Antonie van Leeuwenhoek (2018) 111:1095–1103
https://doi.org/10.1007/s10482-017-1012-6

ORIGINAL PAPER

Nonomuraea lycopersici sp. nov., isolated from the root of tomato plants (*Solanum lycopersicum* L.)

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Received: 25 October 2017 / Accepted: 26 December 2017 / Published online: 3 January 2018
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Abstract Two novel bacterial strains were isolated from the roots of tomato plants (*Solanum lycopersicum* L.) from Dengfeng, Henan Province, China. Phylogenetic analysis of 16S rRNA gene sequences showed that the isolates NEAU-DE8(1)^T and NEAU-HE1(2) are closely related to one another (99.6% similarity) and are closely relate to *Nonomuraea zeae* NEAU-ND5^T (98.3, 98.3%) and *Nonomuraea gerenzanensis* DSM 100948^T (98.3, 98.0%). Phylogenetic trees constructed based on 16S rRNA gene sequences revealed that both strains grouped with *N. zeae* NEAU-ND5^T within the clade comprising the members of the genus *Nonomuraea.* Moreover, key chemotaxonomic properties including major menaquinones, fatty acid composition and phospholipid profiles also confirmed the affiliation of the two strains to the genus *Nonomuraea*. However, DNA–DNA hybridization data, together with physiological and morphological properties, showed that two isolates could be readily distinguished from their close phylogenetic relatives. Thus, on the basis of these phenotypic and genotypic data, strains NEAU-DE8(1)^T and NEAU-HE1(2) are concluded to represent a novel species of the genus *Nonomuraea*, for which the name *Nonomuraea lycopersici* sp. nov. is proposed. The type strain is NEAU-DE8(1)^T (= CGMCC 4.7412^T = DSM 104642^T).

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10482-017-1012-6) contains supplementary material, which is available to authorized users.

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Keywords *Nonomuraea lycopersici* sp. nov. · Polyphasic analysis · 16S rRNA gene · Phenotypic characteristics

Introduction

The genus *Nonomuraea*, which belongs to the family *Streptosporangiaceae*, was first proposed by Zhang et al. (1998). The original spelling of the genus name *Nonomuria* was corrected to *Nonomuraea* by Chiba et al. (1999) in accordance with the International Code of Nomenclature of Bacteria. Members of the genus *Nonomuraea* are aerobic, Gram-positive, non-acid-fast,non-motile actinomycetes that can form extensively branched substrate and aerial mycelia. The aerial hyphae differentiate into hooked, spiral or straight chains of spores or form a single spore, which show a folded, irregular, smooth or warty ornamentation (Quintana et al. 2003; Kämpfer et al. 2005; Zhao et al. 2011; Zhang et al. 2014; Rachniyom et al. 2015; Wu and Liu 2016). However, several spiral spores could cluster to form a pseudosporangia on aerial mycelia (Sripreechasak et al. 2017). The type species of the genus is *Nonomuraea pusilla* (Nonomura and Ohara 1971; Zhang et al. 1998). At the time of writing, there are 47 species and two subspecies of the genus *Nonomuraea* with validly published names included the recently described *Nonomuraea cavernae* (Fang et al. 2017), *Nonomuraea stahlianthi* (Niemhom et al. 2017), *Nonomuraea ceibae* (Wang et al. 2017), *Nonomuraea rhodomycinica* (Sripreechasak et al. 2017) and *Nonomuraea glycinis* (Li et al. 2017) according to the List of Prokaryotic names with Standing in Nomenclature (http://www.bacterio.cict.fr/index.html).

