**Salipaludibacillus aurantiacus** gen. nov., sp. nov. a novel alkali tolerant bacterium, reclassification of *Bacillus agaradhaerens* as *Salipaludibacillus agaradhaerens* comb. nov. and *Bacillus neizhouensis* as *Salipaludibacillus neizhouensis* comb. nov.

Vishnuvardhan Reddy Sultanpuram and Thirumala Mothe

Two novel (S9\(^T\) and S12) Gram-stain-positive, rod shaped, non-motile and endospore forming bacteria were isolated from Narayan Sarovar lake, in India. The high 16S rRNA gene sequence similarity (99.9 %) and DNA–DNA relatedness (86±2 %) indicated that strains S9\(^T\) and S12 were members of a single species. Based on the 16S rRNA gene sequence analysis, these strains were identified as belonging to the class *Firmibacteria* and were most closely related to *Bacillus agaradhaerens* PN-105\(^T\) (96.8 % sequence similarity), *Bacillus neizhouensis* JSM 071004\(^T\) (96.5 %) and *Bacillus luteus* JC167\(^T\) (96.1 %). However, these strains shared only 90.3 % 16S rRNA gene sequence similarity with *Bacillus subtilis* subsp. *subtilis* DSM 10\(^T\), indicating that they might not be members of the genus *Bacillus*. The cell-wall peptidoglycan contained meso-diaminopimelic acid. Polar lipids included diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, one unknown phospholipid and an unknown lipid. The predominant isoprenoid quinone was MK-7. Major fatty acids (>5 %) included anteiso-C\(_{15:0}\), C\(_{16:0}\), iso-C\(_{15:0}\), anteiso-C\(_{17:0}\), iso-C\(_{16:1}\) and summed feature 3. The results of phylogenetic, chemotaxonomic and biochemical tests allowed a clear differentiation of strains S9\(^T\) and S12 from all other members of the family *Bacillaceae*. The strains therefore represent a novel member of a new genus from the family *Bacillaceae*, for which the name *Salipaludibacillus aurantiacus* gen. nov., sp. nov. is proposed. The type strain is S9\(^T\) (=KCTC 33633\(^T\)=LMG 28644\(^T\)). Based on the present study, it is also proposed to transfer *Bacillus agaradhaerens* and *Bacillus neizhouensis* to this new genus as *Salipaludibacillus agaradhaerens* comb. nov. and *Salipaludibacillus neizhouensis* comb. nov.

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Two supplementary figures and one supplementary table are available online. The GenBank/EMBL/DDBJ accession numbers for the 16S rRNA gene sequences of strains S9\(^T\) and S12 are LN827662 and LN812016, respectively.

