Alcanivorax xenomutans sp. nov., a hydrocarbonoclastic bacterium isolated from a shrimp cultivation pond

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Two bacterial strains (JC109T and JC261) were isolated from a sediment sample collected from a shrimp cultivation pond in Tamil Nadu (India). Cells were Gram-stain-negative, motile rods. Both strains were positive for catalase and oxidase, hydrolysed Tween 80, and grew chemoorganoheterotrophically with an optimal pH of 6 (range pH 4–9) and at 30 °C (range 25–40 °C). Based on 16S rRNA gene sequence analysis, strains JC109T and JC261 were identified as belonging to the genus Alcanivorax with Alcanivorax dieseleoli B-5T (sequence similarity values of 99.3 and 99.7 %, respectively) and Alcanivorax balearicus MACLO4T (sequence similarity values of 98.8 and 99.2 %, respectively) as their closest phylogenetic neighbours. The 16S rRNA gene sequence similarity between strains JC109T and JC261 was 99.6 %, respectively. The level of DNA–DNA relatedness between the two strains was 88 %. Strain JC109T showed 31 ± 1 and 26 ± 2 % DNA–DNA relatedness with A. dieseleoli DSM 16502T and A. balearicus DSM 23776T, respectively. The DNA G + C content of strains JC109T and JC261 was 54.5 and 53.4 mol %, respectively. Polar lipids of strain JC109T included diphosphatidylglycerol, phosphatidylglycerol, phosphatidylethanolamine, two unidentified aminophospholipids, two unidentified phospholipids and two unidentified lipids. The major fatty acids were C10 : 0, C12 : 0, C16 : 0, C12 : 0 3-OH, C16:1ω7c, C18:1ω7c and C19:0 cyclo ω8c. Both strains could utilize diesel oil and a variety of xenobiotics as carbon and energy sources. The results of physiological, biochemical, chemotaxonomic and molecular analyses allowed the clear differentiation of strains JC109T and JC261 from all other members of the genus Alcanivorax. Strains JC109T and JC261 are thus considered to represent a novel species, for which the name Alcanivorax xenomutans sp. nov. is proposed. The type strain is JC109T (=KCTC 23751T=NBRC 108843T).

Abbreviations: DPG, diphosphatidylglycerol; ME, minimum-evolution; ML, maximum-likelihood; NJ, neighbour-joining; PE, phosphatidylethanolamine; PG, phosphatidylglycerol.

The GenBank/EMBL/DBJ accession numbers for the 16S rRNA gene sequences of strains JC109T and JC261 are HE601937 and HG974551, respectively.

One supplementary table and two supplementary figures are available with the online version of this paper.
Alcanivorax are Gram-stain-negative, aerobic, motile or non-motile rods, chemo-organotrophic, tolerate high salt concentrations and can thrive in the presence of hydrocarbons (Harayama et al., 2004; Lai et al., 2013). The DNA G+C content of members of the genus ranges from 53 to 66 mol%. They are also characterized by the presence of C16:0, C18:1ω7c and C16:1ω7c as predominant cellular fatty acids (Fernández-Martínez et al., 2003; Lai et al., 2013). Polar lipid profiles of the genus Alcanivorax have not been extensively studied. However, strain JC109T, A. dieselolei DSM 16502T, A. balearicus DSM 23776T, A. borkumensis CIP 105606T and A. marinus R8-12T (Lai et al., 2013) contained diphosphatidyglycerol (DPG), phosphatidylglycerol (PG), phosphatidylethanolamine (PE), unidentified phospholipids, unidentified aminolipids and unidentified lipids.

Strains JC109T and JC261 were isolated from a sediment sample collected from a shrimp cultivation pond in Ramnad, Tamil Nadu, India (9°16′ N 79° 6′ E) during September 2011. Physicochemical parameters including temperature, salinity and pH of the sample were analysed immediately after sample collection. The temperature at the site of sample collection was 29 °C. Salinity and pH of the sample were 2.8% (w/v) and pH 8. One gram of air-dried sediment was serially diluted up to 10⁻⁴ and 100 µl was spread on a growth medium (pH 7.5) containing (per litre): 0.2 g KH₂PO₄, 0.25 g NH₄Cl, 0.5 g KCl, 0.15 g CaCl₂, 2H₂O, 20.0 g NaCl, 0.62 g MgCl₂.6H₂O, 2.84 g Na₂SO₄, 2.83 g HEPES, 3.0 g yeast extract, 3.0 g peptone, 0.5 g Casamino acids, 0.5 g glucose and 3.0 g sodium pyruvate. Purification of the bacteria was achieved by repeated streaking on nutrient agar (HiMedia) containing 2% (w/v) NaCl. Strains JC109T and JC261 were preserved as glycerol stocks and by lyophilization. Unless otherwise mentioned, both strains were grown in nutrient broth or on nutrient agar (HiMedia) supplemented with 1% sodium pyruvate (pH 7.6 at 28 °C) and A. balearicus DSM 23776T was grown in nutrient broth or on nutrient agar with 1.5% (w/v) NaCl (pH 7.2 at 28 °C) as recommended by the culture collection.