During the process of screening the diversity of endophytic actinomycetes in the roots of tomato plants (*Solanum lycopersicum* L.), two novel actinomycetes, strains NEAU-DE8(1)^{T} and NEAU-HE1(2), were isolated from the root of tomato plants (*Solanum lycopersicum* L.) collected from Dengfeng, Henan Province, middle eastern China. We performed a taxonomic analysis of the two strains using a polyphasic approach, and propose that they represent a novel species of the genus *Nonomuraea.*

Materials and methods

Isolation and maintenance of the isolates

The organisms were isolated from the roots of two tomato plants (*S. lycopersicum* L.) taken from the greenhouse of Dengfeng, Henan Province, middle eastern China (45°45′N, 126°41′E). The root specimens were processed as described by Wang et al. (2013) and placed on a plate of Gause's synthetic agar no. 1 (Atlas 1993) supplemented with cycloheximide (50 mg l^{-1}) and nalidixic acid (50 mg l^{-1}). After 2 weeks of aerobic incubation at 28 °C, colonies were transferred and purified on International *Streptomyces* Project (ISP) medium 3 (Shirling and Gottlieb 1966) and maintained as glycerol suspensions (20%, v/v) at − 80 °C. The type strain of *Nonomuraea zeae* NEAU-ND5^{T} was from our laboratory collection (Shen et al. 2016) and cultured under the same conditions for comparative analysis.

Morphological, cultural and physiological characteristics

Morphological characteristics were observed by light microscopy (Nikon ECLIPSE E200) and scanning electron microscopy (Hitachi SU8010) after cultivation on ISP 3 medium at 28 °C for 21 days. Samples for scanning electron microscopy were prepared as described by Guan et al. (2015). Motility was assessed by light microscopic (Nikon ECLIPSE E200) observation of cells suspended in phosphate buffer (pH 7.0, 1 mM). Cultural characteristics were determined after 2 weeks at 28 °C using ISP 1–7, nutrient agar (NA), Bennett's agar (BA) and Czapek's agar (CA) (Shirling and Gottlieb 1966; Jones 1949; Waksman 1967). The ISCC-NBS colour charts were used to determine the designations of colony colours (Kelly 1964). Growth at different temperatures (4, 10, 15, 18, 20, 28, 37, 40 and 45 °C) was determined on ISP 3 medium after incubation for 2 weeks. The pH range for growth from pH 3–12 (at intervals of 1 pH units) was tested in ISP 2 broth using the buffer system described by Xu et al. (2005). Tolerance to NaCl between 0 and 7% (at intervals of 1%) was tested on ISP 2 and observed after 7 and 14 days at 28 °C. Melanin pigment production was determined on ISP 7. Production of catalase, esterase and urease were tested as described by Smibert and Krieg (1994). The utilisation of sole

carbon and nitrogen sources (0.5%, w/v), decomposition of cellulose, hydrolysis of starch and aesculin, reduction of nitrate, peptonisation of milk, liquefaction of gelatin and production of H_2S were examined as described previously (Gordon et al. 1974; Yokota et al. 1993).

Chemotaxonomic characterisation

Biomass for chemical studies was prepared by growing the strains in GY medium (Jia et al. 2013) in shake flasks at 28 °C for 7 days. Cells were harvested by centrifugation, washed with distilled water and freeze-dried. The cell wall diamino acid was determined from whole cell hydrolysates, as described by McKerrow et al. (2000) and analysed by a HPLC method using an Agilent TC-C18 Column (250 × 4.6 mm i.d. 5 μm). Whole organism sugars were analysed according to the procedures developed by Lechevalier and Lechevalier (1980). The presence of mycolic acids was checked by the acid methanolysis method as described previously (Minnikin et al. 1980). The polar lipids were extracted and examined by two-dimensional TLC and identified according to the method of Minnikin et al. (1984). Menaquinones were extracted from freeze-dried biomass and purified according to Collins (1985). Extracts were analysed using an HPLC–UV method (Wu et al. 1989). Fatty acid methyl esters were extracted from the biomass as described by Gao et al. (2014) and analysed by GC–MS using the method of Xiang et al. (2011).

