of sequencing reads was 3,743,297 bp with a sequencing depth of coverage of 414.33X. The genomic sequence of strain BSSL-BM10^T contained five contigs with N50 length of 2,671,820 bp. The complete 16S rRNA gene sequence from the genomic data of strain BSSL-BM10^T was extracted using ContEst16S (Lee et al. 2017). It was found to be identical to respective 16S rRNA gene information previously obtained by Sanger sequencing. This indicated that strain BSSL-BM10^T and its genomic data were not mislabeled. They did not originate from any source of contamination (Chun et al. 2018). Based on its genomic sequence data, the DNA G+C content of strain BSSL-BM10^T was 60.9%, a value in the range reported for *Devosia* species (Ji et al. 2014; Quan et al. 2020; Yoon et al. 2007). The phylogenetic tree based on genomic sequences showed that strain BSSL-BM10^T formed a lineage within the clade comprising type strains of *Devosia* species (Fig. S3). The genomic sequence data of strain BSSL-BM10^T had an ANI value of 77.2% with *D. naphthalenivorans* CM5-1^T and 71.0-78.4% with type strains of *Devosia ginsengisoli*, *Devosia epidermidihirudinis*, *Devosia psychrophila*, *Devosia limi*, *Devosia submarina*, *Devosia marina*, *Devosia indica*, *Devosia subaequoris*, *Devosia elaeis*, *Devosia riboflavina*, *Devosia chinhatensis*, *Devosia lucknowensis*, *Devosia soli*, *Devosia crocina*, *Devosia geojensis*, *Devosia insulae*, and *Devosia enhydra* (Table S1). Strain BSSL-BM10^T had dDDH values of 21.0% with *D. naphthalenivorans* CM5-1^T and 18.8-21.5% with type strains of the above-mentioned 17 *Devosia* species (Table S1). These ANI values (71.0-78.4%) and dDDH values (18.8-21.5%) of genomic sequences between strain BSSL-BM10^T and type strains of *Devosia* species were lower than standard ANI and dDDH values (95-96% and 70%, respectively) recommended for delineation of a bacterial species (Goris et al. 2007; Konstantinidis and Tiedje 2005; Richter and Rosselló-Móra 2009).

Chemotaxonomic Characteristics

The predominant isoprenoid quinone detected in strain BSSL-BM10^T was ubiquinone-10 (Q-10), consistent with results for members of *Devosia* species (Ji et al. 2014; Nakagawa et al. 1996; Quan et al. 2020; Yoon et al. 2007). The major fatty acids (> 10% of total fatty acids in all growth phases) found in strain BSSL-BM10^T were 11-methyl $C_{18:1}$ *ω7c*, $C_{18:1}$ *ω7c*, summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), and $C_{16:0}$ (Table 1). Fatty acid profiles of strain BSSL-BM10^T were similar to those of type strains of *D. naphthalenivorans* and *D. riboflavina*, with 11-methyl $C_{18:1}$ *ω7c*, $C_{18:1}$ *ω7c*, and $C_{16:0}$ being the major fatty acids. Nevertheless, there were differences in proportions of some fatty acids, including summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*) and cyclo $C_{19:0}$ *ω8c*, between strain BSSL-BM10^T and two reference strains (Table 1). Major polar lipids detected in stain BSSL-BM10^T were phosphatidylglycerol and two

unidentified glycolipids. Minor amounts of diphosphatidylglycerol, two unidentified lipids, another unidentified glycolipid, and one unidentified aminolipid were also present (Fig. S4). The polar lipid profile of strain BSSL-BM10^{T} was similar to those of type strains of *D. naphthalenivorans* and *D. riboflavina* in that phosphatidylglycerol and two unidentified glycolipids were major components (Fig. S4; Park et al. 2016).

Table 1

Cellular fatty acid compositions (%) of strain BSSL-BM10^T and the type strains of *Devosia naphthalenivorans* and *Devosia riboflavina*.