Genomic DNA was extracted and purified from strains JC109T and JC261 according to the method of Marmur (1961) and the G+C of the DNA was 54.5 and 53.4 mol%, respectively, as determined by HPLC (Mesbah et al., 1989). Cell material for 16S rRNA gene sequencing was taken from a colony. DNA was extracted and purified by using a QiaGen genomic DNA extraction kit. Recombinant Taq polymerase (Genei) was used for PCR. The almost-complete sequence of the 16S rRNA gene was obtained by sequencing with primers F27 (5′-GTTTGATCCTGGCTCAG-3′) and R1489 (5′-TACCTTGTACGACTTAC-3′) [positions 11–27 and 1489–1506, respectively, according to the Escherichia coli 16S rRNA numbering system of the International Union of Biochemistry (Brosius et al., 1978; Lane et al., 1985)]. PCR amplification was done as described by Imhoff et al. (1998) and Imhoff & Pfennig (2001). 16S rRNA gene sequencing was performed using the BigDye Terminator v1.1 Sequencing kit (Applied Biosystems) in a 3730-DNA-Analysier (Applied Biosystems) as specified by the manufacturer. For sequencing, the primers F27, F790 (5′-GATACCCTGGTATGCTCC-3′) and R1489 were used. Identification of phylogenetic neighbours and calculation of pairwise 16S rRNA gene sequence similarity were achieved using the EzTaxon-e server (Kim et al., 2012). The CLUSTAL W algorithm of MEGA 5.2 was used for sequence alignments and MEGA 5.2 (Tamura et al., 2011) software was used for phylogenetic analysis of the individual sequences. Distances were calculated by using the Kimura correction in a pairwise deletion manner (Kimura, 1980). Neighbour-joining (NJ), maximum-likelihood (ML) and minimum-evolution (ME) methods in the MEGA 5.2 software were used to reconstruct phylogenetic trees. Percentage support values were obtained using a bootstrap procedure based on 1000 replications.

The results of phylogenetic analysis of the 16S rRNA gene sequences (1416 bp for strain JC109T and 1409 bp for strain JC261) suggested that strains JC109T and JC261 formed a clade that is positioned distinctly outside the clades formed by the next most closely related species of the genus Alcanivorax in the family Alcanivoraceae (Fig. 1; nodes that were obtained by all treeing methods are represented by filled circles and open circles represent nodes that were recovered by the NJ and ME methods) and sequence similarities with the nearest phylogenetic members were in agreement with the EzTaxon-e server result. EzTaxon-e server search analysis revealed that strains JC109T and JC261 were related most closely to members of the genus Alcanivorax, and highest sequence similarity was observed with A. dieselolei B-5T (99.3 and 99.7%, respectively), A. balearicus MACL04T (98.8 and 99.2%, respectively) and other members of the genus Alcanivorax (<95%). The 16S rRNA gene sequence similarity between strains JC109T and JC261 was 99.6%.

The taxonomic relationship between strains JC109T, JC261, A. dieselolei DSM 16502T and A. balearicus DSM 23776T was examined using DNA–DNA hybridization studies. Genomic relatedness was determined by the membrane filter technique (Seldin & Dubnau, 1985; Tourova & Antonov, 1988) using a DIG High Prime DNA labelling and Detection Starter kit II (Roche). Hybridization was performed with three replications for each sample (control: reversal of strains was used for binding and labelling), and the results are presented as means ± SD. The DNA–DNA reassociation value between strains JC109T and JC261 was 88%, while the level of relatedness between strain JC109T and A. dieselolei DSM 16502T and A. balearicus DSM 23776T was only 31 ± 2 and 26 ± 2% (based on DNA–DNA hybridization), respectively; these hybridization values are within the recommended standards to delineate a bacterial species (Stackebrandt & Goebel, 1994).

Cells of strains JC109T, JC261, A. dieselolei DSM 16502T, A. balearicus DSM 23776T and A. borkumensis CIP 105606T...
Alcanivorax xenomutans sp. nov.

