The members of the genus *Methylobacterium* are strictly aerobic, Gram-negative rods that belong to the class *Alphaproteobacteria*. At the time of writing, the genus *Methylobacterium* comprised 44 species with validly published names (http://www.bacterio.net/methylobacterium.html), with *Methylobacterium organophilum* as the type species (Patt et al., 1976; Green, 2006). Members of this genus can grow on diverse one-carbon or multicarbon compounds, and some of them on methylated amines or halogenated one-carbon compounds (Green, 1992; Kayser et al., 2002; Lidstrom, 2006; Schäfer et al., 2007), but none of them on methane (Dedys et al., 2004). Bacteria of the genus *Methylobacterium* are common leaf epiphytes and endophytes (Holland, 1979; Elbeltagy et al., 2000; Pirttilä et al., 2000; Lindow & Brandl, 2003; Mano et al., 2007; Schauer & Kutschera, 2008; Andreote et al., 2009) and benefit from the methanol produced by plants by means of methylophytes (Chistoserdova et al., 2003; Sy et al., 2005; Abanda-Nkwatt et al., 2006; Schmidt et al., 2010), in turn promoting plant growth by synthesizing phytohormones (Basile et al., 1985; Trotsenko et al., 2001; Koenig et al., 2002), production of siderophores (Idris et al., 2004) and synthesis of enzymes that modulate plant growth (Holland & Polacco, 1992; Madhaiyan et al., 2006, 2007a). Potential advantages of this association for the plant host have been discussed in different reports (Trotsenko et al., 2001; Holland et al., 2002; Koenig et al., 2002; Lidstrom & Chistoserdova, 2002; Idris et al., 2004; Omer et al., 2004; Kutschera, 2007; Madhaiyan et al., 2007a, 2009). In addition, a non-pigmented strain of *Methylobacterium* has been shown to form a root-nodulating nitrogen-fixing symbiosis with a legume (Sy et al., 2001; Jourand et al., 2004). In previous studies, we analysed pink-pigmented, facultative methylotroph diversity from variety of crop species (Madhaiyan et al., 2007b, 2012). The data presented in this paper include the formal taxonomic description of two novel species of the genus *Methylobacterium*, which were isolated from the bamboo phyllosphere, and these bacteria promote plant growth and development by production of phytohormones.

Fresh leaf samples, i.e. the top knot of new shoots from healthy plants (>10 years old), were collected from Tamilnadu Agriculture University campus, Coimbatore, Tamilnadu, India. Strains BL36<sup>T</sup> and BL47<sup>T</sup> were isolated from the phyllopole of leaves on selective ammonium mineral salts (AMS) medium (Whittenbury et al., 1970) supplemented with filter-sterilized cycloheximide (10 µg ml<sup>-1</sup>) and methanol (0.5 %, v/v) at 28 °C by the leaf
imprinting method (Chanprame et al., 1996). These isolates were preserved at −80 °C in nutrient broth (Difco) with 1% (v/v) methanol or on AMS medium with 0.5% methanol with 50% (v/v) glycerol or by lyophilization. Cellular phenotypic characters were determined according to standard protocols described by Gerhardt et al. (1994). The test for swarming motility was performed on one-tenth-strength R2A broth (Difco) supplemented with 0.2% agar. Indole production was tested on motility-indole-lysine (MIL) medium (Difco) according to the manufacturer’s instructions. Growth at 5–45 °C and pH 4, 5, 6, 7, 8, 9 and 10 was monitored in R2A broth. The requirement for NaCl was tested in R2A broth supplemented with 0, 2, 3, 5 and 7% (w/v) NaCl. The type strains Methylobacterium phyllosphaerae CBMB27T, M. oryzae CBMB20T, M. fujisawense KACC 10744T, M. radiotolerans DSM 1819T, M. mesophilicum DSM 1708T, M. brachiatum NBRC 103629T, M. tardum NBRC 103632T, M. longum DSM 23933T, M. zatmanii DSM 5688T, M. extorquens DSM 1337T, M. organophilum DSM 760T, M. iners KACC 11765T and M. platani KCTC 12901T were included as reference strains for the investigation of the phenotypic properties of the leaf isolates BL36T and BL47T under the same laboratory conditions. Nutritional features were determined as described previously by using Biolog GN2 MicroPlates (Madhaiyan et al., 2007a) and utilization of carbon sources not included on the Biolog plates was determined as described by Green & Bousfield (1982). Various physiological and biochemical tests were carried out using the API ZYM, API 20NE and API 32GN galleries (bioMérieux) following the manufacturer’s instructions. Urease activity was tested using urea broth (Difco) according to the manufacturer’s instructions. Scanning electron microscope observations were performed on fixed material prepared for routine examinations as described by Bozolla & Russell (1998). Samples were critical-point-dried, mounted on stubs, sputter-coated with gold/palladium and visualized by using a Hitachi S-2500C scanning electron microscope with a GEMINI column equipped with a field-emission electron source. For transmission electron microscope observations, the cells were negatively stained with 1% (w/v) phosphotungstic acid and, after air-drying, grids were examined with a transmission electron microscope (model CM-20; Philips).