Fatty acid	**1**	**2**	**3**	**4**	**5**
Straight-chain					
$C_{14:0}$	0.8	1.1	1.1	0.7	TR
$C_{16:0}$	11.0	13.4	12.8	8.0	21.5
$C_{17:0}$	1.5	2.3	2.3	–	TR
Cyclo $C_{17:0}$	–	–	–	TR	1.3
$C_{18:0}$	8.1	7.0	6.9	7.9	4.1
Unsaturated					
$C_{18:1}$ *ω7c*	29.5	24.8	26.1	41.2	32.4
$C_{20:1}$ *ω7c*	TR	TR	TR	TR	0.6
Hydroxy					
$C_{10:0}$ 3-OH	–	–	–	1.1	1.4
$C_{18:0}$ 3-OH	2.4	2.7	–	4.0	TR
11-methyl $C_{18:1}$ ω7c	33.5	34.9	36.8	23.4	31.3
Cyclo $C_{19:0}$ ω8c	–	–	–	2.6	4.7
Summed feature[a]					
3	11.5	12.7	12.0	7.6	1.5

Strains: 1, BSSL-BM10^T (3 days); 2, BSSL-BM10^T (5 days); 3, BSSL-BM10^T (7 days); 4, *D. naphthalenivorans* JCM 32509^T (5 days); 5, *D. riboflavina* DSM 7230^T (5 days). All data obtained from this study. Fatty acids that represented < 0.5% in all columns were omitted. Fatty acids that represented > 10.0% were indicated in bold. TR, Traces (< 0.5%). −, Not detected.

[a]Summed feature is fatty acids that cannot be resolved reliably from another fatty acid using the chromatographic conditions chosen. The MIDI system groups these fatty acids together as one feature with a single percentage of the total. Summed feature 3 contains $C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*.

Morphological, Cultural, Physiological And Biochemical Characteristics

Strain BSSL-BM10^T showed a Gram-negative, non-spore-forming, and non-flagellated properties and its cellular morphology was rod-shaped. Phenotypic characteristics of strain BSSL-BM10^T are given in the species description, Table 2, or Fig. S5. Strain BSSL-BM10^T grew well on TSA and MA. Although the type strain of *D. naphthalenivorans* also grew well on MA, it grew poorly on TSA. Strain BSSL-BM10^T was resistant to gentamicin, whereas type strains of *D. naphthalenivorans* and *D. riboflavina* were susceptible to gentamicin (Table 2). Strain BSSL-BM10^T produced trypsin, *α*-glucosidase, and *α*-fucosidase, but the type strains of *D. naphthalenivorans* and *D. riboflavin* did not produce these three enzymes (Table 2).

Table 2

Differential characteristics of strain BSSL-BM10^T and the type strains of *Devosia naphthalenivorans* and *Devosia riboflavina*.

Characteristic	1	2	3
Nitrate reduction	–	+	–
Arginine dihydrolase	–	–	+
Acid production from D-glucose	–	–	+
Utilization of			
L-Arabinose, D-cellobiose, D-fructose, D-galactose, D-glucose, maltose, D-mannose, sucrose, D-trehalose, D-xylose, acetate, pyruvate, succinate, salicin	+	–	+
Citrate, L-malate	+	–	–
Susceptibility to			
Cephalothin	–	–	+
Gentamicin	–	+	+
Penicillin G	+	–	+
Polymyxin B	–	–	+
Enzyme activity (API ZYM)			
Valine arylamidase	+	+	–
Trypsin	+	–	–
Acid phosphatase	+	–	+

