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ORIGINAL PAPER

Nonomuraea basaltis sp. nov., a siderophore-producing actinobacteria isolated from surface soil of basaltic parent material

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Abstract

A Gram-stain-positive, aerobic, spore-forming actinobacterial strain, designated 160415^T, was isolated from a surface soil sample, which was formed on basaltic parent material, collected from Samsun, Turkey. Phylogenetic analysis based on 16S rRNA gene sequences showed that strain 160415^T clustered closely with species of the genus *Nonomuraea*, and showed the highest sequence similarity to *Nonomuraea zeae* NEAU-ND5^T, *Nonomuraea candida* HMC10^T and *Nonomuraea turkmeniaca* DSM 43926^T with 99.1%, 98.9% and 98.7%, respectively. Chemotaxonomic properties including major menaquinones, diaminopimelic acid, sugar and phospholipid profiles also confirmed the affiliation of the strain to the genus *Nonomuraea*. The DNA G+C content of strain 160415^T was 69.6 mol%. DNA–DNA hybridization and average nucleotide identity values between the strain and closely related type strains were less than the recommended cut-off values. On the basis of phylogenetic relationships, genotypic and phenotypic characterizations, strain 160415^T represents a novel species of the genus *Nonomuraea*, for which the name *Nonomuraea basaltis* sp. nov. is proposed. The type strain is 160415^T (=KCTC 39875^T=DSM 104309^T).

Keywords *Actinobacteria* · Basaltic parent material · *Nonomuraea* · Whole-genome

Introduction

The genus *Nonomuraea*, which belongs to the family *Streptosporangiaceae,* was first proposed by Zhang et al. (1998) and the genus has been consecutively emended by Nakaew et al. (2012) and Cao et al. (2019). Members of the genus form extensively branched substrate and aerial mycelia. Aerial hyphae differentiate into hooked, spiral or straight chains of spores (Goodfellow and Quintana 2006; Kämpfer 2012). At the time of writing, the genus comprises 51 species with validly published names have been described (https://www.bacterio.net/nonomuraea.html). Members of this genus are widespread in different type soil, including acidic soil (Li et al. 2012), cave soil (Nakaew et al. 2012), desert soil (Saygin et al. 2020), forest soil (Sripreechasak et al. 2017; Saricaoglu et al 2018), mangrove soil (Huang et al. 2018) and rhizosphere soil (Wang et al 2011; Cao et al. 2019).

In the course of the investigation of novel actinobacteria from the surface soil sample, which was formed on basaltic parent material, 160415^T was isolated. We describe the

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taxonomic position of the strain using a polyphasic approach based on genome analyses.

Materials and methods

Isolation and maintenance of the microorganisms

A surface soil sample, formed on basaltic parent material, was collected from Samsun (GPS coordinates 41°27.421′ N and 36°02.421′ E), Turkey. At first, the soil sample was air-dried at room temperature for 2 weeks to aim of isolation for actinobacteria. After drying, the sample was prepared using the standard dilution plate method and spread onto Czapek-Dox Agar (Weyland 1969) supplemented with nystatin (50 µg/ml) and rifampicin (5 µg/ml). Following to 4 weeks of aerobic incubation at 28 ℃, an actinobacteria like colony was picked considering the colony morphology, transferred and purified on the N-Z Amine Medium (DSMZ Medium No. 554), and stored in glycerol stock solutions (35%, v/v) at − 80 ℃. The reference strains, *Nonomuraea candida* DSM 45086^T, *Nonomuraea zeae* DSM 100528^T and *Nonomuraea turkmeniaca* DSM 43926^T were obtained from the Deutsche Sammlung von Mikroorganismen und Zellkulturen (DSMZ). These strains were also cultured under the same conditions for comparative analysis.

DNA preparation, amplification and determination of 16S rRNA gene sequence

The genomic DNA of strain 160415^T was extracted using the DNA extraction kit (Invitrogen) according to the manufacturer's instructions and the 16S rRNA was amplified as described by Weisburg et al. (1991). Phylogenetic trees were generated using the neighbour-joining (Saitou and Nei 1987), maximum-likelihood (Felsenstein 1981) and maximum-parsimony (Fitch 1971) algorithms in MEGA X (Kumar et al. 2018). Evolutionary distances were calculated using the model of Jukes and Cantor (1969). Topologies of the resultant tree were evaluated by bootstrap analyses (Felsenstein 1985) based on 1000 resamplings. The almost full-length 16S rRNA gene sequence of strain 160415^T (1480 nt) was compared with the corresponding sequences available on the EzTaxon-e server (Yoon et al. 2017a).