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

Extraction of chromosomal DNA and PCR amplification of the 16S rRNA gene sequences were carried out according to the procedure developed by Kim et al. (2000). The PCR products were purified and cloned into the vector pMD19-T (Takara) and sequenced using an Applied Biosystems DNA sequencer (model 3730XL). Almost full-length 16S rRNA gene sequences of strains NEAU-DE8(1)^T (1512 bp) and NEAU-HE1(2) (1512 bp) were obtained and aligned with multiple sequences obtained from the GenBank/EMBL/DDBJdatabases using Clustal X 1.83 software. Phylogenetic trees were constructed with the neighbour-joining (Saitou and Nei 1987), maximum likelihood (Felsenstein 1981) and maximum-parsimony (Fitch 1971) algorithms using molecular evolutionary genetics analysis (MEGA) software version 6.06 (Tamura et al. 2013). The stability of the topology of the phylogenetic trees was assessed using the bootstrap method with 1000 repetitions (Felsenstein 1985), and the distance matrix was generated using Kimura's two prameter model (Kimura 1980). All positions containing gaps and missing data were eliminated from the dataset (complete deletion option). 16S rRNA gene sequence similarities between strains were calculated on the basis of pairwise alignments using the EzTaxone server (Kim et al. 2012).

DNA base composition and DNA–DNA hybridization

The G+C content of the genomic DNA was determined using the thermal denaturation (*Tm*) method (Mandel and Marmur 1968) with *Escherichia coli* JM109 DNA used as the control. *N. zeae* NEAU-ND5^T was used as reference strain in the DNA–DNA relatedness test. DNA–DNA relatedness tests were carried out as described by De Ley et al. (1970) under consideration of the modifications described by Huss et al. (1983), using a model Cary 100 Bio UV/VIS-spectrophotometer equipped with a Peltier-thermostatted 6 × 6 multicell changer and a temperature controller with in situ temperature probe (Varian). The DNA samples used for hybridizations were diluted to OD_{260} around 1.0 using 0.1 × SSC (saline sodium citrate buffer), then sheared using a JY92-II ultrasonic cell disruptor (ultrasonic time 3 s, interval time 4 s, 90 times). The DNA renaturation rates were determined in 2 × SSC at 70 °C. The experiments were performed with three replications and the DNA–DNA relatedness value was expressed as mean of the three values.

Results and discussion

Strains NEAU-DE8(1)^T and NEAU-HE1(2) were observed to be aerobic, Gram-stain positive and non-motile actinomycetes. Morphological observations by scanning electron microscopy of three-week cultures grown on ISP 3 revealed that tightly closed spiral chains or hook structure of 5–20 spores were observed on the aerial hyphae and pseudosporangia were

formed as well (Fig S1). The spores (0.4–0.8 × 0.6–1.1 μm) are non-motile with a wrinkled and prominently ridged surface. Production of melanoid pigment was not observed on ISP 7 medium. Strain NEAU-DE8(1)^T was observed to grow well on ISP 2, ISP 3, ISP 4, ISP 7, NA and BA media; moderately on ISP 1, ISP 5 and ISP 6 media; and poorly on CA medium. For isolate NEAU-HE1(2), good growth was observed on ISP 2, ISP 3, ISP 7 and BA medium; moderate growth on ISP 1, ISP 5, ISP 6 and NA media; poor growth was observed on ISP 4 and CA media. The colours of the substrate mycelium were from light yellow to moderate yellow green on different tested media and the colour of aerial hyphae was yellowish white (Table S1). The colour of substrate mycelium is an obvious distinction of the both strains compared with the closely related species *N. zeae* NEAU-ND5^T and *N. gerenzanensis* DSM 100948^T (Table 1). Growth of both strains was observed at 15–40 °C, pH 4.0–10.0 and in the presence of 0–3% (w/v) NaCl, with optimum growth at 28 °C, pH 7.0 and in 1% (w/v) NaCl. The physiological and biochemical properties of the two strains are given in Table 1 and the species description.