The moderately halophilic bacteria are frequently isolated from saline and hypersaline environments such as saline soils and other saline aquatic habitats (Arahal & Ventosa, 2002; de la Haba et al., 2011). These bacteria are represented by heterogeneous physiological and taxonomic groups of both Gram-negative and Gram-positive micro-organisms (Ventosa et al., 1998; Ventosa, 2006). Among them, the order *Bacillales* within the class *Bacilli* (or *Firmibacteria*) represents an extremely heterogeneous bacterial taxon (Euzéby, 2011). In this group, fundamentally different physiological types such as aerobic or anaerobic, psychrophilic or thermophilic, halophilic or non-halophilic or endospore-forming and non-endospore-forming bacteria are combined (Seiler et al., 2013). The family *Bacillaceae* is one of the largest taxa in the order *Bacillales* in which several novel genera have been reported. Some of these recently described genera include *Streptohalobacillus* (Wang et al., 2011), *Allobacillus* (Sheu et al., 2011), *Natribacillus* (Echigo et al., 2012), *Domibacillus* (Seiler et al., 2013), *Saliterribacillus* (Amoozegar et al., 2013), *Fictibacillus* (Glaeser et al., 2013), *Simibacillus* (Yang & Zhou, 2014), *Thermolongibacillus* and others.
CLUSTAL W sequence similarity were achieved using the EzTaxon-e server search analysis revealed that strains S9T and S12 were most closely related to Bacillus agaradhaerens PN-105T (96.8 % sequence similarity), Bacillus neizhouensis DSM 071004T (96.5 %) and Bacillus luteus JC167T (96.1 %). However, strains S9T and S12 shared only 90.3 % 16S rRNA gene sequence similarity with Bacillus subtilis subsp. subtilis DSM 10T, a value lower than those obtained with respective species of the genera Salisediminibacterium (93.4 %), Alteribacillus (93.1 %), Virgibacillus (92.2 %), Scopulibacillus (92.0 %), Anaerobacillus (91.7 %), Alkalibacillus (91.7 %), Piscibacillus (91.6 %), Pullulanibacillus (91.5 %), Gracilibacillus (91.4 %), Filobacillus (91.1 %) and Lentibacillus (90.8 %). Further, some of the closely related neighbours (from the genera Bacillus) of strains S9T and S12 also shared low values of 16S rRNA gene sequence similarities with B. subtilis subsp. subtilis DSM 10T: B. agaradhaerens PN-105T (92.1 %), B. neizhouensis DSM 071004T (90.3 %), B. luteus JC167T (89.2 %), B. dahlensis DLS13T (90.4 %), B. clarkii PN-102T (92.1 %), B. polygoni YN-1T (91.7 %), ‘B. daqingensis’ X1-10 (90.2 %), B. saliphilus 6AGT (91.0 %) and B. selenitireducens MLS10T (91.3 %). These 16S rRNA gene sequence similarity values are lower than those with some of the species from other genera, Lentibacillus kapidus PN7T (92.5 %) and Virgibacillus sediminis YIM kkn3T (93.0 %). The results of phylogenetic analysis of the 16S rRNA gene sequences showed that strains S9T and S12 clustered with B. agaradhaerens and B. neizhouensis (a composite tree is shown as Fig. 1) and the sequence similarities with the nearest phylogenetic members were in agreement with the EzTaxon-e server result. The G+C content of the DNA of strains S9T and S12 was 42.4±2 mol% and 42.5±1 mol%, respectively. These values are slightly higher than that of B. agaradhaerens PN-105T (39.3 mol%) (Nielsen et al., 1995), B. neizhouensis DSM 071004T (40.8 %) (Chen et al., 2009) and B. luteus JC167T (40.9 %) (Subhash et al., 2014).

The phenotypic features of strains S9T and S12 were determined following the minimum standards for describing new taxa of aerobic, endospore-forming bacteria recommended by Logan et al. (2009). Morphological properties, such as, cell shape, cell size and motility were observed by phase-contrast light microscopy (Magnus MLX). The pH (range pH 6.0–12.0, with intervals of 0.5, with KH2PO4/KH2PO4 buffer for pH 6.0–8.0, NaHCO3/NaOH buffer for pH 8.5–11.0 and Na2CO3/NaOH buffer for pH 11.5–12.0), temperature (0, 4, 10, 16, 20, 28, 35, 37, 40, 45, 50, 55, 60, 65 and 70 °C) and salt concentration (0–30 %, w/v, with intervals of 0.5 %, w/v) ranges for growth were examined in alkaline nutrient broth as described earlier and the results were recorded after 48 h of incubation. Growth was measured turbidometrically at 540 nm in a colorimeter (Systronics). The tests for temperature and salt concentration were performed in the emended medium so as to get pH 9.0. Growth under anaerobic conditions was determined on modified nutrient agar, (g l⁻¹) peptone (5), NaCl (5), beef extract (1.5), yeast extract (1.5), agar (15) with a final
Fig. 1. Phylogenetic tree, based on the maximum-likelihood algorithm, of strains S9\textsuperscript{T} and S12 with other closely related strains, based on 16S rRNA gene sequences available from the EMBL database (accession numbers are given in parentheses), reconstructed using MEGA 5 software and rooted by using *Marinococcus halophilus* HK 718\textsuperscript{T} (X90835) as the outgroup. Bootstrap values based on 1000 replications are listed as percentages at the branching points. Bar, 0.01 nucleotide substitutions per nucleotide position. Filled circles at the branching points indicate that the same branching was obtained when the neighbour-joining, minimum-evolution, maximum-likelihood and maximum-parsimony algorithms were used.