Phylogeny and genome features based on whole-genome sequencing

The genomes of strain 160415^T, *N. zeae* DSM 100528^T and *N. turkmeniaca* DSM 43926^T were sequenced externally (MicrobesNG, Birmingham, UK) with Illumina HiSeq 2500 next-generation sequencing platform with 250× bp paired-end protocol. The raw data of the genomes were assembled using full Spades assemble strategy on PATRIC webserver (Wattam et al. 2016). Following deposition to National Center for Biotechnology Information (NCBI) under the accession numbers VCJS00000000, VCKX00000000 and VCKY00000000 for the strain 160415^T, *N. zeae* DSM 100528^T and *N. turkmeniaca* DSM 43926^T, respectively; the draft genome sequences annotated on RAST annotation server (Aziz et al. 2008). The genome sequence data were uploaded to the Type (Strain) Genome Server (TYGS), a free bioinformatics platform available under https://tygs.dsmz.de (Meier-Kolthoff and Göker 2019) to obtain the genomic tree. The digital DNA–DNA hybridization (dDDH) and Average Nucleotide Identity (ANI) values between the strain 160415^T and closely related type strains were determined using formula 2 of the GGDC web server (Meier-Kolthoff et al. 2013) and online ANI Calculator (Yoon et al. 2017b), respectively. Biosynthetic gene clusters (BGCs) of the strains were revealed using antiSMASH webserver (Blin et al. 2019).

Morphological, cultural and physiological characteristics

Cultural characteristics in terms of growth, spore colour, colours of the aerial mycelium and soluble pigmentation of strain 160415^T were observed after cultivation at 28 ℃ for 14 days on the International *Streptomyces* project (ISP) media 2, 3, 4, 5, 6, and 7 (Shirling and Gottlieb 1966), and four additional media, namely modified Bennett's agar (MBA; Jones 1949), Czapek's agar (CA; Waksman 1967), nutrient agar (NA; Waksman 1961) and tryptic soy agar (TSA; Difco) using the ISCC-NBS Colour Charts (Kelly 1964) to determine colour designation. Colony morphology and micromorphological properties were determined by scanning electron microscopy (JEOL JSM 6060) using colonies grown on ISP 7 medium at 28 ℃ for 28 days. The temperature range for growth was tested on ISP 2 at various temperatures (4, 10, 20, 28, 37, 40, 45, 50 and 55 ℃). Optimal conditions for growth such as pH (4.0–11.0 at intervals of 1.0 pH unit using buffers) and NaCl concentrations (up to 10%, w/v, at intervals of 1.0% unit) were examined on yeast extract-malt extract (ISP 2) agar (Shirling and Gottlieb 1966). The utilization of sole carbon and nitrogen sources, decomposition of cellulose, various degradation tests, reduction of nitrate, hydrolysis of arbutin, allantoin and urea were examined as described previously methods (Goodfellow 1971; Gordon et al. 1974; Williams et al. 1983; Nash and Krent 1991). The closely related type strains, *N. candida* DSM 45086^T, *N. turkmeniaca* DSM 43926^T and *N. zeae* DSM 100528^T were also included for comparison in all tests.

Chemotaxonomic characterisation

Biomass for chemotaxonomic studies was prepared by growing the strain in N-Z Amine broth in flasks on a rotary shaker at 200 rpm for 10 days at 30 ℃. Biomass was harvested by centrifugation, washed twice in distilled water, recentrifuged and freeze-dried. Analysis of the diaminopimelic acid isomers in the cell wall and whole-cell sugars were performed as described by Staneck and Roberts (1974) and Lechevalier and Lechevalier (1970) by thin-layer chromatography (TLC), respectively. The menaquinones were extracted and purified using the method of (Collins 1985) and analysed by high-performance liquid chromatography (HPLC) (Kroppenstedt 1982). Polar lipids were extracted, separated by two-dimensional TLC and identified according to procedures proposed by Minnikin et al. (1984). Cellular fatty acids were extracted, methylated and separated according to the standard protocol of the Sherlock Microbial identification (MIDI) system (Sasser 1990; Kämpfer and Kroppenstedt 1996) and the fatty acid methyl ester peaks were quantified using the TSBA 5.0 database.