Strains: 1, BSSL-BM10^T; 2, *D. naphthalenivorans* JCM 32509^T; 3, *D. riboflavina* DSM 7230^T. Data of columns 1 and 2 obtained from this study unless otherwise indicated and data of column 3 obtained from Park *et al*. [12]. +, positive; –, negative; w, weakly positive. All strains are positive for activity of urease; aesculin hydrolysis; *β*-galactosidase (hydrolysis of 4-nitrophenyl-*β*-D-galactopyranoside); susceptibility to ampicillin, carbenicillin, chloramphenicol, neomycin, novobiocin, oleandomycin and tetracycline; and activity of alkaline phosphatase (weak for *D. riboflavina* DSM 7230^T), esterase (C4), esterase lipase (C8), leucine arylamidase (weak for *D. riboflavina* DSM 7230^T) and *β*-glucosidase. All strains are negative for indole production; gelatin hydrolysis; utilization of benzoate, formate and L-glutamate; susceptibility to kanamycin, lincomycin and streptomycin; and activity of lipase (C14), cystine arylamidase, *α*-chymotrypsin, *α*-galactosidase, *β*-glucuronidase and *α*-mannosidase.

[a]Data from genomic sequences.

Characteristic	1	2	3
Naphthol-AS-BI-phosphohydrolase	+	+	–
β-Galactosidase (hydrolysis of 2-naphthyl-*β*-D-galactopyranoside)	+	–	+
α-Glucosidase	+	–	–
N-Acetyl-*β*-glucosaminidase	+	–	+
α-Fucosidase	+	–	–
DNA G+C content (%)[a]	60.9	61.4	61.8

Strains: 1, BSSL-BM10^T; 2, *D. naphthalenivorans* JCM 32509^T; 3, *D. riboflavina* DSM 7230^T. Data of columns 1 and 2 obtained from this study unless otherwise indicated and data of column 3 obtained from Park *et al*. [12]. +, positive; –, negative; w, weakly positive. All strains are positive for activity of urease; aesculin hydrolysis; *β*-galactosidase (hydrolysis of 4-nitrophenyl-*β*-D-galactopyranoside); susceptibility to ampicillin, carbenicillin, chloramphenicol, neomycin, novobiocin, oleandomycin and tetracycline; and activity of alkaline phosphatase (weak for *D. riboflavina* DSM 7230^T), esterase (C4), esterase lipase (C8), leucine arylamidase (weak for *D. riboflavina* DSM 7230^T) and *β*-glucosidase. All strains are negative for indole production; gelatin hydrolysis; utilization of benzoate, formate and L-glutamate; susceptibility to kanamycin, lincomycin and streptomycin; and activity of lipase (C14), cystine arylamidase, *α*-chymotrypsin, *α*-galactosidase, *β*-glucuronidase and *α*-mannosidase.

[a]Data from genomic sequences.

Conclusion

Combined results obtained from phylogenetic, genomic, and chemotaxonomic analyses made it reasonable to assign strain BSSL-BM10^T as a member of the genus *Devosia* (Fig. 1; Figs. S1, S2 and S3; Table 1). Strain BSSL-BM10^T was distinguished from type strains of *D. naphthalenivorans* and *D. riboflavina* by differences in several phenotypic characteristics, including nitrate reduction, acid production from D-glucose, utilization of some substrates, susceptibility to some antibiotics, and activities of some enzymes (Table 2). Distinguished phenotypic properties, 16S rRNA gene sequence similarities, and genetic distinctiveness based on ANI values and dDDH values suggest that strain BSSL-BM10^T is separated from recognized species of genus *Devosia* (Chun et al. 2018; Goris et al. 2007; Konstantinidis and Tiedje 2005; Richter and Rosselló-Móra 2009). Based on polyphasic taxonomic data presented, strain BSSL-BM10^T is considered to represent a novel *Devosia* species, for which we propose the name *Devosia litorisediminis* sp. nov.

Description of Devosia litorisediminis **sp. nov.**

Devosia litorisediminis (li.to.ri.se.di'mi.nis. L. n. *litus – oris* the seashore, coast; L. n. *sedimen – inis* sediment; N.L. gen. n. *litorisediminis* of a coastal sediment, tidal flat sediment).