Isolates NEAU-DE8(1)^T and NEAU-HE1(2) were found to contain meso-diaminopimelic acid as the cell wall diamino acid. Whole cell hydrolysates were found to contain madurose, glucose and ribose. The polar lipid profile of both strains was found to consist of diphosphatidylglycerol, phosphatidylethanolamine, hydroxyl phosphatidylethanolamine, phosphatidylinositol mannosides, phosphatidylinositol and unidentified glucosamine-containing phospholipids (Supplementary Fig. S2). The menaquinones were identified as MK-9(H_0) (39.5, 43%), MK-9(H_2) (32.8, 41.9%) and MK-9(H_4) (27.7, 15.1%). Mycolic acids were not detected. The major fatty acids (> 5%) of strain NEAU-DE8(1)^T were identified as 10-methyl $C_{17:0}$ (24.1%), iso-$C_{16:0}$ (19.4%), $C_{16:0}$ (12.7%), $C_{17:1}\omega7c$ (10.2%), $C_{17:0}$ (7.8%), $C_{15:0}$ (6.5%) and $C_{18:0}$ (5.6%). 10-Methyl $C_{17:0}$ (22.3%), iso-$C_{16:0}$ (18.6%), $C_{16:0}$ (10.2%), $C_{17:1}\omega7c$ (13.4%), $C_{17:0}$ (9.4%) and $C_{15:0}$ (8.0%) were identified as major fatty acids for strain NEAU-HE1(2). Detailed fatty acid compositions are shown in Supplementary Table S2. Chemotaxonomic analyses revealed that the two isolates exhibited characteristics which are typical of members of the genus *Nonomuraea*.

For the phylogenetic analysis, the almost-complete 16S rRNA gene sequences of strains NEAU-DE8(1)^T (1512 bp) and NEAU-HE1(2) (1512 bp) were determined. Isolates NEAU-DE8(1)^T and NEAU-HE1(2) are closely related to one another (99.6% similarity) and are closely related to *N. zeae* NEAU-ND5^T (98.3, 98.3%) and *Nonomuraea gerenzanensis* DSM 100948^T (98.3, 98.0%). In the neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, the two strains formed a stable clade with the closely related species *N. zeae* NEAU-ND5^T, which was supported by a bootstrap value of 73% (Fig. 1). This relationship was also supported using the maximum-likelihood and maximum-parsimony methods (Figs. S4, S5). However, the relationship between the two novel isolates and *N. gerenzanensis* DSM100948^T was distant according to the three phylogenetic trees. *Nonomuraea* species typically have high 16S rRNA gene sequence similarities (97.6–99.4%), but low DNA–DNA relatedness values (Fischer et al. 1983; Poschner et al. 1985; Tamura et al. 2000; Kämpfer et al. 2005; Qin et al. 2009). DNA hybridization was only employed between the two isolates and the closely related strain *N. zeae* NEAU-ND5^T. The results showed a low relatedness value of 39.6 ± 3.5% between strain NEAU-DE8(1)^T and *N. zeae* NEAU-ND5^T which is below the 70% cut-off point recommended for the delineation of prokaryotic genomic species (Wayne et al. 1987). Meanwhile, DNA–DNA relatedness between strains NEAU-DE8(1)^T and NEAU-HE1(2) was 85.71 ± 3.8%, indicating that they belong to the same novel *Nonomuraea* species, supported by the homogeneous phylogenetic and biochemical characteristics. The DNA G+C content of the DNA of strain NEAU-DE8(1)^T was determined to be 72.8 mol% and that of strain NEAU-HE1(2) to be 71.8 mol%.