pH of 7.5, supplemented with 0.5 % (w/v) glucose and with or without 0.1 % (w/v) nitrate using an anaerobic system (Himedia). Various biochemical tests, such as those to determine hydrolysis of starch, casein, tyrosine, xanthine, hypoxanthine and gelatin, as well as urease activity, nitrate reduction, Voges–Proskauer test, methyl red test, H\textsubscript{2}S production, indole production, and oxidase and catalase activities, were carried out as described by Smibert & Krieg (1981, 1994, in the alkaline nutrient agar medium described above or the specified medium. In both cases 10 % NaHCO\textsubscript{3} was autoclaved separately and only added after sterilization. Utilization of various substrates as sole carbon and energy sources or carbon, nitrogen and energy sources was determined using a basal medium with the following composition (g l\textsuperscript{−1}): yeast extract, 0.01; KH\textsubscript{2}PO\textsubscript{4}, 0.5; MgSO\textsubscript{4}·7H\textsubscript{2}O, 0.2; (NH\textsubscript{4})\textsubscript{2}HPO\textsubscript{4}, 1.0; NaCl, 60. To this liquid medium, 0.1 % (w/v) filter-sterilized substrate was added. Carbohydrates were used at a final concentration of 0.2 % (w/v), and the tests for their utilization were performed as described by Ventosa et al. (1982). Antibiotic sensitivity tests of the strains were performed using the standard disc assay method (Ventosa et al., 1982).

Colonies of both strains S9\textsuperscript{T} and S12 grown on alkaline nutrient agar were orange, circular (1.2–2.0 mm in diameter), convex and opaque with entire margin. Cells of strains S9\textsuperscript{T} and S12 were Gram-stain-positive and non-motile rods with 0.3–0.9 μm diameter and 1.7–2.2 μm length. The strains also formed sub-terminal endospores (Fig. S1, available in the online Supplementary Material). Growth of both strains occurred within a pH range of 8.0–11.0 with an optimum of pH 9.0. A minimal amount of NaCl (0.5 %, w/v) was essential for growth of both strains, and they could grow with up to 22 % (w/v) with optimum growth at 3–5 % (w/v). Optimum growth of both strains occurred at 37°C with a range of 20–45°C. Casein, aesculin, DNA, starch, cellulose, hippurate, Tween 20 and tyrosine were not hydrolysed, whereas xanthine and hypoxanthine were hydrolysed by both strains. Gelatin was not liquefied. Oxidase, catalase and urease activities were positive, whereas lipase activity was negative for both strains. Indole production from tryptophan was negative for both strains. Strains S9\textsuperscript{T} and S12 produced H\textsubscript{2}S and showed positive Voges-Proskauer tests but were negative for nitrate reduction, citrate utilization and the methyl red test. Fermentative growth of strains S9\textsuperscript{T} and S12 was not observed, and the substrates which supported growth of both these strains (S9\textsuperscript{T} and S12) are included in the species description. Strains S9\textsuperscript{T} and S12 were sensitive to gentamycin (120 μg), vancomycin (30 μg), tetracycline (30 μg), streptomycin (10 μg), penicillin (10 μg), erythromycin (15 μg), ciprofloxacin (5 μg) and ampicillin (10 μg) and resistant to kanamycin (30 μg) and nalidixic acid (30 μg). However, amikacin (30 μg) gave a varied result with the two strains; strain S9\textsuperscript{T} was sensitive to it, whereas strain S12 showed resistance to this antibiotic. The differentiating characteristics of strain S9\textsuperscript{T} from the related species are summarized in Table 1.

