

Flavobacterium nitrogenifigens sp. nov., isolated from switchgrass (*Panicum virgatum*)

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A yellow, nitrogen-fixing bacterial strain, NXU-44^T, isolated from the rhizosphere of switchgrass (*Panicum virgatum*) in Auburn, Alabama, USA, was studied to determine its taxonomic position. Cells of the isolate were rod-shaped and Gram-stain-negative. A comparison of the 16S rRNA gene sequence with the sequences of the type strains of the most closely related species showed that the strain belongs to the genus *Flavobacterium* with highest sequence similarities to the type strains of *Flavobacterium ginsenosidimutans* (97.9 %), *Flavobacterium phragmitis* (97.6 %) and *Flavobacterium anhuiense* (97.5 %). The 16S rRNA gene sequence similarities to all other species of the genus *Flavobacterium* were below 97.5 %. The fatty acid profile of strain NXU-44^T consisted of the major fatty acids iso-C_{15:0}, iso-C_{15:0} 2-OH/C_{16:1ω7c} and iso-C_{17:0} 3-OH. The major compounds in the polar lipid profile were phosphatidylethanolamine, phosphatidylserine, one aminolipid and two polar lipids. The quinone system was composed exclusively of menaquinone MK-6. The polyamine pattern contained the major compound *sym*-homospermidine and only minor amounts of other polyamines. The diagnostic diamino acid of the peptidoglycan was *meso*-diaminopimelic acid. These data and the differential biochemical and chemotaxonomic properties show that strain NXU-44^T represents a novel species of the genus *Flavobacterium* for which the name *Flavobacterium nitrogenifigens* sp. nov. is proposed. The type strain is NXU-44^T (=LMG 28694^T=CIP 110894^T).

Members of the original genus *Flavobacterium*, described by Bergey *et al.* (1923), have undergone numerous taxonomic rearrangements since its proposal. The genus, as it is now defined, is growing rapidly with respect to the numbers of species proposed and in recent years many novel species have been added, for example: *Flavobacterium caeni* (Liu *et al.*, 2010), *Flavobacterium reichenbachii* (Ali *et al.*, 2009), *Flavobacterium chungangense* (Kim *et al.*, 2009), *Flavobacterium cheniae* (Qu *et al.*, 2008) and *Flavobacterium aquidurensense* (Cousin *et al.*, 2007). Species of the genus *Flavobacterium* have been isolated from many different locations including fresh and salt water, soil, sediment, sea ice, diseased fish and microbial mats (Bernardet & Bowman, 2006). Members of the genus are generally Gram-negative, aerobic, non-spore-forming, yellow, rod-shaped bacteria, which usually show gliding motility. We report here the results of the characterization of a yellow isolate (NXU-44^T) originating from the rhizosphere of switchgrass grown in Auburn, Alabama, USA, and

originally cultured on NFb semisolid medium (Bashan *et al.*, 1993), which supports the growth of presumptive nitrogen-fixing bacteria. The isolate was further studied and subcultivated on nutrient agar (NA; Oxoid) at 30 °C for 48 h and subsequently underwent analysis of the 16S rRNA gene sequence, fatty acid methyl ester composition of the whole-cell hydrolysate, polar lipid and polyamine profiles and further phenotypic features in comparison with the most closely related species (on the basis of 16S rRNA gene sequence similarities).

Because of the high 16S rRNA gene sequence similarity to *Flavobacterium ginsenosidimutans* THG 01^T, which has been previously studied in detail (Yang *et al.*, 2011), and to the type strains of *Flavobacterium phragmitis* (Liu *et al.*, 2011) and *Flavobacterium anhuiense* (Liu *et al.*, 2008) these strains were chosen for physiological, biochemical and fatty acid composition comparison tests.