The data from chemotaxonomic examinations showed that strains NEAU-DE8(1)^T and NEAU-HE1(2) had typical characteristics of the genus *Nonomuraea*, such as: MK-9(H_4) and MK-9(H_2) as predominant menaquinones; hydroxyl phosphatidylethanolamine, phosphatidylethanolamine and unidentified glucosamine-containing phospholipids as polar lipids; 2-OH $C_{15:0}$ and 2-OH $C_{16:0}$ among the fatty acid components. Moreover, phylogenetic analysis based on 16S rRNA gene sequences indicated that the two isolates fall within the genus *Nonomuraea* (Figs. 1, S3, S4). These results indicated that strains

Table 1 Differential characteristics of strain NEAU-DE8(1)^T, NEAU-HE1(2) and closely related type strains

Characteristic	1	2	3	4
Growth on ISP2				
Aerial mycelium	Yellowish white	Yellowish white	Pink white	None
Substrate mycelium	Pale yellow	Pale yellow	Deep reddish orange	Brown
Growth on ISP3				
Aerial mycelium	Yellowish white	None	Pink white	Whitish
Substrate mycelium	Moderate yellow green	Moderate yellow green	Strong pink	Red-voliet
Hydrolysis of starch	−	−	+	−
Peptonisation of milk	+	+	−	−
Use as sole nitrogen source:				
L-Arginine	+	+	−	ND
L-Glutamic acid	+	−	+	ND
L-Glutamine	−	−	+	ND
L-Aspartic acid	+	+	−	ND
L-Proline	+	−	−	ND
L-Serine	+	−	+	ND
L-Threonine	+	−	+	ND
L-Tyrosine	−	−	+	+
Use as sole carbon source				
D-Glucose	−	−	+	ND
Maltose	−	−	+	+
D-Mannitol	−	−	+	+
D-Raffinose	−	+	+	+
D-Rhamnose	−	−	−	+
D-Sorbitol	−	+	+	+
Lactose	−	−	+	+
L-Arabinose	−	−	+	+
Temperature for growth (°C)	15–40	15–40	15–35	22–40

Strains *1* NEAU-DE8(1)^T, *2* NEAU-HE1(2), *3 N. zeae* NEAU-ND5^T, *4 N. gerenzanensis* ATCC 39727^T. Data for strains 1–3 are from this study, data for strain 4 are from Dalmastri et al. (2016). + positive, − negative, *ND* no data avalible

NEAU-DE8(1)^T and NEAU-HE1(2) should be affiliated to the genus *Nonomuraea*. Phenotypic comparison between strains NEAU-DE8(1)^T/NEAU-HE1(2) and closely related type strains of the genus *Nonomuraea* are shown in Table 1. The two strains can be easily distinguished from their closely related species by cultural characteristics on ISP 2 and ISP 3 (Table 1). Similarity, the two novel strains cannot utilise L-arabinose, maltose, D-mannitol or D-sorbitol as a sole carbon source, while the reference strains *N. zeae* NEAU-ND5^T and *N. gerenzanensis* DSM 100948^T can. Both organisms have the ability to peptonise of milk, while the reference strains *N. zeae* NEAU-ND5^T and *N. gerenzanensis* DSM100948^T could not. NEAU-DE8(1)^T and NEAU-HE1(2) cannot utilise L-tyrosine as the sole nitrogen source, whilst *N. zeae* NEAU-ND5^T and *N. gerenzanensis* DSM100948^T can. In addition, the absence of phosphatidylmethylethanolamine and hydroxy-phosphatidylmethylethanolamine in the phospholipid profiles of strains NEAU-DE8(1)^T and NEAU-HE1(2) also differentiates them from *N. zeae* NEAU-ND5^T and *N. gerenzanensis* DSM100948^T.