Results and discussion

Morphology, physiology and biochemical analysis

Strain 160415^T formed irregular spores differentiated from aerial mycelia. The spores were 0.5–0.7 × 0.7–1.0 µm in size with a smooth surface (Fig. S1, available in the online version of this article). Strain 160415^T was able to grow on all the tested media especially grow well on ISP 2, ISP 3, ISP 6, MBA and CA agar with generally brown substrate mycelia color. No diffusible pigments were observed on any of the media tested for the isolate (Table 1). Growth of strain 160415^T occurred in the range of 10–37 ℃, with the optimum growth temperature of 28 ℃. Strain 160415^T grew well between pH 6.0 and 9.0, with an optimum pH of 7.0. Strain 160415^T grew in the presence of 0–2% NaCl (w/v) and optimally at 0% (w/v). Detailed physiological and biochemical properties of strain 160415^T are presented in the species description and Table 2.

Chemotaxonomic characterisation

Strains 160415^T showed chemical markers typical of the members of the genus *Nonomuraea* (Kämpfer 2012). The diamino acid in the cell wall of strain 160415^T was *meso*-diaminopimelic acid and the whole-cell sugars were glucose, madurose, mannose and ribose. Diphosphatidylglycerol and phosphatidylglycerol were detected as major polar lipids with four unidentified phosphoglycolipids, three unidentified phospholipids, two unidentified aminolipids, five unidentified glycolipids and five unidentified lipids (Fig. S2). The major menaquinone was MK-9(H_4) (69%), followed by MK-9(H_6) (14%), MK-9(H_2) (5%) and MK-9 (4%). Iso-$C_{16:0}$ (31.6%), $C_{17:0}$ 10-methyl (17.9%), iso-$C_{16:1}$ G (14.6%) and iso-$C_{15:0}$ (10%) were the major fatty acids in this strain and the detailed fatty acid profile of strain and those of the type strains of closely related *Nonomuraea* species are shown in Table S1.

Genome sequencing and phylogenetic analysis

An almost-complete 16S rRNA gene sequence (1480 bp) of strain 160415^T was obtained. The BLAST search result of the EzBioCloud database of 16S rRNA gene sequences showed that strain 160415^T had high sequence similarities to the *Nonomuraea* species, *N. zeae* DSM 100528^T (99.1%), *N. candida* HMC10^T (98.9%) and *N. turkmeniaca* DSM 43926^T (98.8%); similarities to other type strains of species of the genus *Nonomuraea* were found to be less than 98.7%, which is the threshold for delineation of novel species proposed by Stackebrandt and Ebers (2006). The results of phylogenetic analyses with type strains of related *Nonomuraea* species showed strain 160415^T formed a monophyletic clade with *N. zeae* DSM 100528^T on the neighbour-joining tree and this topology was also supported by maximum-parsimony and maximum-likelihood trees (Fig. 1).

The assembled genome sequence of strain 160415^T was found to be 14,334,648 bp long, composed of 671 contigs with an N50 of 50,765 bp, a DNA G+C content of 69.6 mol% and a 76 sequencing depth of coverage. A total of 15,210 protein-coding genes and 75 RNA loci were detected. The digital DDH values between strain 160415^T and *N. zeae* DSM 100528^T, *N. candida* NRRL B-24552^T and *N. turkmeniaca* DSM 43926^T were 31.7 ± 2.4, 30.3 ± 2.4 and 36.8 ± 2.4%, respectively. The ANI values between strain 160415^T and its closely related strains, *N. zeae* DSM 100528^T, *N. candida* NRRL B-24552^T and *N. turkmeniaca* DSM 43926^T, were 85.90, 84.78 and 88.30%, respectively. The dDDH and ANI values were well below the 70 and 95% cut-off point recommended for delineating novel species (Wayne et al. 1987; Goris et al. 2007; Chun et al. 2018) and these values confirmed that strain 160415^T represents a novel species within the genus *Nonomuraea.* In addition, the phylogenomic tree (Fig. 2) reconstructed on the TYGS server provided further evidence for the taxonomic position of the strain in the genus *Nonomuraea*.