The cultural and morphological characteristics were recorded from cultures grown on NA for 48 h at 30 °C. The Gram stain reaction was tested on the basis of a modified method of Gerhardt *et al.* (1994) and the motility test was carried out

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain NXU-44^T is KP711654.

under a light microscope (Axiophot 2, Carl Zeiss AG, Germany) on cells grown for 3 days in nutrient broth (Oxoid) at 30 °C. The oxidase reaction was carried out with oxidase reagent (bioMérieux), according to the instructions of the manufacturer. Catalase activity was recorded by observation of gas formation after dropping H₂O₂ on fresh biomass grown for 48 h on NA. In addition, growth was studied at different temperatures (4, 8, 10, 30, 37, 45 and 50 °C) on NA. Tolerance to NaCl was investigated in trypticase soy broth (TSB; Oxoid) supplemented with 0.5–8.0 % (w/v) NaCl and pH tolerance in TSB adjusted to pH 4.5–12.5 (increasing in increments of 1.0 pH unit) by the addition of HCl or NaOH.

Isolate NXU-44^T was Gram-stain-negative and formed visible (diameter about 2 mm) yellowish colonies within 48 h at 30 °C. The colonies were translucent, glistening and had entire edges. A bright yellow pigment of the flexirubin type (KOH method according to Reichenbach, 1992) was produced on NA. Strain NXU-44^T was positive for oxidase activity and was non-motile, and microscopic examination showed non-spore-forming rods (approximately 1 µm wide and 2 µm long).

Good growth was recorded on NA, as well as on brain heart infusion agar, R2A agar and TSA, but no growth was observed on MacConkey agar (Oxoid). No growth was observed below 10 °C or above 36 °C. Growth at 10 and 36 °C was very weak. Strain NXU-44^T grew in TSB at 28 °C in the presence of 1 %, but not 2 % (w/v) NaCl, and in TSB adjusted to pH 5.5–10.5, but not at pH 4.5 or pH 11.5.

Detailed physiological characterization and biochemical tests were performed to assess the carbon source utilization pattern, acid formation from different sugars and/or sugar-related compounds and hydrolysis of chromogenic substrates as described by Kämpfer *et al.* (1991). In addition, other biochemical tests were performed, such as production of H₂S, indole reaction with Ehrlich's and Kovacs' reagents, activity of arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase, β-galactosidase (ONPG) and urease on Christensen's urea agar [all performed with the Micronaut E kit (Kämpfer, 1990)], and hydrolysis of casein, gelatin (plate method), starch and tyrosine (Smibert & Krieg, 1994). Isolate NXU-44^T utilized few carbon sources, similarly to species of the genus *Flavobacterium* with validly published names, but was able to produce acid from D-glucose, maltose and L-arabinose and to produce acid weakly from D-xylose, D-mannose and D-cellulose. The isolate was also able to hydrolyse many chromogenic substrates. Detailed biochemical and physiological data are given in Table 1 and in the species description.

To confirm the capacity to fix N₂ and the presence of the nitrogenase gene, the strain was subcultured on NFb solid agar (Bashan *et al.*, 1993) and subjected to an acetylene reduction analysis (Holguin *et al.*, 1992). A suspension was created in sterile water using biomass of isolate NXU-44^T grown on NFb agar. From this suspension 100 µl was used as an inoculum in 4.0 ml NFb semi-solid medium. This culture was incubated at 28 °C for 7 days, after which the tube cap was replaced with a rubber

Table 1. Comparison of the physiological characteristics of strain NXU-44^T with those of other species of the genus *Flavobacterium*

Strains: 1, NXU-44^T; 2, *F. ginsenosidimutans* THG 01^T; 3, *F. phragmitis* BLN2^T; 4, *F. anhuiense* D3^T; 5, *F. defluvii* EMB117^T; 6, *F. denitrificans* ED5^T; 7, *F. daejeonense* GH1-10^T; 8, *F. johnsoniae* UW101^T. Data for taxa 1 and 2 are from this study; all other data are from Yang *et al.* (2011), except where indicated otherwise. All strains were Gram-stain-negative, rod-shaped, catalase- and oxidase-positive, and tolerated 1 % (w/v) NaCl. +, Positive; (+), weakly positive; –, negative.