Alcanivorax venustensis ISO4T (AF328762)
Alcanivorax marinus R8-12T (KC415169)
Alcanivorax pacificus W11-5T (DQ659451)
Alcanivorax hongdengensis A-11-3T (EU438901)
Alcanivorax borkumensis SK2T (AM286690)
Alcanivorax jadensis T9T (AJ001150)
Alcanivorax xenomutans JC109T (HE601937)
Alcanivorax xenomutans JC261 (HG974551)
Alcanivorax dieselolei B-5T (AY683537)
Halomonas ventosae A12T (AY268080)
Marinobacter zhejiangensis CN74T (EU293413)
Haella chejuensis KCTC 2396T (CP000155)
Microbulbifer thermotolerans JAMB A94T (AB124836)
'Marinimicrobium haloxylanilyticum' SX15 (GQ920839)
'Gilviminus agarilicus' M5c (GQ872424)
Azotobacter beijerinckii ATCC 19360T (AJ308319)
Pseudomonas segetis FR1439T (AY770691)
Rhodospirillum sulfurexigenes JA143T (AM710622)

Fig. 1. Phylogenetic tree based on 16S rRNA gene sequences showing the relationship of strains JC109T and JC261 within the family Alcanivoracaceae. The tree was reconstructed by the NJ method using the MEGA 5.2 software and rooted by using Rhodospirillum sulfurexigenes JA143T as the outgroup. Numbers at nodes are the percentage of bootstrap support (based on 1000 resamplings). GenBank accession numbers for 16S rRNA gene sequences are shown in parentheses. Bar, 2 nucleotide substitutions per 100 nt. Filled circles indicate that the corresponding nodes were obtained by all treeing methods (NJ, ME and ML). Open circles indicate that the corresponding nodes were obtained by the NJ and ME methods.

(representing the type species of the genus *Alcanivorax*) were grown in 250 ml conical flasks containing 100 ml mineral salts medium [consisting of (per litre): 0.5 g KH₂PO₄, 0.2 g MgSO₄.7H₂O, 20.0 g NaCl, 0.6 g NH₄Cl, 0.05 g CaCl₂.2H₂O and 5 ml of ferric citrate solution (0.1 %, w/v)] with pyruvate (22 mM) as carbon source at 28 °C under shaking at 100 r.p.m. 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 and the pellet was used for fatty acid and polar lipid analysis. Cellular fatty acids were methylated, separated and identified according to the instructions for the Microbial Identification System [Microbial ID; MIDI 6.0 version; Agilent: 6850; peak identification was done based on the RTSBA6 database (Sasser, 1990); http://www.midi-inc.com/] which was outsourced to Royal Research Laboratories, Secunderabad, India. Whole-cell fatty acid analysis of strain JC109T revealed that C₁₀:₀, C₁₂:₀, C₁₆:₀, C₁₂:₀ 3-OH, C₁₆:₁ω7c, C₁₈:₁ω7c and C₁₉:₀ cyclo ω8c were the major fatty acids with minor amounts of C₁₄:₀, C₁₂:₀ 2-OH and C₁₇:₀ cyclo (Table S1, available in the online Supplementary Material). The fatty acid profile of strain JC261 was qualitatively identical to that of strain JC109T. Strains JC109T and JC261 shared the presence of major fatty acids with the closely related type strains of *A. dieselolei* and *A. balearicus*. However, significant differences in the relative amounts of C₁₈:₁ω7c were found between strains JC109T and JC261 and the type strains of *A. dieselolei* and *A. balearicus*.

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). The lipids were separated using silica gel TLC (Kieselgel 60 F254; Merck) by two-dimensional chromatography using chloroform/methanol/water (65 : 25 : 4, by vol.) in the first dimension and chloroform/methanol/acetic acid/water (80 : 12 : 15 : 4, by vol.) in the second dimension (Tindall et al., 1987; Tindall, 1990; Oren et al., 1996). Total polar lipids 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 reagent (quaternary nitrogen) or α-naphthol (specific for sugars) (Kates, 1972; Oren et al., 1996). Polar lipids of strain JC109T included DPG, PG, PE, two unknown
aminophospholipids (APL1, APL2), two unknown phospholipids (PL1, PL2) and two unknown lipids (L2, L3) (Fig. S1a). The polar lipid profile of strain JC109T was similar to that of the type species of the genus *Alcanivorax*, *A. borkumensis* CIP 105606T, which contained DPG, PG and PE as major compounds along with minor amounts of PL2, L1 and L3 (Fig. S1d). Differences were the presence of APL1, APL2, PL1 and L2 in strain JC109T and the absence of L1. Polar lipids of strain JC109T differ from those of *A. dieselolei* DSM 16502T in the presence of APL1, APL2 and L2 (Fig. S1b). Polar lipids of strain JC109T also differ from *A. balearicus* DSM 23776T in the presence of APL2 (Fig. S1c).