The SEED analysis of strain 160415^T and closely related type strains revealed that strain 160415^T contained more genes associated with iron acquisition and metabolism compared to close relative species. Strain 160415^T has 23 genes associated with the iron acquisition and metabolism, while reference strains *N. zeae* DSM 100528^T, *N. candida* NRRL B-24552^T and *N. turkmeniaca* DSM 43926^T have

Table 1 Cultural characteristics of the 160415^T and closely related type strains grown at 28 °C for 14 days

Strains	Characteristics	ISP 2	ISP 3	ISP 4	ISP 5	ISP 6	ISP 7	MBA	TSA	CA	NA
1	Growth	+++	+++	+	++	+++	++	+++	+	+++	++
	Aerial mycelium	–	–	–	–	–	–	–	–	–	–
	Substrat mycelium	Light brown	Brown	Brown	Dark brown	Brown	Brown	Brown	Brown	Brown	Brown
	Soluble pigment	–	–	–	–	–	–	–	–	–	–
2	Growth	+++	++	++	No growth	++	+	+++	+++	No growth	++
	Aerial mycelium	White	White	–		–	–	–	–		–
	Substrat mycelium	Dark brown	Gray	Claret red		Brown	Orange	Brown	Purple		Red
	Soluble pigment	–	–	–		–	–	–	–		–
3	Growth	+++	+++	No growth	No growth	+++	++	+++	+++	No growth	+++
	Aerial mycelium	Cream	Cream			–	Cream	Gray	–		–
	Substrat mycelium	Dark brown	Brown			Black	Orange	Dark brown	Orange		Dark brown
	Soluble pigment	Brown	–			Light brown	–	Sarı	–		Light brown
4	Growth	+++	+++	No growth	No growth	No growth	+	++	–	+++	++
	Aerial mycelium	–	Cream				–	–	–	–	–
	Substrat mycelium	Brown	Purple				Dark green	Light brown	–	Orange	Orange
	Soluble pigment	–	Light purple				–	–	–	–	–

Strains: 1, 160415^T; 2, *N. zeae* DSM 100528^T; 3, *N. candida* DSM 45086^T; 4, *N. turkmeniaca* DSM 43926^T. All data were obtained in this study

Table 2 Differential characteristics of strain 160415^T and type strains of closely related species of the genus *Nonomuraea*

	1	2	3	4
NaCl tolerance (%, w/v)	0–2	0–3	0–2	0–1
pH tolerance	6–9	6–10	7–11	7–9
Temperature range (°C)	10–37	10–37	28–45	28–37
Nitrogen source utilization (0.1%, w/v)				
L-Arginine	−	+	+	+
L-Cysteine	−	+	+	−
Glycine	−	+	+	+
L-Histidine	−	+	+	−
Carbon source utilization (1.0%, w/v)				
D-Arabinose	+	+	−	−
D-Fructose	−	+	+	+
D-Sorbitol	+	−	+	+
D-Ribose	−	+	−	−
Dextran	+	−	+	−
L-Sorbose	−	−	+	+
L-Rhamnose	+	−	+	−
Lactose	+	−	+	−
myo-Inositol	+	−	+	−
Succinic acid (0.1%)	−	+	−	−
Xylitol	−	−	+	+
Degradation of (%, w/v)				
Adenine	−	−	+	−
Guanine	+	−	+	−
Hypoxanthine	+	−	+	−
Starch	+	+	−	+
Tween 20	−	+	+	+
Xanthine	−	+	+	+
Xylan	+	−	+	+
Biochemical tests				
Arbutin hydrolysis	+	+	−	+
Urea hydrolysis	−	−	−	+
Nitrate reduction	+	−	−	−
Major menaquinones (> 10%)	MK-9(H_4), MK-9(H_6)	MK-9(H_4), MK-9(H_2), MK-9(H_0)[a]	ND	ND
Polar lipids	DPG, PG	DPG, PME, PE, OH-PE, OH-PME, PI, PIM[a]	ND	ND
Major fatty acids (> 10%)	Iso-$C_{16:0}$, $C_{17:0}$ 10-methyl, iso-$C_{16:1}$ G, iso-$C_{15:0}$	Iso-$C_{16:0}$, $C_{17:0}$ 10-methyl	Iso-$C_{16:0}$, $C_{17:0}$ 10-methyl	Iso-$C_{16:0}$, $C_{17:0}$ 10-methyl
Whole-cell sugars	Glu, mad, man, rib	Glu, mad, rib[a]	ND	ND