Characteristic	1	2	3	4	5	6	7	8
Indole production	–	–	–*	–	–	–	+	–
API 20NE/ID 32GN tests:								
Nitrate reduction to nitrite	+	–	–*	–	–	+	–	+
Assimilation of carbon sources:								
Malate	–	–	+	+	–	–	+	–
Melibiose	–	(+)†	+	+	–	+	–	–
Salicin	–	(+)†	–	–	+	–	–	–
Sucrose	–	(+)†	+	–	–	+	–	+
API ZYM results:								
N-Acetyl-β-glucosaminidase	+	–	–	–	–	–	–	+
Acid phosphatase	+	+	+	–	+	+	–	+
Alkaline phosphatase	+	+	+	+	+	+	+	–
Leucine arylamidase	+	+	–	–	–	–	+	+
Naphthol-AS-BI-phosphohydrolase	+	–	–	–	+	–	+	+
Valine arylamidase	+	+	+	–	+	+	–	–

*Data from Liu *et al.* (2011).

†Positive in the API system, but negative according to the method of Kämpfer *et al.* (1991).

cap to create a seal. Then 10 % (v/v) of the air in the culture tube was removed by syringe and replaced with 10 % (v/v) acetylene. The tubes were then incubated for 24 h and an air sample from the tube was analysed with a Hewlett Packard 5890 Series II gas chromatograph (Agilent Technologies) equipped with a GASPRO column (60 m × 0.320 mm) and a flame ionizing detector to quantify the amount of ethylene converted from acetylene. The isolate generated 48.0 nmol ethylene 24 h⁻¹ ml⁻¹ (mean of three replications), confirming the presence of the nitrogenase gene, which is also responsible for nitrogen fixation (Lopez *et al.*, 2011).

For phylogenetic identification, the nearly full-length 16S rRNA gene of strain NXU-44^T was amplified and sequenced using the universal primers 8F and 1492R (Lane, 1991). After manual sequence correction, the sequence used for analysis had a length of 1380 nt spanning gene termini 6–1467, according to *Escherichia coli* numbering (Brosius *et al.*, 1978). The EzTaxon server (<http://www.ezbiocloud.net/eztaxon>; Kim *et al.*, 2012) was used to determine 16S rRNA gene sequence similarities to the most closely related type strains. A phylogenetic tree including all type strains of species of the genus *Flavobacterium* was calculated with the ARB software package release 5.2 (Ludwig *et al.*, 2004) and the 'All-Species Living Tree' Project (LTP; Yarza *et al.*, 2008) database release LTPs119 (November 2014). Sequences not included in the database were added after the sequences were aligned with the SILVA Incremental Aligner (SINA; v. 1.2.11; Pruesse *et al.*, 2012). The alignment of all sequences used for tree reconstruction was checked manually considering information about the secondary structure of the 16S rRNA gene. A maximum-likelihood tree was generated using RAxML v7.04 (Stamatakis, 2006) with GTR-GAMMA and rapid bootstrap analysis (100 resamplings) and was based upon 16S rRNA gene sequence positions 96–1400 (according to Brosius *et al.*, 1978) and on 100 replications (bootstrap analysis; Felsenstein, 1985). All type strains of species of the genus *Flavobacterium* with validly published names were included in the phylogenetic analysis. Only the cluster containing the most closely related species is depicted here (Fig. 1); all other sequences were removed from the tree without affecting the overall tree topology.

The type strains of *F. ginsenosidimutans* (97.9 %), *F. phragmitis* (97.6 %) and *F. anhuiense* (97.5 %) shared the highest 16S rRNA gene sequence similarities with strain NXU-44^T; sequence similarity to all other species of the genus *Flavobacterium* was below 97.5 %. The maximum-likelihood tree showed clearly that strain NXU-44^T should be placed within the genus *Flavobacterium*. A distinct clustering with other type strains of species of the genus *Flavobacterium* was not observed. Strain NXU-44^T, however, clustered without high bootstrap support closest to the type strains of *F. ginsenosidimutans*, *F. phragmitis* and *F. anhuiense*, which showed highest 16S rRNA gene sequence similarities to strain NXU-44^T.

DNA–DNA hybridization experiments were not performed because the 16S rRNA gene sequence similarities were <97.8 %. This level corresponds to a maximum probability of error of 0.25 % (Meier-Kolthoff *et al.* 2013). Kim *et al.* (2014) recently recommended a threshold of 98.65 %.