Fatty acids, quinones and polar lipids of strains S9\textsuperscript{T}, S12, *B. agaradhaerens* DSM 8721\textsuperscript{T} and *B. neizhouensis* KCTC 13187\textsuperscript{T} were analysed from cells grown in alkaline nutrient
medium at 37 °C with pH 9.0 and 3% (w/v) NaCl. The strain *B. subtilis* ssp. *subtilis* MTCC 121 T was used as a reference strain in the chemotaxonomic studies. Cells were harvested by centrifugation (10,000 g for 15 min at 4 °C) on reaching a cell density of 70% of the maximum optical density (100% = 0.8 OD540) and the lyophilized pellet was used for analysis. Cellular fatty acids of all the strains were methylated, separated and identified according to the instructions for the Microbial Identification System (version 6.0; MIDI; peak identification was done based on RTSBA6 data base) (Sasser, 1990; revised-www.midi-inc.com). Fatty acid methyl ester analysis was outsourced to Zeal Biologicals, Secunderabad, India. Polar lipids were extracted from 1 g freeze-dried cells with methanol/chloroform/saline (2:1:0.8, by vol.) as described by Kates (1986) and were separated using silica gel TLC (Kieselgel 60 F254; Merck) by two-dimensional chromatography using chloroform/methanol/water (75:32:4, by vol.) in the first dimension and chloroform/methanol/acetic acid/water (86:16:15:4, by vol.) in the second dimension (modified after Tindall, 1990a, b; Oren et al., 1996). Total polar lipids profiles were detected by spraying with 5% ethanolic molybdophosphoric acid and further characterized by spraying with ninhydrin (specific for amino groups), molybdenum blue (specific for phosphates), Dragendorff’s reagent (quaternary nitrogen) or *α*-naphthol (specific for sugars) (Kates, 1972; Oren et al., 1996). Quinones of all the strains were determined by extraction with chloroform/methanol (2:1, v/v) mixture, purified by TLC and analyzed by HPLC (Tamaoka et al., 1983). The peptidoglycans of all the strains were isolated after disruption of the cells by shaking with glass beads and subsequent trypsin digestion, according to the method of Schleifer (1985). The cell wall was hydrolysed for amino acid analysis and analysed as described by Schleifer & Kandler (1972) and Hasegawa et al. (1983).

Whole-cell fatty acid analysis of strains S9 T, S12, *B. agaradhaerens* DSM 8721 T, *B. neizhouensis* KCTC 13187 T and *B. subtilis* ssp. *subtilis* MTCC 121 T revealed that anteiso-C15:0 (37.9%, 40.2%, 51.9% and 40.7%, respectively) was the predominant fatty acid present in all these cultures. However, some major differences were observed between all the other strains and *B. subtilis* ssp. *subtilis* MTCC 121 T, which included the absence of C12:0 and C14:0, low

### Table 1. Characteristics used to distinguish strains S9 T and S12 from the type strains of phylogenetically related species

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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<tr>
<td>Colony pigmentation</td>
<td>Orange</td>
<td>White</td>
<td>Pale yellow</td>
<td>Orange</td>
<td>White</td>
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<tr>
<td>Motility</td>
<td>–</td>
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<td>–</td>
<td>–</td>
<td>+</td>
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<tr>
<td>Spore shape</td>
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<td>Ellipsoidal</td>
<td>Oval</td>
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<td>Endospore position</td>
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<td>Sub-terminal</td>
<td>Sub-terminal</td>
<td>Terminal</td>
<td>Sub-terminal</td>
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<td>NaCl range (%) (w/v)</td>
<td>0.5–22</td>
<td>0–15</td>
<td>0.5–10 †</td>
<td>0–6 †</td>
<td>0–7</td>
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<tr>
<td>NaCl optimal (%) (w/v)</td>
<td>3–5</td>
<td>2–3</td>
<td>2–4 †</td>
<td>0–3 †</td>
<td>0–0.5</td>
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<tr>
<td>pH range</td>
<td>8.0–11.0</td>
<td>7.5–9.7</td>
<td>6.5–10.0 †</td>
<td>6.8–9.8 †</td>
<td>7.0–8.0</td>
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<tr>
<td>pH optimum</td>
<td>9.0</td>
<td>8.5–9.0</td>
<td>8.5 †</td>
<td>8.0–9.0 †</td>
<td>7.5</td>
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<td>Temp. range (°C)</td>
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<td>10–45</td>
<td>4–30 †</td>
<td>10–45 †</td>
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<td>Temp. optimum (°C)</td>
<td>37</td>
<td>37</td>
<td>25 †</td>
<td>27–37 †</td>
<td>35–37</td>
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<td>Anaerobic growth</td>
<td>–</td>
<td>+</td>
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<td>H₂S production</td>
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<td>Urease</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
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<tr>
<td>Citrate utilization</td>
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<td>–</td>
<td>+</td>
<td>+</td>
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<td>Nitrate reduction</td>
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<td>+</td>
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<td>Hydrolysis of:</td>
<td>DNA</td>
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<td>–</td>
<td>+</td>
<td>–</td>
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<td>Aesculin</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
<td>–</td>
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<td>Tween 20</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
<td>–</td>
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<td>DNA G+C content (mol%)</td>
<td>42.4±1</td>
<td>39.3–39.5 †</td>
<td>40.8 †</td>
<td>40.9 †</td>
<td>42.8</td>
</tr>
</tbody>
</table>