Strains: 1, 160415^T; 2, *N. zeae* DSM 100528^T; 3, *N. candida* DSM 45086^T; 4, *N. turkmeniaca* DSM 43926^T. All data were obtained from this study unless indicated

+ positive, − negative, *ND* not determined, *glu* glucose, *mad* madurose, *man* mannose, *rib* ribose, *DPG* diphosphatidylglycerol, *PG* phosphatidylglycerol, *PME* phosphatidylmonomethylethanolamine, *PE* phosphatidylethanolamine, *OH-PME* hydroxy-phosphatidylmonomethylethanolamine, *OH-PE* hydroxy-phosphatidylethanolamine, *PI* phosphatidylinositol, *PIM* phosphatidylinositol mannoside

[a]Data taken from: Shen et al. (2016)

only 2, 12 and 5 genes, respectively (Table S2). Moreover, the draft genome sequence of strain 160415^T contains 35 potential biosynthetic gene clusters and three of the gene clusters are siderophore type. Thus, it is speculated that these genes could facilitate the weathering of rocks (Ahmed and Holmström 2014) and the strain 160415^T could be found in the surface soil on the basaltic parent material thanks to having these genes.

The phylogenetic analyses, morphological and chemotaxonomic properties indicate that strain 160415^T belongs

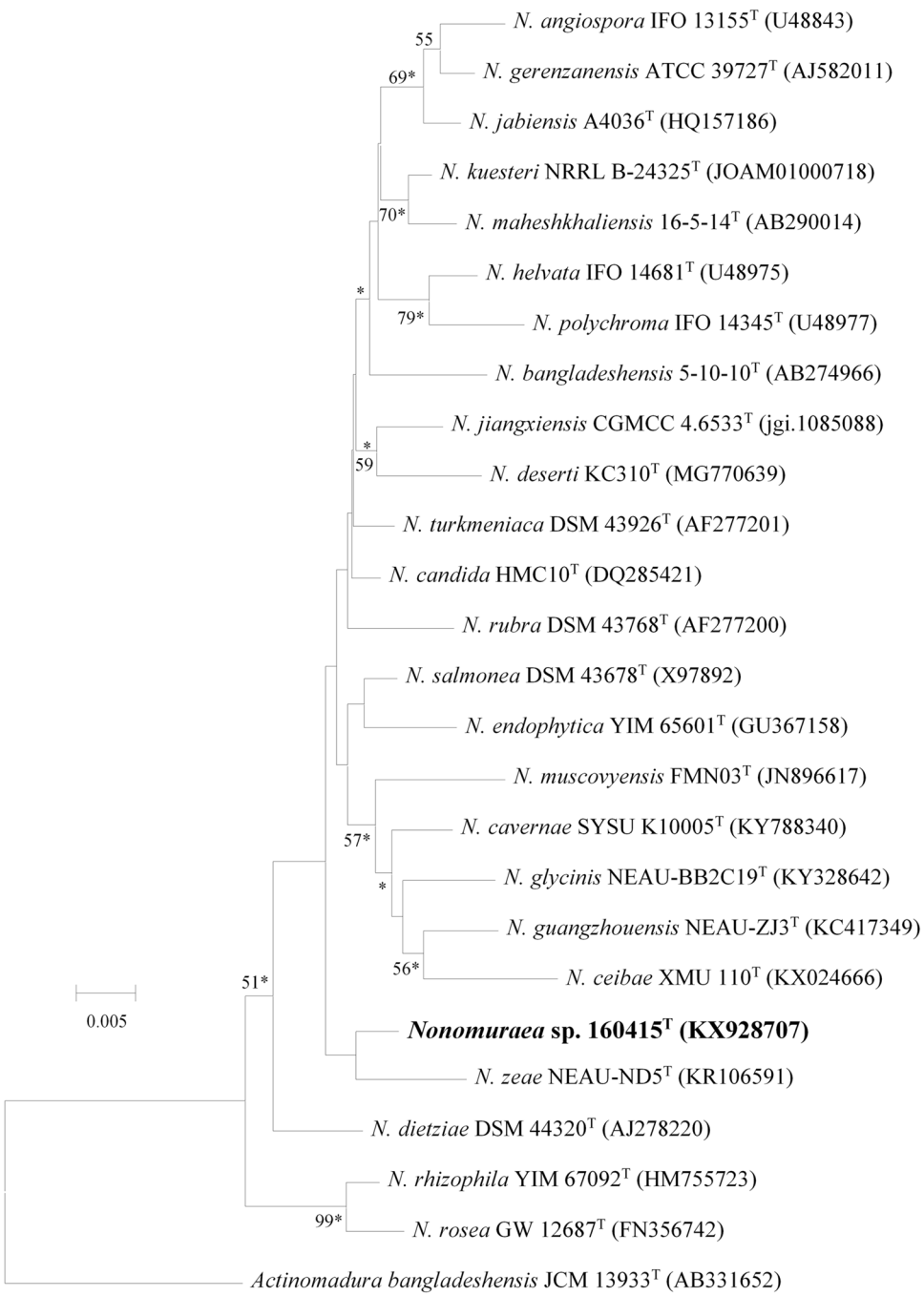

Fig. 1 Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences showing relationships between strain 160415^T and type strains of closely related *Nonomuraea* species. Evolutionary distances were computed using the Jukes–Cantor