Analysis of the cellular fatty acid profiles was performed as described previously (Kämpfer & Kroppenstedt, 1996). An HP gas chromatograph (HP 6890) with Sherlock MIDI software version 2.11 and a TSBA peak naming table version 4.1 were used, after growth of the strain on NA for 48 h at 28 °C, and showed the most abundant fatty acids were as follows: iso-C_{15:0}, iso-C_{17:0} 3-OH, iso-C_{17:1} ω9c and iso-C_{15:0} 2-OH [detected as summed feature 3 (iso-C_{15:0} 2-OH/C_{16:1} ω7c), but as shown in several previous studies clearly identified as iso-C_{15:0} 2-OH (Vandamme *et al.*, 1994; Montero-Calasanz *et al.*, 2013)].

The complete fatty acid pattern of NXU-44^T also showed slight, mainly quantitative differences and is shown in Table 2 in comparison with those of the type strains of the most closely related species of the genus *Flavobacterium*.

The biomass used to extract and analyse the quinones, polar lipids, polyamines and the characteristic diamino acid of the peptidoglycan was grown on 3.3 × PYE [1.0 % (w/v) peptone from casein, 1.0 % (w/v) yeast extract, pH 7.2]. For analysis of quinones, polar lipids and the diamino acid of the peptidoglycan, biomass was harvested at the stationary growth phase, whereas polyamines were extracted from biomass harvested at the late exponential growth phase as recommended by Busse & Auling (1988). Quinones and polar lipids were extracted and analysed by applying the integrated procedure reported by Tindall (1990a, b) and Altenburger *et al.* (1996). Polyamines were extracted as reported by Busse & Auling (1988) and analysed according to the conditions reported by Busse *et al.* (1997). HPLC analyses were carried out using the equipment reported by Stolz *et al.* (2007). The presence of the diagnostic diamino acid of the peptidoglycan was analysed according to Schumann (2011) and identified as *meso*-diaminopimelic acid. The polar lipid profile contained the major lipids phosphatidylethanolamine, one unidentified aminolipid (AL1) and two polar lipids (L2, L3) only detectable in total polar lipid staining. Furthermore, minor to moderate amounts of phosphatidylserine, one polar lipid (L1) and two aminolipids (AL2, AL3) were detected (Fig. 2). This profile is similar to that reported for *Flavobacterium cutihirudinis* (Glaeser *et al.*, 2013). The quinone system was exclusively composed of menaquinone MK-6. The polyamine pattern contained the major compound *sym*-homospermidine [31.0 μmol (g dry weight)⁻¹]. Other polyamines were present only in very low amounts [0.1–1.4 μmol (g dry weight)⁻¹], including putrescine, cadaverine, *sym*-norspermidine, spermidine and spermine. Both the quinone system and polyamine pattern are in good accordance with the emended description of the genus *Flavobacterium* (Bernardet *et al.*, 1996).