*a* Data from Chen et al. (2009).  
† Data from Subhash et al. (2014).  
‡ Data from Nielsen et al. (1995).
percentage of C16:0 and high percentages of anteiso-C17:0 and iso-C17:0 (Table S1). The major (>5%) fatty acids of the strains apart from anteiso-C15:0 were as follows: strain S9 contained C16:0 (14.9%), iso-C15:0 (9.0%), anteiso-C17:0 (6.8%), iso-C16:0 (6.7%) and summed feature 3 (C16:1ω6c and/or C16:1ω7c) (5.9%); B. agaradhaerens DSM 8721T analysis revealed iso-C15:0 (23.2%), anteiso-C17:0 (11.5%), iso-C17:0 (6.8%) and C16:0 (6.3%); B. neizhouensis KCTC 13187T analysis revealed iso-C15:0 (14.4%), C16:1ω11c (6.8%), C16:0 (6.1%) and iso-C16:0 (5.5%); whereas, B. subtilis subsp. subtilis MTCC 121T analysis revealed iso-C15:0 (18.8%), iso-C17:0 (15.4%) and anteiso-C17:0 (14.9%) (Table S1). The major polar lipids of all the strains included diphosphatidylglycerol (DPG), phosphatidylglycerol (PG) and phosphatidylethanolamine (PE). However, there was a clear differentiation of all the other strains when compared with B. subtilis subsp. subtilis MTCC 121T, by the absence of the characteristic glycolipid (Fig. S2). The major quinone of strains S9T and S12 was MK-7 (92%); MK-6 was also present (8%). Similar was the case with all the related strains except B. subtilis subsp. subtilis MTCC 121T, which only had MK-7 (100%). The proportions of MK-7:MK-6 were 96:4 and 98:2 in B. agaradhaerens DSM 8721T and B. neizhouensis KCTC 13187T, respectively. The peptidoglycan cell-wall of all the strains contained m-DAP as the diagnostic diamino acid. The respiratory quinones and peptidoglycan diamino acid of the cell wall of all the strains were typical of those found in the members of the genera Bacillus as well as the other related genera within the phylum Firmicutes (Didari et al., 2012).

In summary, several phenotypic features (Table 1) as well as phylogenetic studies separate the novel strains S9T and S12 from closely related species (B. agaradhaerens, B. neizhouensis and B. luteus). However, there is a clear consensus that the genus Bacillus sensu stricto should be restricted to species that share high 16S rRNA gene sequence similarities with the type strain, B. subtilis (Kämpfer et al., 2006; Albert et al., 2007; Didari et al., 2012); hence, strains S9T, S12, B. agaradhaerens and B. neizhouensis do not fit into the genus Bacillus and are more closely related to each other (Fig. 1). Similarly, a number of closely related members of the genus Bacillus (including B. luteus and others) also share a very low value of 16S rRNA gene sequence similarity with the type strain of the genus Bacillus, B. subtilis, and are phylogenetically different from B. subtilis as well as strains S9T, S12, B. agaradhaerens and B. neizhouensis (Fig. 1). Hence, representatives of these species require an in-depth analysis before concluding their taxonomic positions. Further, the novel strains S9T and S12 along with the related strains of B. agaradhaerens and B. neizhouensis differed remarkably in fatty acid, quinone and polar lipid compositions when compared with B. subtilis subsp. subtilis MTCC 121T, the type strain of the genus Bacillus. Therefore, on the basis of their phenotypic, chemotaxonomic and genotypic distinctiveness, strains S9T and S12 represent a new member of the family Bacillaceae for which, the name Salipaludibacillus aurantiacus is proposed. A reclassification of the related species B. agaradhaerens and B. neizhouensis as Salipaludibacillus agaradhaerens comb. nov. and Salipaludibacillus neizhouensis comb. nov., respectively, is also proposed based upon the present studies.