method (Jukes and Cantor 1969) and are in the units of the number of base substitutions per site. The analysis was based on 26 nucleotide sequences. Positions containing gaps and missing data were eliminated from the data set. There were a total of 1331 positions in the final dataset. Asterisks indicate corresponding nodes recovered in the maximum-likelihood and maximum-parsimony trees. Numbers at the nodes indicate percentage levels of bootstrap support, only values over 50% are shown. Bar, 0.005 substitutions per nucleotide position

to the genus *Nonomuraea*. The cultural and phenotypic characteristics which were listed in Tables 1 and 2 as well as the low ANI and DDH values provide sufficient evidence to differentiate the strain 160415^T from its closely related strains. Therefore, based on a combination of chemotaxonomic, morphological, molecular and physiological data, strain 160415^T represents a novel species of the genus *Nonomuraea*, for which the name *Nonomuraea basaltis* sp. nov. is proposed.

Description of *Nonomuraea basaltis* sp. nov.

Nonomuraea basaltis (ba.sal'tis. L. masc. gen. n. basaltis of basaltic parent material, pertaining to the source of isolation).

Aerobic, Gram-stain-positive, non-motile actinobacterium that forms extensively branched substrate and aerial mycelia. Aerial hyphae differentiated into irregular spore (0.5–0.7 × 0.7–1.0 µm) chains with smooth surfaces. Good