Colonies of strains JC109T and JC261 grown on nutrient agar (HiMedia) were creamish white, circular and convex with entire margin. Morphological properties such as cell shape, cell size and motility were observed by phase-contrast light microscopy (Olympus BH-2). Cells of strain JC109T were rod-shaped (1.8 × 0.3 μm), motile and divided by binary fission. For scanning electron microscopy, cells were prepared by fixing with 2% (v/v) glutaraldehyde and 1% (w/v) osmium tetroxide (OsO₄) as previously described (Priefer et al., 2007). The dry specimen was mounted on a specimen stub and fixed using an electrically conductive double-sided adhesive carbon tape and sputter-coated with gold/palladium alloy before examination in the field emission scanning electron microscope (Zeiss Ultra 55). Cells of strain JC109T were rod-shaped and showed pilus formation (Fig. S2). Cells of strain JC109T were larger than those of *A. dieselolei* DSM 16502T and *A. balearicus* DSM 23776T.

The pH range for growth was tested using nutrient broth, adjusted to different pH values (pH 4.0–11.0, intervals of 0.5 units) by using the appropriate biological buffers as described by Xu et al. (2005). The buffer systems used were: pH 4.0–5.0, 0.1 M citric acid/0.1 M sodium citrate; pH 6.0–8.0, 0.1 M KH₂PO₄/0.1 M NaOH; pH 9.0–10.0, 0.1 M NaHCO₃/0.1 M Na₂CO₃; pH 11.0, 0.05 M Na₂HPO₄/0.1 M NaOH. Final pH was determined by using a pH indicator (Fisher Scientific).

NaCl [0.5–22% (w/v) at 0.5% intervals] and temperature (4, 10, 15, 25, 30, 37, 40 and 45 °C) ranges for growth were examined in nutrient broth and growth was measured turbidimetrically at 540 nm in a colorimeter (Systronic). Strains JC109T and JC261 grew at a pH range of 4–9 with optimum at pH 6 and differed from *A. dieselolei* DSM 16502T and *A. balearicus* DSM 23776T which have a pH range of 6–9. NaCl was required for growth of the two strains and they were able to tolerate up to 20% (w/v), while *A. borkumensis* CIP 105606T, *A. dieselolei* DSM 16502T and *A. balearicus* DSM 23776T are less tolerant (Table 1). The temperature range for growth further differentiated strains JC109T and JC261 from their closest phylogenetic neighbours (Table 1).

Various biochemical tests [on specified media containing 2% (w/v) NaCl] such as hydrolysis of starch, casein, gelatin and Tween 80, oxidase, catalase and urease, nitrate reduction, nitrite reduction, H₂S production, acid production from carbohydrates, and methyl red and Voges–Proskauer tests were performed by the procedures as outlined by Cappuccino & Sherman (1999). Arginine dihydrolase, phenylalanine deaminase, ornithine decarboxylase and lysine decarboxylase activities were absent. Negative for acid production from D-glucose, mannose, malic acid, arabinose, cellobiose and salicine. Glutamate, glutamine, methionine, aspartate, peptone, Casamino acids and urea could not be used as sole source of carbon, nitrogen and energy. +, Positive; W, weakly positive; −, negative.

### Table 1. Differential characteristics between strains JC109T and JC261 and their closest phylogenetic neighbours in the genus *Alcanivorax*

<table>
<thead>
<tr>
<th>Characteristic</th>
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<th>3</th>
<th>4</th>
<th>5</th>
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<tr>
<td>Motility</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
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<tr>
<td>Temperature range (°C)</td>
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<td>25–40</td>
<td>15–45</td>
<td>4–37</td>
<td>4–37</td>
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<tr>
<td>NaCl range for growth (%), (w/v)</td>
<td>0.5–20</td>
<td>0.5–20</td>
<td>1–15</td>
<td>0–15</td>
<td>1.0–15</td>
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<td>Na⁺ requirement</td>
<td>+</td>
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<td>+</td>
<td>−</td>
<td>+</td>
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<tr>
<td>Hydrolysis of Tween 80</td>
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<td>+</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>Utilization of compounds as sole source of carbon and energy</td>
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<tr>
<td>L-Arabinose</td>
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<td>−</td>
<td>w</td>
<td>−</td>
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<td>w</td>
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<tr>
<td>DNA G+C content (mol%)</td>
<td>54.5</td>
<td>55.3</td>
<td>62.1</td>
<td>62.8</td>
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</table>