Cells are rod-shaped measuring approximately 0.3-0.8 μm in diameter and 0.8-4.0 μm in length. Gram-staining reaction is negative. Spore is not formed. No flagellum is found. Colonies on TSA are circular, convex, smooth, glistening, grayish yellow in colour, and 0.5-1.0 mm in diameter after incubation at 30°C for 5 days. Grows optimally at 30°C and pH 7.0-8.0. Growth occurs at 4 °C to 37°C, but not at 40°C and occurs at pH 5.0, but not at pH 4.5. Growth occurs in the presence of 0.5-5.0% (w/v) NaCl with an optimum of approximately 1.0-2.0% (w/v) NaCl. Anaerobic growth does not occur on TSA or TSA supplemented with nitrate. It is catalase- and oxidase-positive. Nitrate is not reduced to nitrite. Aesculin, hypoxanthine, urea, and xanthine are hydrolyzed, while casein, gelatin, starch, Tween 80, and L-tyrosine are not. L-Arabinose, D-galactose, D-glucose, maltose, D-cellobiose, D-fructose, D-mannose, sucrose, D-trehalose, D-xylose, acetate, citrate, succinate, L-malate, pyruvate, and salicin are utilized as carbon and energy sources, but benzoate, formate, and L-glutamate are not. Susceptible to ampicillin (10 μg), carbenicillin (100 μg), chloramphenicol (100 μg), neomycin (30 μg), novobiocin (5 μg), oleandomycin (15 μg), penicillin G (20 IU), and tetracycline (30 μg), but resistant to cephalothin (30 μg), gentamicin (30 μg), kanamycin (30 μg), lincomycin (15 μg), polymyxin B (100 IU), and streptomycin (50 μg). In assays with API 20NE system, it is positive for activity of urease and hydrolysis of 4-nitrophenyl-*β*-D-galactopyranoside, but negative for indole production, arginine dihydrolase, and acid production from D-glucose and gelatin hydrolysis. In assays with the API ZYM system, activities of esterase (C4), esterase lipase (C8), leucine and valine arylamidases, trypsin, alkaline and acid phosphatases, naphthol-AS-BI-phosphohydrolase, *β*-galactosidase, *α*-glucosidase, *β*-glucosidase, *N*-acetyl-*β*-glucosaminidase, and *α*-fucosidase are present, but activities of other enzymes are absent. The predominant ubiquinone is Q-10. The major fatty acids (> 10% of total fatty acids) are 11-methyl $C_{18:1}$ *ω7c*, $C_{18:1}$ *ω7c*, summed feature 3 ($C_{16:1}$ *ω7c* and/or $C_{16:1}$ *ω6c*), and $C_{16:0}$. The major polar lipids are phosphatidylglycerol and two unidentified glycolipids.

The type strain, BSSL-BM10^T (= KACC 21633^T = NBRC 115152^T), was isolated from a sand dune at Boryeong on the Yellow Sea, Republic of Korea. The DNA G+C content of the type strain is 60.9% (from genome sequence data). The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence and GenBank accession number for the whole genome shotgun sequence of strain BSSL-BM10^T are MN872411and JAGXTP000000000, respectively.

Abbreviations

ANI, average nucleotide identity; dDDH, digital DNA-DNA hybridization; GC, Gas chromatograph

Declarations

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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Figures