In conclusion, it is evident from the genotypic and phenotypic data that strain NEAU-DE8(1)^T and NEAU-HE1(2) represent a novel species of the genus

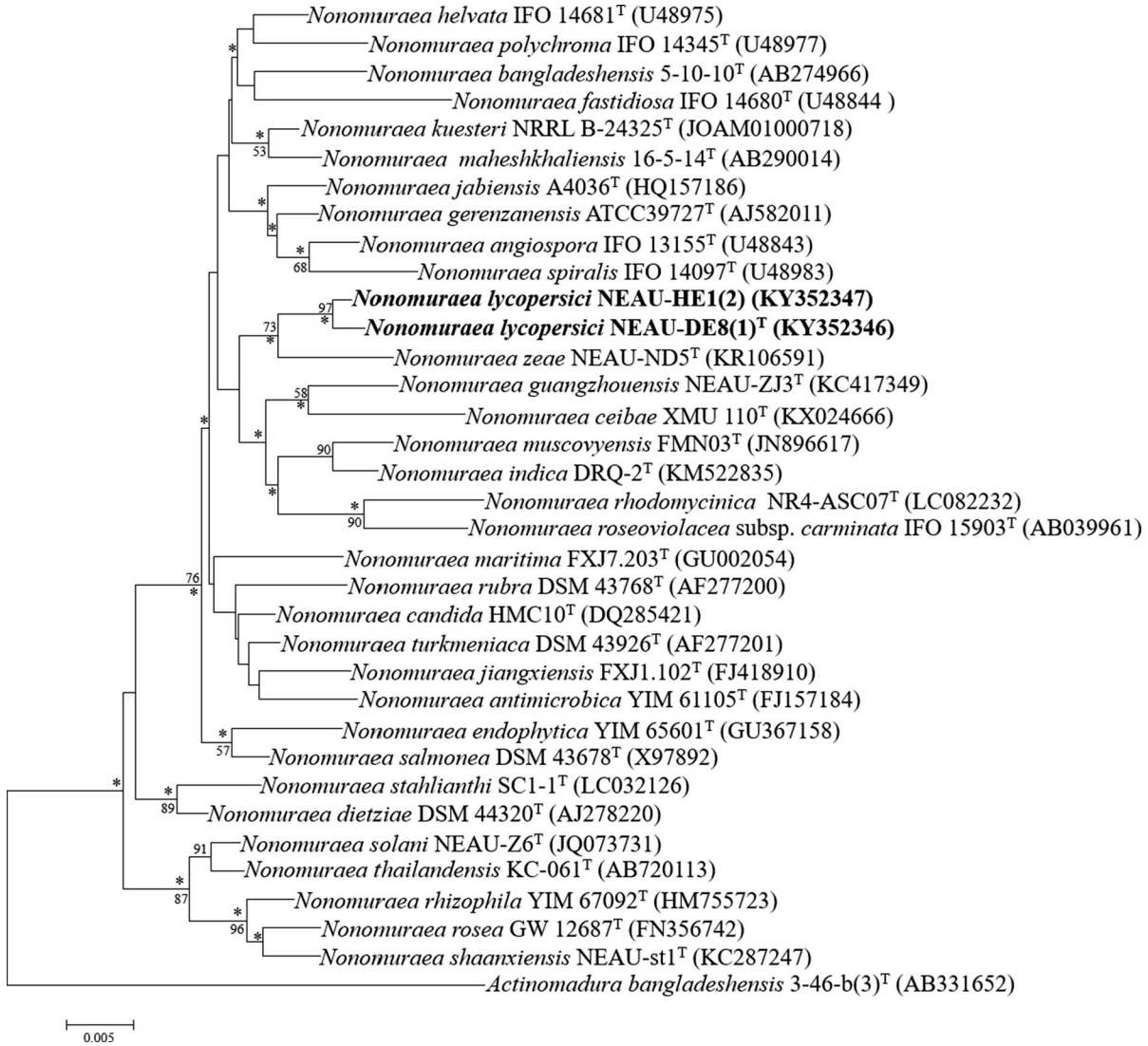

Fig. 1 Neighbour-joining tree based on 16S rRNA gene sequence showing relationship between strains NEAU-DE8(1)^T (1366 bp) and NEAU-HE1(2) (1366 bp) and related taxa. Only bootstrap values above 50% (percentages of 1000 replications) are indicated. Asterisks indicate branches also recovered in the maximum-likelihood tree; *Actinomadura bangladeshensis* was used as the outgroup. Bar, 0.005 nucleotide substitutions per site

Nonomuraea, for which the name *Nonomuraea lycopersici* sp. nov. is proposed. The Digital Protologue database (Rosselló-Móra et al. 2017) TaxoNumber for strain NEAU-DE8(1)^T is TA00364.