*Data for strains 3, 4 and 5 were from Liu & Shao (2005), Rivas et al. (2007) and Yakimov et al. (1998), respectively.*
carbon compounds as carbon and energy source for organoheterotrophic growth was also tested in a mineral medium as previously described (Lakshmi et al., 2011) containing specific organic compounds (0.35%, w/v or v/v) replacing sodium pyruvate. Growth was measured turbidometrically (OD540) after 48 h. Nitrogen source utilization was tested by replacing ammonium chloride with different nitrogen sources (NaNO3, NaNO2, glutamate, aspartate, glutamine and urea). Utilization of glutamate, glutamine, methionine, aspartate, peptone, Casamino acids and urea as sole source of carbon, nitrogen and energy was also determined. The results are given in the species description and Table 1. Strains JC109T, JC261, A. borkumensis CIP 105606T and A. dieseloel DSM 16502T all grew well in a minimal medium containing diesel oil, octane or xylene as sole source of carbon and energy. In addition, strains JC109T and JC261 grew in the presence of hexane, benzene and toluene as sole source of carbon, while nitrogendated (nitrobenzene, nitrobenzoic acid) and halogenated aromatic hydrocarbons (chlorobenzene, 2,4-dichlorophenoxy acetic acid) did not support growth. None of the compounds tested above supported the growth of A. balearicus DSM 23776T.

Strains JC109T and JC261 showed phenotypic and genotypic distinctiveness from their closest phylogenetic neighbours, A. dieseloel DSM 16502T, A. balearicus DSM 23776T and other members of the genus Alcanivorax (Table 1) and hence they are considered to represent a novel species of the genus Alcanivorax, for which we propose the name Alcanivorax xenomutans sp. nov.

Description of Alcanivorax xenomutans sp. nov.

Alcanivorax xenomutans [xe.no.mu’tans. Gr. adj. xenos foreign; L. part. adj. mutans transforming, converting; N.L. part. adj. xenomutans transforming foreign (xenobiotic) compounds].

Cells are short rods, 1.8 × 0.3 μm, motile, non-endospore-forming and Gram-stain-negative. Forms bright creamish-white colonies on nutrient agar. Hydrolyses Tween 80; oxidase activity is weak at 2% but positive at 5% NaCl concentration; catalase-positive. Hydrolysis of casein, gelatin, aesculin and starch are negative. Nitrate and nitrite concentration; catalase-positive. Hydrolysis of casein, gelatin, aesculin and starch are negative. Nitrate and nitrite are negative. Acid is not produced from D-glucose, mannose, galactose, arabinose, cellobiose or salicin. Facultatively anaerobic. Chemo-organoheterotrophic is the only growth mode. Temperature range for growth is 25–40 °C (optimum 30 °C). Growth occurs with 0.5–20% (w/v) NaCl (optimum 2–5%) and at pH 4–9 (optimum pH 6). Able to degrade diesel oil and other hydrocarbons. Oxidizes cis-aconitic acid, methyl pyruvate, monomethyl succinate, sebacic acid, γ-hydroxybutyric acid, β-hydroxybutyric acid, 2,3-butanediol, Tween 40 and Tween 80. Can grow using sucrose, mannitol, citrate, adipate, malate, valerate, arabinose, thioglycolate and phenylacetate as sole carbon and energy source. Glycerol, proline, ethanol, glucose and lactate are not used as sole source of carbon and energy. Ammonium chloride is used as sole nitrogen source; cannot use glutamine or glutamate as sole source of carbon, nitrogen and energy. The polar lipid profile includes DPG, PG, PE, aminophospholipids, two unknown phospholipids and two unknown lipids. Major fatty acids include C10:0, C12:0, C16:0, C12:0 3-OH, C16:1ω7c, C18:1ω7c and C19:0 cyclo ω8c. Minor amounts of C14:0, C12:0 2-OH and C17:0 cyclo are present.

The type strain is JC109T (=KCTC 23751T=NBRC 108843T), which was isolated from a sediment sample of a shrimp cultivation pond, Ramnad, Tamil Nadu, India. JC261, isolated from the same pond, is a second strain of the species. The DNA G+C content of the type strain is 54.5 mol% and of strain JC261 is 53.4 mol%.

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References