Both strains were strictly aerobic, Gram-negative, motile and rod-shaped. Colonies were smooth, circular, convex, pink to red and 0.5–1.8 mm in diameter. Growth was observed at 20–37 °C (optimum 28–30 °C) and pH 5–9 (optimum pH 7) and not in the presence of NaCl concentrations of 2% or more. Both strains grew on R2A (Difco), mineral salt medium plus 1% (v/v) methanol, PYG, succinate medium, glycerol peptone, plate count agar and nutrient agar but did not grow on trypticase soy agar (Difco) or MacConkey agar (Difco). Both strains could be differentiated clearly from their close relatives by several phenotypic characteristics such as oxidase, urease, nitrate reduction, substrate assimilation and enzyme activities (Table 1).

To determine the cellular fatty acid composition, all strains were grown on R2A at 30 °C for 72 h. The fatty acids were extracted, derivatized to methyl esters and analysed by gas chromatography (Hewlett Packard 6890) using the Microbial Identification System (MIDI; Microbial ID) software package, according to the standard protocols (Kroppenstedt, 1985; Sasser, 1990). Fatty acid methyl esters were identified and quantified by using the TSBA6 database (version 6.10) of the Sherlock Microbial Identification System (Microbial ID Inc.). The G+C content of genomic DNA was determined by HPLC analysis of individual nucleosides using a reversed-phase column (Supelcosil LC-18S; Supelco) as described previously (Mesbah et al., 1989). Quinones were extracted and analysed as described by Minnikin et al. (1984). Both strains had C18:1ω7c as the major fatty acid. These were consistent with the major fatty acids of M. longum 440T, M. platani PBM02T, M. oryzae CBMB20T, M. brachiatum NBRC 103629T, M. tardum NBRC 103632T, M. phyllosphaerae CBMB27T, M. gossipicola Gh-105T, M. iners KACC 11765T and M. aerolatum KACC 11766T (Kang et al., 2007; Madhaiyan et al., 2007a; Kato et al., 2008; Weon et al., 2008; Madhaiyan et al., 2009; Madhaiyan et al., 2012; Knief et al., 2012); however, strains BL36T and BL47T could be distinguished on the basis of qualitative and quantitative differences for these and other fatty acids (Table 1). The DNA G+C content of strain BL36T was 69.4 mol% and that of strain BL47T was 69.8 mol%. The major respiratory quinone was identified as Q-10.

Strains BL36T and BL47T were grown in 100 ml AMS liquid medium supplemented with 0.5% methanol as the carbon source and incubated at 30 °C for 72 h. The culture supernatant was used and the extraction was carried out with dichloromethane as for TLC. The residues were resuspended in small volumes of dichloromethane for GC-MS analysis and stored at −20 °C. GC-MS analyses were performed using a model CP-3800 GC system (Varian) interfaced to a 1200L Quadrupole MS-MS detector (Varian). Conditions were as follows: injector temperature 200 °C; transfer line temperature 280 °C; electron energy 70 eV; injection volume 1 μl. The GC was programmed as follows: 5 min at 150 °C and then increasing to 275 °C at 15 °C min−1 and operated in a split mode. The carrier gas was helium at 0.8 ml min−1. The mass spectrometer was run in full scan mode (m/z 15–800) and in SIM mode (m/z 143). Identification of compounds was performed by comparison of mass spectra and retention times with authentic compounds. Data analysis was carried out with MS workstation SP1 version 6.5 (Varian). Synthetic homoserine lactones (HSLs), namely N-3-hexanoyl-DL-homoserine lactone (C6-HSL), N-heptanoyl-DL-homoserine lactone (C7-HSL), N-octanoyl-DL-homoserine lactone (C8-HSL), N-decanoyl-DL-homoserine lactone (C10-HSL), N-dodecanoyl-DL-homoserine lactone (C12-HSL) and
N-tetradecanoyl-DL-homoserine lactone (C_{14}-HSL) used as reference standards were obtained from Fluka and Sigma-Aldrich.