Description of *Nonomuraea lycopersici* sp. nov.

Nonomuraea lycopersici (ly.co.per'si.ci. N.L. gen. n. *lycopersici*, of *lycopersicum*, the systematic name of the tomato *Solanum lycopersicum*; *Lycopersicon esculentum*).

Aerobic, Gram-positive, non-motile actinomycetes that form extensively branched substrate mycelia and bear yellowish-white aerial hyphae on ISP 3. Tightly closed spiral spore chains or hook structures are produced on aerial mycelia. Pseudosporangia are observed. The spores (0.4–0.8 × 0.6–1.1 μm) are non-motile with a wrinkled and prominently ridged surface. Melanoid pigment is not observed on ISP 7 medium. Good growth is observed on ISP 2, ISP 3, ISP 7 and BA media; moderate growth ISP 1, ISP 5 and ISP 6 media; poor growth on CA medium. Growth on ISP 4 is

poor to good and on NA is moderate to good. Growth occurs at initial pH values between 4.0 and 10.0, the optimum being pH 7.0. Tolerates up to 3.0% NaCl and grows at temperatures between 15 and 40 °C, with an optimum temperature of 28 °C. Positive for production of catalase and urease, peptonisation of milk and hydrolysis of aesculin, but negative for reduction of nitrate, hydrolysis of starch, liquefaction of gelatin, decomposition of cellulose and production of H_2S. D-Fructose, D-mannose and sucrose are utilised as sole carbon sources but L-arabinose, D-galactose, D-glucose, lactose, maltose, D-mannitol, myo-inositol, D-rhamnose and D-xylose are not. The results of utilisation of D-ribose, D-raffinose and D-sorbitol are variable. L-Alanine, L-arginine, glycine and L-aspartic acid are utilised as sole nitrogen sources but L-asparagine, creatine, L-glutamine and L-tyrosine are not. L-Glutamic acid, L-proline, L-serine and L-threonine are variably utilised as sole nitrogen sources. The cell wall contains *meso*-diaminopimelic acid and the whole cell sugars are glucose, ribose and madurose. Mycolic acids are not present. The menaquinones are MK-9(H_4), MK-9(H_2) and MK-9(H_0). The polar lipids profile contains diphosphatidylglycerol, hydroxyl phosphatidylethanolamine, phosphatidylethanolamine, phosphatidylinositol, phosphatidylinositol mannosides (PIMs) and unidentified glucosamine-containing phospholipids. The predominant fatty acids (> 10%) are 10-methyl $C_{17:0}$, iso-$C_{16:0}$, $C_{16:0}$ and $C_{17:1}\omega7c$. The DNA G+C content of the type strain is 72.8 mol%.

The type strain is NEAU-DE8(1)^T (= CGMCC 4.7412^T = DSM 104642^T), which was isolated from the root of a tomato plant (*Solanum lycopersicum* L.) collected in Dengfeng, Henan Province, China. The GenBank/EMBL/DDBJ database accession numbers for the 16SrRNA gene of strains NEAU-DE8(1)^T and NEAU-HE1(2) are KY352346 and KY352347 respectively.

Acknowledgements This work was supported in part by Grants from the National Natural Science Foundation of China (No. 31471832), Chang Jiang Scholar Candidates Program for Provincial Universities in Heilongjiang (CSCP).

Compliance with ethical standards

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

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

Informed consent The formal consent is not required in this study.

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