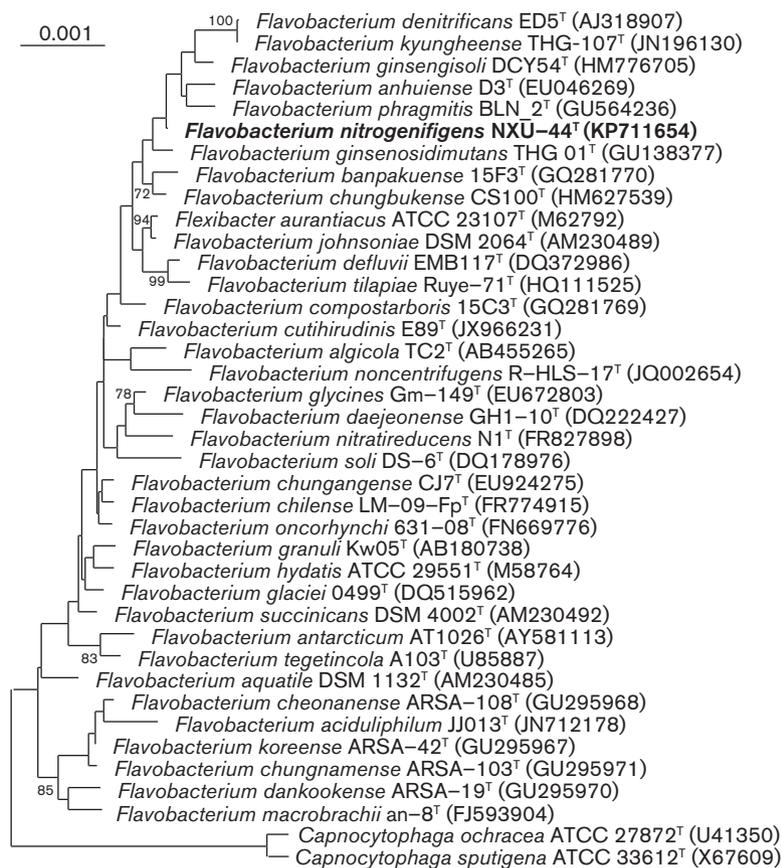


Fig. 1. Maximum-likelihood tree based on nearly full-length 16S rRNA gene sequences showing the phylogenetic position of strain NXU-44^T among the most closely related species of the genus *Flavobacterium*. The tree was calculated in ARB using RAxML with GTR-GAMMA, rapid bootstrap analysis and 100 replications. The analyses included all type strains of species of the genus *Flavobacterium* and nucleotide sequences between gene termini 96 and 1400 [*E. coli* numbering, Brosius *et al.* (1978)] were included in the analysis. Bootstrap values above 70 % are shown at branch nodes. Asterisks represent nodes with high bootstrap support, also present with high bootstrap support in the maximum-parsimony tree. Two type strains of species of the genus *Capnocytophaga* were used as outgroups. Bar, 0.001 nt substitutions per site.

On the basis of these results strain NXU-44^T warrants description as representing a novel species of the genus *Flavobacterium* for which the name *Flavobacterium nitrogenifigens* sp. nov. is proposed.

Description of *Flavobacterium nitrogenifigens* sp. nov.

Flavobacterium nitrogenifigens (ni.tro.ge.ni.fi'gens. N.L. n. *nitrogenium* nitrogen; L. part. adj. *Figens* fixing; N.L. part. adj. *nitrogenifigens* referring to the ability of this organism to fix nitrogen).

Gram-stain-negative, non-motile, non-spore-forming rods, approximately 1 µm in width and 2 µm in length. Aerobic, oxidase-positive, catalase-positive. Good growth occurs after 48 h on NA, brain heart infusion agar, TSA and R2A agar but not on MacConkey agar at 30 °C. Growth occurs on NA at 15–30 °C, but only weakly at 10 and

36 °C, and not at 40 °C. Cells grow at 28 °C in the presence of 1.0 % (w/v) NaCl as an additive ingredient of TSB, but not at 2 %, and at pH 5.5–10.5, but not at pH 4.5 or 11.5. Colonies on NA are smooth, yellowish, circular, translucent and glistening with entire edges. Colonies become mucoid, and cannot be identified as single entities after prolonged incubation. The yellow pigment of the flexirubin type is non-diffusible and non-fluorescent. Able to fix N₂, produces acid from D-glucose, L-arabinose and maltose, and weakly produces acid from D-xylose, D-mannose and D-cellulose. No acid is produced from adonitol, D-arabitol, dulcitol, erythritol, *i*-inositol, lactose, D-mannitol, melibiose, methyl α-D-glucoside, raffinose, L-rhamnose, salicin, D-sorbitol, sucrose or trehalose. Urease production and the hydrolysis of casein, gelatin, starch, DNA and tyrosine are positive, while the production of brown diffusible pigments on tyrosine agar, H₂S production, indole production from tryptophan, the activities of arginine dihydrolase, lysine decarboxylase, ornithine decarboxylase,

Table 2. Cellular fatty acid profiles of strain NXU-44^T and the type strains of phylogenetically related species of the genus *Flavobacterium*

Strains: 1. NXU-44^T; 2, *F. phragmitis* BLN2^T; 3, *F. ginsenosidimutans* THG 01^T; 4, *F. anhuiense* D3^T; 5, *F. defluvii* EMB117^T; 6, *F. denitrificans* ED5^T; 7, *F. daejeonense* GH1-10^T; 8, *F. johnsoniae* UW101^T. Data for taxa 1 and 3 (in parentheses) are from this study. Data for *F. phragmitis* are from Liu *et al.* (2011). All other data are from Yang *et al.* (2011), but obtained under exactly the same conditions. Cells were cultured on NA for 2 days at 28 °C. Fatty acids that account for <0.5 % of the total fatty acids are not shown. –, Not found.