Since methylotrophic bacteria tend to form aggregates on the aerial parts of plants (Sy et al., 2005), the phenomenon of quorum sensing, which affects the multicellular behaviour of bacteria in a community, gains importance. Our previous study showed that the occurrence of quorum-sensing systems in species of the genus Methylobacterium is widespread (Poonguzhali et al., 2007). In Methylobacterium extorquens AM1, two quorum-sensing systems responsible for the production of short- and long-chain N-acyl homoserine lactones (AHLs) have been described (Nieto Penalver et al., 2006), with the long-chain molecules being detected with Pseudomonas putida F117 (pRK-C12), a gfp-based monitoring system. GC-MS analysis of the AHL extracts revealed strain-level differences among species of the genus Methylobacterium similar to other bacteria studied so far (Poonguzhali et al., 2007). Strain BL36^T contained two known compounds (C_{6}-HSL and C_{7}-HSL), and no known compounds were detected in strain BL47^T (Fig. S1, available in the online Supplementary Material).

Chromosomal DNA was extracted according to the kit instructions (QIAamp DNA mini kit; Qiagen). The 16S rRNA gene was amplified using universal primers 27F and 1492R (DeLong, 1992). Cycling conditions were as follows: 95 °C for 10 min, 30 cycles of 95 °C for 1.5 min, 55 °C for 1.5 min and 72 °C for 1.5 min and a final extension for 10 min at 72 °C. Sequencing was carried out with the fluorescent dye terminator method using the ABI Prism Big Dye terminator cycle sequencing ready reaction kit (version 2.2, Applied Biosystems). The 16S rRNA gene was amplified using universal primers 27F and 1492R (DeLong, 1992), and sequences were aligned using the CLUSTAL W tool in MEGA version 5.05 (Tamura et al., 2011). Phylogenetic analyses were performed by the neighbour-joining (Saitou & Nei, 1987), maximum-likelihood (Felsenstein, 1981) and maximum-parsimony (Fitch, 1971) methods using MEGA.

<table>
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<th>Table 1. Differential characteristics of the strains characterized in this study and their closest phylogenetic neighbours</th>
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<td>Strains: 1, BL36^T; 2, BL47^T; 3, M. phyllosphaerae CBMB27^T; 4, M. oryzae CBMB20^T; 5, M. fujisawaense KACC 10744^T; 6, M. radiotolerans DSM 1819^T; 7, M. mesophilicum DSM 1708^T; 8, M. brachiatum NBRC 103629^T; 9, M. tardum NBRC 103632^T; 10, M. longum DSM 23933^T; 11, M. zatmanii DSM 5688^T; 12, M. extorquens DSM 1337^T; 13, M. organophilum DSM 760^T; 14, M. iners KACC 11765^T; 15, M. platani KCTC 12901^T; 16, M. gossypicola Gh-105^T. +, Positive; –, negative; w, weakly positive. All data were obtained in this study. Fatty acids representing less than 0.3 % in all strains were omitted. All strains were grown on R2A medium for 3 days at 30 °C.</td>
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<td><strong>Characteristic</strong></td>
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<td><strong>L-Arabinose</strong></td>
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<td><strong>L-Araskanate</strong></td>
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<td><strong>Fatty acids (%) of total</strong></td>
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<td>C_{18:0}</td>
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<td>C_{18:1} 3-OH</td>
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<td>Summed feature 2§</td>
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<td>Summed feature 3§</td>
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*LP, Light pink; P, pink; PP, pale pink; PR, pink to red; WP, whitish pink.
†Discrepancies were found between this study and the following previous studies: a, Kato et al. (2008); b, Green (1992); c, Van Aken et al. (2004); d, Weon et al. (2008).
§Summed features represent groups of two or three fatty acids that could not be separated by GLC with the MIDI system. Summed feature 2 contained iso-C_{16:1} I and/or C_{14:0} 3-OH; summed feature 3 contained C_{16:1} 07c and/or iso-C_{15:0} 2-OH.
version 5.05 (Tamura et al., 2011) with bootstrap values set at 1000 replications (Felsenstein, 1985). mxaF gene sequences were determined as described previously (McDonald & Murrell, 1997; Madhaiyan et al., 2009).