**Description of Salipaludibacillus gen. nov.**

Salipaludibacillus (Sa.li.pal.lu.di.ba.ci.lus. L. n. sal salis salt; L. n. palus paludis a swamp; L. masc. n. bacillus a rod; N.L. masc. n. Salipaludibacillus a rod from a salt marsh).

Cells are non-motile, rod shaped, Gram-stain-positive and form oval or ellipsoidal endospores at the sub-terminal position. Aerobic or facultatively anaerobic. Positive for catalase and oxidase activities. Nitrate reduction is variable. The major isoprenoid quinone is MK-7 with minor traces of MK-6. The peptidoglycan is based on m-DAP as the diagnostic diamino acid. The major polar lipids present are DPG, PG and PE. Major fatty acids are anteiso-C15:0, C16:0 and iso-C15:0. Phylogenetically, belongs to the family Bacillaceae. The DNA G+C content is 39.3–42.4 mol%. The type species is Salipaludibacillus aurantiacus.

**Description of Salipaludibacillus aurantiacus sp. nov.**

Salipaludibacillus aurantiacus (au.ran.ti.a’cus. N.L. masc. adj. aurantiacus orange-coloured, referring to the orange colour of the colonies).

In addition to the characteristics described above in the genus description, cells are 0.3–0.9 µm diameter and 1.7–2.2 µm length and form sub-terminal endospores, which are ellipsoidal in shape, in non-swollen sporangia. Fermentative growth is absent. Negative for nitrate and nitrite reduction and gelatin liquefaction. Optimal growth occurs after 48 h of incubation on alkaline nutrient agar at 37°C (range 20–45°C). Growth occurs between pH 8.0 and pH 11.0 (optimum pH 9.0). A minimal amount of NaCl (0.5%) is essential for growth; optimal growth occurs at 3–5% and cells can tolerate up to 22% NaCl. Casein, tyrosine, cellulose, starch, aerosol, hippurate, Tween 20 and DNA are not hydrolysed. Xanthine and hypoxanthine are hydrolysed. Lipase activity is negative, but urease activity is positive. Indole production from tryptophan, the methyl red test and citrate utilization are negative, but H2S is produced and the Voges–Proskauer test is positive. Growth as sole carbon and energy is supported by maltose, raffinose, fructose, D-arabinose, melibiose, mannose, D-glucose, cellobiose, D-xyllose, D-galactose, D-mannitol and sucrose, but, they do not yield either gas or acid. Inulin, inositol, trehalose, D-sorbitol and salicin do not support growth as a sole carbon source. The utilization of lactose and rhamnose as sole carbon and energy source is variable. Ammonium chloride and urea are the most suitable nitrogen sources, but, no growth is observed with nitrate, nitrite, glutamate or aspartate.
Type strain is S9T (=KCTC 33633T =LMG 28644T). The DNA G+C content of the type strain is 42.4±2 mol%. An additional strain (S12) with DNA G+C content of 42.5±1 mol% was also isolated in this study.

Description of Salipaludibacillus agaradhaerens comb. nov.

Salipaludibacillus agaradhaerens (a.gar.ad.hae’rens. Malayan n. agar gelling polysaccharide from brown algae; L. part. adj. adhaerens adherent; N.L. part. adj. agaradhaerens adhering to agar).


The description is identical to that given for Bacillus agaradhaerens by Nielsen et al. (1995). In addition, major fatty acids (>5%) include anteiso-C15:0, iso-C15:0, anteiso-C17:0, iso-C17:0 and C16:0. Major polar lipids include DPG, PG, PE and a phospholipid (PL1). Major quinone is MK-7. The peptidoglycan cell-wall contains m-DAP acid.

The type strain is PN-105T (=ATCC 700163T =DSM 17948T =DSM 8721T).
Syst Evol Microbiol

structure of murein.


Evol Microbiol