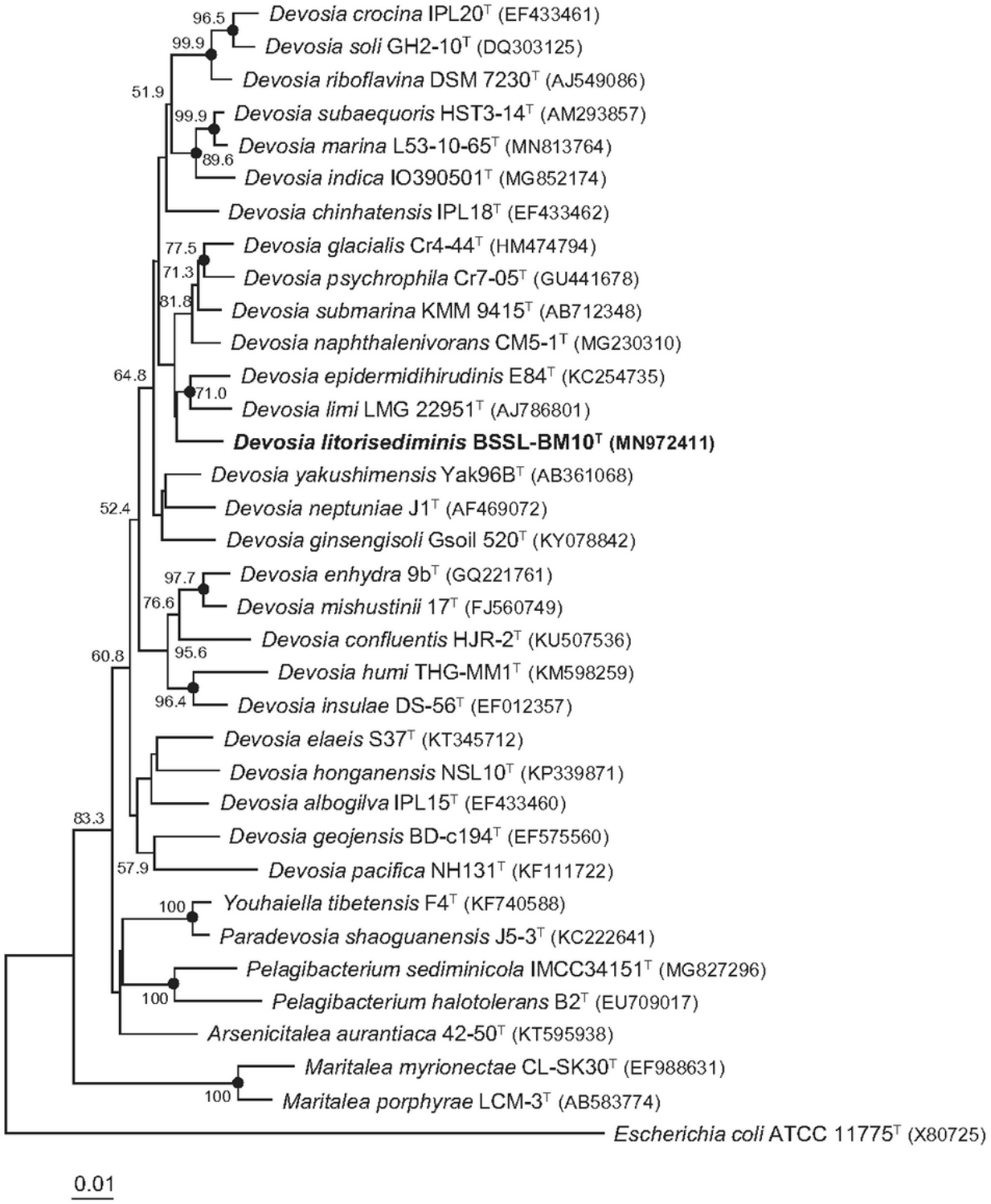

Figure 1

Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing the positions of Devosia litorisediminis BSSL-BM10T, the type strains of Devosia species and representatives of some other related taxa. Only bootstrap values greater than 50% are shown at branching points. Filled circles indicate that the corresponding nodes were also recovered in the trees generated with the maximum-likelihood and maximum-parsimony algorithms, while open circles indicate that the corresponding nodes

were also recovered in the tree generated with the maximum-parsimony algorithm. Escherichia coli ATCC 11775T (GenBank accession number, X80725) was used as an outgroup. Bar, 0.01 substitutions per nucleotide position.

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