DNA–DNA hybridization was carried out to find the relatedness of the strains to their closest relatives following the filter hybridization method (Seldin & Dubnau, 1985) with some modifications. DNA–DNA hybridization was done by the membrane filter technique using the DIG High Prime DNA Labelling and Detection Starter kit II (Roche Molecular Biochemicals) and hybridized DNA was visualized using the DIG luminescent detection kit (Roche Diagnostics). Genomic DNA (200 ng) was denatured by the alkaline method and immobilized on a nylon membrane (Hybond-N+; Amersham) by applying a low vacuum and the DNA preparations (1 mg) were labelled using the DIG High Prime DNA Labelling and Detection Starter kit II according to the manufacturer’s protocol. The membranes were prehybridized in a hybridization solution at 52 °C for 30 min. The actual hybridization was carried out in a hybridization solution containing labelled DNA (25 ng ml⁻¹) at 52 °C for 16 h. After hybridization, the membranes were washed twice in primary washing solution (2 × SSC, 0.1% SDS) and subsequently washed twice in a secondary solution (0.5 × SSC, 0.1% SDS) at 68 °C. Detection reagents were added to the membranes for 5 min at room temperature, and the excess liquid was then squeezed out. The membranes were exposed to autoradiography film (Hyperfilm-ECL; Amersham) for 10 min, and the signal intensities were quantified by using a densitometer (Bio-Rad) and analysed with the TINA 2.0 program. The signal produced by self-hybridization of the probe with homologous target DNA was taken as 100 %, and percentage relatedness values were calculated for the duplicate samples.