Fatty acid	1	2	3	4	5	6	7	8
Saturated								
C ₁₀ :0	0.8	–	3.6 (1.9)	2.6	3.1	2.3	2.7	2.4
C ₁₄ :0	0.9	1.3	1.2 (1.2)	1.2	–	1.2	1.4	1.3
C ₁₅ :0	7.6	–	– (7.5)	–	–	–	–	–
C ₁₆ :0	3.9	8.9	4.7 (3.2)	9.6	2.0	7.6	5.9	5.7
Unsaturated								
C ₁₅ :1ω6c	2.4	2.4	3.0 (2.3)	1.7	1.8	2.5	1.4	5.1
C ₁₅ :1ω8c	–	–	– (–)	–	–	–	–	1.1
C ₁₆ :1ω5c	–	–	– (–)	–	–	–	–	1.0
C ₁₇ :1ω6c	2.8	2.5	1.4 (2.5)	1.2	2.0	1.8	–	2.8
C ₁₇ :1ω8c	1.2	1.4	1.2 (0.8)	1.5	2.4	1.5	–	1.6
iso-C ₁₇ :1ω9c	2.5	1.5	– (1.3)	–	–	–	–	–
Branched chain								
iso-C ₁₄ :0	–	–	– (–)	–	–	–	1.0	–
iso-C ₁₅ :0	17.3	20.7	24.7 (20.8)	21.8	25.4	20.9	25.3	23.7
iso-C ₁₅ :0 3-OH	8.3	7.0	8.5 (8.7)	6.5	10.7	6.6	5.4	3.8
iso-C ₁₅ :1 G	5.9	2.0	5.2 (5.1)	3.8	4.4	4.6	4.5	6.2
iso-C ₁₆ :0	0.7	–	– (0.8)	–	1.7	–	–	–
iso-C ₁₆ :0 3-OH	1.7	1.6	1.0 (2.2)	1.3	1.5	–	1.3	1.6
iso-C ₁₆ :1 H	–	–	– (–)	–	–	–	–	1.1
iso-C ₁₇ :0 3-OH	10.2	8.7	8.2 (9.1)	7.5	15.4	6.3	8.8	3.1
anteiso-C ₁₅ :0	–	2.3	1.5 (0.8)	–	1.4	1.0	7.8	3.4
anteiso-C ₁₉ :0	–	–	2.1 (–)	1.7	2.6	–	1.4	–
Hydroxy								
C ₁₅ :0 2-OH	1.5	–	– (1.3)	–	–	–	–	–
C ₁₅ :0 3-OH	1.5	1.8	1.7 (1.5)	2.2	2.8	1.8	1.3	2.2
C ₁₆ :0 3-OH	5.4	9.1	5.7 (6.4)	8.9	1.0	7.9	4.8	2.3
C ₁₇ :0 3-OH	0.9	1.0	– (–)	–	1.2	–	–	–
Summed features*								
2	1.6	–	1.1 (1.8)	1.2	–	1.5	–	–
3	21.0	19.6	14.6 (18.3)	15.6	5.7	19.0	16.7	19.6
9	–	–	1.6 (–)	2.2	6.8	1.9	1.2	3.0

*Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 2 comprised iso-C₁₆:1 I and/or C₁₄:0 3-OH; summed feature 3 comprised C₁₆:1ω7c and/or C₁₆:1ω6c; summed feature 9 comprised iso-C₁₇:1ω9c and/or 10-methyl C₁₆:0.