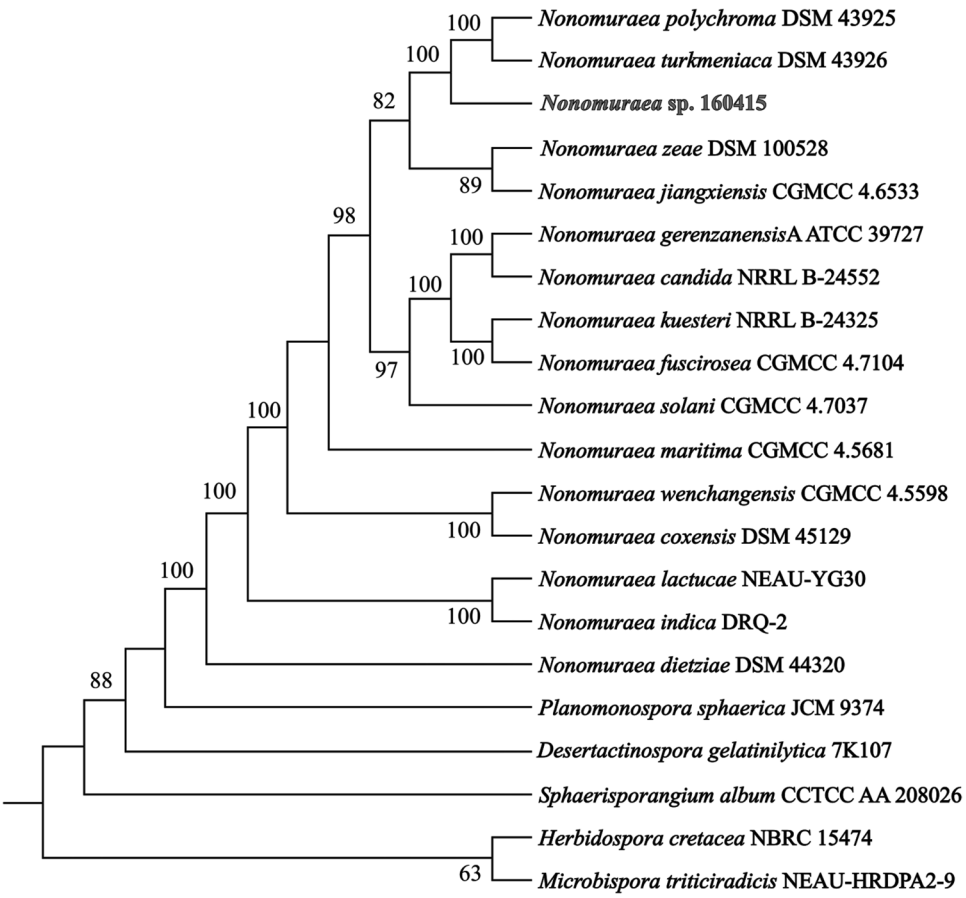

Fig. 2 Phylogenomic tree based on whole genome sequence data of strain 160415^T and closely related type strains reconstructed on the Type (Strain) Genome Server (TYGS). The tree was inferred with FastME 2.1.6.1 (Lefort et al. 2015) from GBDP distances calculated from genome sequences and was rooted at the midpoint (Farris 1972). The branch lengths are scaled in terms of GBDP distance formula d_5. The numbers above branches are GBDP pseudo-bootstrap support values from 100 replications

growth occurs on ISP 2, ISP 3, ISP 6, modified Bennett's and Czapek's agars, moderate growth on ISP 5, ISP 7 and nutrient agars, weak growth on ISP 4 and tryptic soy agars. Substrate mycelia produce pigments in brown tones. Melanoid pigments are not produced on ISP 6 agar and diffusible pigments are not produced on all media tested. Grow from 10–37 °C (optimum, 28 ℃), from pH 6.0–9.0 (optimum, pH 7.0), in the presence of NaCl up to of 2% (w/v). Hydrolyses allantoin and arbutin, reduces nitrate but does not hydrolyse urea. Guanine, hypoxanthine, starch and xylan are degraded, but not adenine, Tweens 20, 40 or 80 or xanthine. D-Arabinose, D-cellobiose, dextrin, dextran, D-galactose, D-glucose, L-glutamine, myo-Inositol, inulin, lactose, maltose, mannitol, D-mannose, D-melezitose, D-melibiose, L-rhamnose, D-sorbitol, sucrose and xylose are utilized as sole carbon and energy sources, but not D-fructose, D-ribose, L-sorbose, sodium succinate or xylitol. L-Alanine, L-asparagine, L-hydroxyproline, α-isoleucine, L-lysine, L-methionine, L-phenylalanine, L-proline, L-serine, L-threonine and L-tyrosine are utilized as sole nitrogen sources, but not L-arginine, L-cysteine, glycine, L-histidine. The major menaquinones are MK-9(H_4) and MK-9(H_6). The polar lipids profile includes diphosphatidylglycerol, phosphatidylglycerol, phosphoglycolipids, phospholipids, aminolipids, glycolipids and lipids. Whole-cell hydrolysates contain *meso*-A_2pm, glucose, madurose, mannose and ribose. The major fatty acids are iso-$C_{16:0}$, $C_{17:0}$ 10-methyl, iso-$C_{16:1}$ G and iso-$C_{15:0}$. The DNA G+C content of strain 160415^T is 69.6 mol% and the genome size is 14.33 Mbp.

The type strain 160415^T (= KCTC 39875^T = DSM 104309^T) was isolated from a soil sample, which was formed on basaltic parent material, collected from Samsun, Turkey. The GenBank accession number for the 16S rRNA gene sequence of the strain is KX928707 and that of the draft genome sequence accession number VCJS00000000. The version described in this paper is version VCJS00000000.1.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants and/or animals performed by any of the authors. The formal consent is not required in this study.

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