The 16S rRNA gene sequence similarities between strain BL36T and the type strains of all recognized species of the genus Methylobacterium were in the range 93.6–98.5 %; its closest relatives were M. mesophilicum JCM 2829T (98.5 % sequence similarity), M. brachiatum B0021T (98.4 %), M. phyllophaeae CBMB27T (97.9 %), M. oryzae CBMB20T (97.4 %), M. fujisawaense DSM 5686T (97.3 %), M. tardum RB677T (97.2 %), M. longum 440T (97.2 %) and M. radiotolerans JCM 2813T (97.2 %). Strain BL47T showed sequence similarity of 92.8–99.0 % with all type strains of the genus Methylobacterium. It revealed ≥97 % sequence similarity with M. phyllophaeae CBMB27T (99.0 %), M. longum 440T (98.8 %), M. tardum RB677T (98.4 %), M. oryzae CBMB20T (98.2 %), M. fujisawaense DSM 5686T (98.1 %), M. radiotolerans JCM 2813T (98.1 %), M. mesophilicum JCM 2829T (97.4 %) and M. brachiatum B0021T (97.4 %). According to the neighbour-joining tree (Fig. 1), strain BL36T formed a compact cluster with M. mesophilicum JCM 2829T and M. brachiatum B0021T (99 % bootstrap support). A fully expanded neighbour-joining tree is shown in Fig. S2. Strain BL47T clustered with M. phyllophaeae CBMB27T and M. longum 440T. The topologies of phylogenetic trees built using the maximum-parsimony algorithm also supported the notion that these isolates belong to the genus Methylobacterium. Sequencing of the mxaF gene from strains BL36T and BL47T resulted in a product of ~550 bp in a continuous stretch and, when compared with representative species of the genus Methylobacterium, revealed a compact cluster with the type strains of M. iners, M. platani and M. brachiatum (Fig. 2). DNA–DNA hybridization between the two novel isolates, BL36T and BL47T, was below 15 % (reciprocal 21 %). Strain BL36T showed low levels of DNA–DNA relatedness with M. phyllophaeae CBMB27T (40 %, reciprocal 43 %), M. longum DSM 23933T (35 %, reciprocal 39 %), M. tardum NBRC 103632T (33 %, reciprocal 41 %), M. oryzae CBMB20T (38 %, reciprocal 48 %), M. fujisawaense KACC 10744T (32 %, reciprocal 37 %), M. radiotolerans DSM 1819T (18 %, reciprocal 24 %), M. mesophilicum DSM 17081T (42 %, reciprocal 45 %), M. brachiatum NBRC 103629T (44 %, reciprocal 49 %), M. zatmannii DSM 5688T (12 %, reciprocal 17 %), M. extorquens DSM 13375T (12 %, reciprocal 17 %), M. organophilum DSM 760T (16 %, reciprocal 18 %), M. iners KACC 11765T (18 %, reciprocal 26 %), M. platani KCTC 12901T (45 %, reciprocal 49 %) and M. gossypiicola Gh-105T (13 %, reciprocal 16 %). Strain BL47T also showed low levels of DNA–DNA relatedness with M. phyllophaeae CBMB27T (42 %, reciprocal 51 %), M. longum DSM 23933T (44 %, reciprocal 45 %), M. tardum NBRC 103632T (36 %, reciprocal 40 %), M. oryzae CBMB20T (38 %, reciprocal 43 %), M. fujisawaense KACC 10744T (39 %, reciprocal 46 %), M. radiotolerans DSM 1819T (40 %, reciprocal 41 %), M. mesophilicum DSM 17081T (37 %, reciprocal 42 %), M. brachiatum NBRC 103629T (36 %, reciprocal 39 %), M. zatmannii DSM 5688T (21 %, reciprocal 28 %), M. extorquens DSM 13375T (18 %, reciprocal 21 %), M. organophilum DSM 760T (18 %, reciprocal 19 %), M. iners KACC 11765T (17 %, reciprocal 24 %), M. platani KCTC 12901T (39 %, reciprocal 47 %) and M. gossypiicola Gh-105T (19 %, reciprocal 23 %). These results indicate that strains BL36T and BL47T do not belong to any of the above species when the recommendation of a threshold value of 70 % DNA–DNA relatedness for species definition is considered (Wayne et al., 1987). On the basis of this polyphasic taxonomic analysis, the names Methylobacterium pseudosasicola sp. nov. and Methylobacterium phyllostachyos sp. nov. are proposed to accommodate these two novel strains.

**Description of Methylobacterium pseudosasicola sp. nov.**

Methylobacterium pseudosasicola (pseu.do.sa.si’co.la. N.L. n. Pseudosasa a botanical genus name; L. suff. -cola inhabitant, dweller, N.L. n. pseudosasicola an inhabitant of Pseudosasa, referring to the isolation of the type strain from *Pseudosasa japonica*).

Gram-negative, non-endospore-forming, motile, strictly aerobic rods (1.4–2.5 × 0.4–0.5 μm) occurring singly, in pairs or in rosettes (Fig. 3). Colonies are pink, convex and translucent with regular edges, growing slowly and 0.8–1.4 mm in diameter after 96 h at 28 °C on AMS. Grows on...
nutrient agar, R2A, PYG, succinate, glycerol peptone and plate count agar media and does not grow in the presence of 2 % NaCl or higher. Growth occurs at 20–37 °C (optimum 28–30 °C) and at pH 5–9 (optimum pH 7). Catalase, oxidase and urease are positive. Nitrate reduction and methyl red and Voges–Proskauer tests are negative. Gelatin, starch, glycerol tributyrate, casein and aesculin are not hydrolysed. Hydrogen sulfide is not produced. Simmons' citrate test is positive. Weak growth on diethylamine, methylamine, ethanol, trimethylamine and diethanolamine but not formaldehyde or dichloromethane. The following compounds are utilized as sole carbon and energy sources (Biolog): α-cyclodextrin, dextrin, glycogen, Tweens 40 and 80, N-acetyl-D-galactosamine, N-acetyl-D-glucosamine, adonitol, L-arabinose, D-arabitol, cellobiose, D-fructose, L-fucose, D-galactose, gentiobiose, myo-inositol, α-D-glucose, lactose, lactulose, maltose, D-mannitol, D-mannose, L-rhamnose, D-sorbitol, trehalose, turanose, xylitol, pyruvic acid methyl ester, succinic acid monomethyl ester, cis-aconitic acid, citric acid, D-galacturonic acid, D-glucosaminic acid, D-glucuronic acid, α-hydroxybutyric acid, β-hydroxybutyric acid, γ-hydroxybutyric acid, D-lactic acid, quinic acid, D-saccharic acid, sebacic acid, bromosuccinic acid, L-asparagine, glycyl L-aspartic acid, glycylL-glutamic acid, L-serine, γ-aminobutyric acid, urocanic acid, glycerol, DL-α-glycerol phosphate, α-D-glucose 1-phosphate and D-glucose 6-phosphate. In API ZYM assays, esterase (C4), esterase lipase (C8), leucine arylamidase, acid phosphatase, trypsin and naphthol-AS-BI-phosphohydrolase are present. The major respiratory quinone is ubiquinone Q-10 and a low level of Q-9 is present. The major fatty acid is C18:1 ω7c.