urease and ONPG are all negative. The following compounds are very weakly utilized as the sole source of carbon: D-glucose, N-acetylglucosamine, L-arabinose, cellobiose, D-galactose, maltose, D-mannose, L-rhamnose, D-xylose, L-malate, fumarate, L-ornithine and L-aspartate. The following compounds are not utilized as sole source of carbon: acetate, propionate, N-acetylgalactosamine, L-arbutin, gluconate, D-fructose, sucrose, trehalose, glycerol, D-mannitol, maltitol, α-melibiose, D-ribose, salicin, adonitol, i-inositol, D-sorbitol, putrescine, cis-aconitate, trans-aconitate, 4-aminobutyrate, adipate, azelate, glutarate, DL-3-hydroxybutyrate, itaconate, DL-lactate, 2-oxoglutarate,

pyruvate, suberate, citrate, mesaconate, L-alanine, β-alanine, L-ornithine, L-phenylalanine, L-serine, L-histidine, L-leucine, L-proline, L-tryptophan, 3-hydroxybenzoate, 4-hydroxybenzoate and phenylacetate. The following chromogenic substrates are hydrolysed: p-nitrophenyl-α-D-glucopyranoside, p-nitrophenyl-β-D-glucopyranoside (weakly), p-nitrophenyl-β-D-galactopyranoside, p-nitrophenyl-β-D-xylopyranoside, bis(p-nitrophenyl)-phosphate, bis(p-nitrophenyl)phenyl-phosphonate, bis(p-nitrophenyl)phosphorylcholine, 2-deoxythymidine-2'-p-nitrophenyl-phosphate, L-alanine-p-nitroanilide, γ-L-glutamate-p-nitro-anilide and L-proline-p-nitroanilide; p-nitrophenyl-β-D-glucuronide is

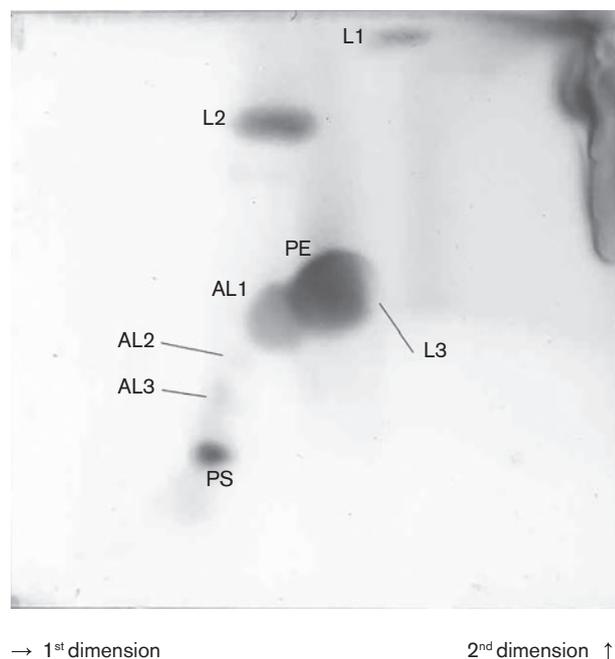


Fig. 2. Polar lipid profile of strain NXU-44^T after separation by two-dimensional TLC and detection using 5% (v/v) ethanolic molybdato-phosphoric acid. PE, phosphatidylethanolamine; PS, phosphatidylserine; AL1–3, unidentified aminolipids; L1–3, unidentified polar lipids not detectable with any of the spray reagents specific for lipids containing a phosphate group, an amino group or a sugar moiety.

not hydrolysed. The major cellular fatty acids are iso-C_{15:0}, iso-C_{15:0} 2-OH detected as summed feature 3 (iso-C_{15:0} 2-OH/C_{16:1ω7c}), iso-C_{17:1ω9c} and iso-C_{17:0} iso 3-OH. The diagnostic diamino acid of the peptidoglycan is *meso*-diaminopimelic acid. The polyamine pattern contains the major compound *sym*-homospermidine; very low amounts of putrescine, cadaverine, *sym*-norspermidine, spermidine and spermine are present. The quinone system is menaquinone MK-6. The polar lipid profile is composed of the major compounds phosphatidylethanolamine, one unidentified aminolipid (AL1) and two polar lipids (L2, L3). Furthermore, moderate to minor amounts of phosphatidylserine, one polar lipid (L1) and two aminolipids (AL2, AL3) are present.

The type strain is NXU-44^T (=LMG 28694^T=CIP 110894^T), isolated from the rhizosphere of switchgrass (*Panicum virgatum*) in Auburn, Alabama, USA.

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