The type strain, BL36T (=NBRC 105203T = ICMP 17621T), was isolated from an arrow bamboo leaf (Pseudosasa japonica) collected from TNAU campus, Coimbatore, Tamilnadu, India.

Fig. 1. Phylogenetic tree based on 16S rRNA gene sequence comparison showing the position of strains BL36T and BL47T and related members of the genus Methylobacterium. Filled circles at nodes indicate generic branches that were also recovered by using the maximum-parsimony algorithm. Numbers at nodes indicate percentages of occurrence in 1000 bootstrapped trees; bootstrap values below 50% are not shown. Bar, 0.5% substitutions.
Methylobacterium phyllostachyos sp. nov.

Methylobacterium phyllostachyos (phyl.lo.sta’chy.os. N.L. n. Phyllostachys a botanical genus name; N.L. gen. n. phyllostachyos of Phyllostachys, referring to the isolation of the type strain from Phyllostachys aureosulcata).

Gram-negative, non-endospore-forming, motile, strictly aerobic rods (1.3–2.5 × 0.4–0.7 μm) occurring singly or in
Colonies are pink to red, convex, translucent with regular edges, growing slowly and 0.5–1.8 mm in diameter after 96 h at 28 °C on AMS. Grows on nutrient agar, R2A, PYG, succinate, glycerol peptone and plate count agar media and does not grow in the presence of 2 % NaCl or higher. Growth occurs at 20–37 °C (optimum 28 °C) and at pH 5–9 (optimum pH 7). Catalase, oxidase and urease are positive. Nitrate reduction and methyl red and Voges–Proskauer tests are negative. Gelatin, starch, glycerol tributyrate, casein and ascinulc are not hydrolysed. Hydrogen sulfide is not produced. Simmons’ citrate test is positive. Weak growth on diethylamine, methylamine, ethanol, trimethylamine, and diethanolamine but not formaldehyde or dichloromethane. The following compounds are utilized as sole carbon and energy sources (Biolog): dextrin, glycogen, D-arabinose, D-galactose, α-D-glucose, L-rhamnose, pyruvic acid methyl ester, succinic acid monomethyl ester, cis-aconitic acid, β-galactonic acid lactone, D-gluconic acid, β-hydroxybutyric acid, γ-hydroxybutyric acid, α-ketoglutaric acid, DL-lactic acid, D-saccharic acid, succinic acid, bromosuccinic acid, succinic acid, 1,3-alaninamide, L-asparagine, L-aspartic acid, L-glutamic acid, L-pyroglutamic acid, D-serine, L-serine, L-threonine, γ-aminobutyric acid, glycerol, DL-α,DL-β-glycerol phosphate and D-glucose 6-phosphate. In API ZYM assays, esterase (C4), esterase lipase (C8), leucine arylamidase, acid phosphatase, trypsin and naphthol-AS-BI-phosphohydrolase are present. The major respiratory quinone is ubiquinone Q-10; a low level of Q-9 is present. The major fatty acid is C18:1ω7c.

The type strain, BL47T (=NBRC 105206T=ICMP 17619T), was isolated from a bamboo leaf (Phyllostachys aureosulcata) collected from TNAU campus, Coimbatore, Tamilnadu, India.

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References


