Polycyclic aromatic hydrocarbons (PAHs), including naphthalene, biphenyl, phenanthrene and pyrene, cause serious environmental concerns because of their persistence, resistance to biodegradation, toxicity, mutagenicity and carcinogenicity (Haeseler et al., 1999). PAH-degrading bacteria that play important roles in PAH biodegradation have been isolated mainly from terrestrial habitats, but they have increasingly been isolated from marine habitats (Collins et al., 1998; Geiselbrecht et al., 1998; Hedlund et al., 1999; Jeon et al., 2003; Sohn et al., 2004; Jin et al., 2012).

The genus *Alteromonas* Baumann et al. 1972 contains phylogenetically and phenotypically diverse, Gram-negative, marine bacteria that are heterotrophic, motile rods with a single polar flagellum. Members of genus *Alteromonas* are distributed globally in marine environments, copiotrophic and *r*-strategists that dominate heterotrophic blooms (Acinas et al., 1999; García-Martínez et al., 2002; López-López et al., 2005; Vandecandelaere et al., 2008). Currently, the genus *Alteromonas* includes 13 species, although a number of additional species have been transferred to other genera (Parte, 2014; Matsuyma et al., 2015). Previous studies showed that some members of the genus are probably responsible for hydrocarbon biodegradation, including PAH compounds, in marine environments contaminated by crude oil spills (Cui et al., 2008; Jin et al., 2012; Gutierrez et al., 2013). Tidal flats consist of coastal muddy sediment that is exposed to air and flooding by seawater, and may play an important role in the bioremediation of marine environments (Math et al., 2012; Jin et al., 2013, 2015; Lo et al., 2014). In this study, a novel PAH-degrading bacterium, strain SN2<sup>T</sup>, belonging to the genus *Alteromonas* was isolated from tidal-flat sediment contaminated with crude oil and its taxonomic properties were characterized using a polyphasic approach.

A tidal-flat sediment sample was obtained from the Taean coastal area of South Korea (36°48’50.82”N 126°11’09.56”E) and strain SN2<sup>T</sup>, capable of PAH biodegradation, was isolated according to previously described procedures (Jin et al., 2012). Strain SN2<sup>T</sup> was routinely cultivated and grown in nutrient broth (Difco Laboratories, Detroit, MI, USA) supplemented with 5% (w/v) crude oil. Strain SN2<sup>T</sup> was further identified using the GenBank/EMBL/DDBJ accession number of 16S rRNA gene sequence of strain SN2<sup>T</sup> is GU166736. Two supplementary figures and two supplementary tables are available with the online Supplementary Material.
aerobically on marine agar 2216 (MA; BD) at 30 °C for 36 h, except where indicated, and stored at −80 °C in marine broth 2216 (MB; BD) supplemented with 15 % (v/v) glycerol for extended preservation. *Alteromonas stellipolaris* DSM 15691<sup>T</sup>, *A. addita* KCTC 12195<sup>T</sup>, *A. macleodii* LMG 2843<sup>T</sup>, *A. marina* KCCM 41638<sup>T</sup> and *A. hispanica* LMG 22958<sup>T</sup> were selected on the basis of 16S rRNA gene sequence similarities and phylogenetic relatedness and used as reference strains for comparisons of phenotypic properties and fatty acid compositions. In addition, *Alteromonas halophila* KCTC 22164<sup>T</sup>, *A. genovensis* DSM 23844<sup>T</sup>, *A. litorea* JCM 12188<sup>T</sup>, *A. tagae* JCM 13895<sup>T</sup> and *A. mediterranea* DSM 17117<sup>T</sup> were used for matrix-assisted laser desorption ionization time-of-flight mass spectrometry (MALDI-TOF MS) analysis.

The complete 16S rRNA gene sequence (1540 nt) of strain SN2<sup>T</sup> was obtained from the whole-genome sequence of strain SN2<sup>T</sup> available in GenBank (Jin et al., 2011) and similarities to sequences of type strains of all validly named species were evaluated using the Nucleotide Similarity Search program in the EzTaxon-e server (Kim et al., 2012). The 16S rRNA gene sequences of strain SN2<sup>T</sup> and closely related type strains were aligned using the fast secondary-structure-aware Infernal aligner available from the Ribosomal Database Project (Nawrocki & Eddy, 2007). Phylogenetic trees based on the neighbour-joining (NJ) and maximum-parsimony algorithms were reconstructed using the PHYLIP software (version 3.695; Felsenstein, 2002) and their topologies were evaluated through a bootstrap analysis based on 1000 resamplings. Maximum-likelihood analysis with bootstrap values was conducted using RAxML-HPC BlackBox (version 8.1.11) from the Cyber-Infrastructure for Phylogenetic Research project (http://www.phyl.org; Stamatakis et al., 2005). Sequence information for the *dnaK*, *sucC*, *rpoB*, *gyrB* and *rpoD* genes of strain SN2<sup>T</sup> and type strains of other species of the genus *Alteromonas* was obtained from GenBank for multilocus phylogenetic analysis (MLPA). A phylogenetic tree was reconstructed using the *neigh*bor module of PROTDIST, available in the PHYLIP software, based on the concatenated sequences of these five genes (~3350 bp). MALDI-TOF MS analysis of strain SN2<sup>T</sup> and other members of the genus *Alteromonas* was carried out according to previously described procedures (Ng et al., 2013; Ivanova et al., 2015). A dendrogram based on the MALDI-TOF MS results was reconstructed using the MALDI Biotyper version 3.0 software package (Bruker Daltonik).

Comparative analysis based on the 16S rRNA gene sequences revealed that strain SN2<sup>T</sup> was most closely related to *A. stellipolaris* LMG 21861<sup>T</sup>, *A. addita* R105W13<sup>T</sup> and *A. macleodii* ATCC 27126<sup>T</sup>, with 99.5, 99.3 and 98.4 % sequence similarity, respectively. Phylogenetic analysis based on the NJ algorithm showed that strain SN2<sup>T</sup> forms a phylogenetic lineage with *A. stellipolaris* LMG 21861<sup>T</sup> and *A. addita* R105W13<sup>T</sup> with a bootstrap value of 100 % (Fig. 1). Phylogenetic analyses based on the maximum-parsimony and maximum-likelihood algorithms also confirmed that strain SN2<sup>T</sup> forms a phylogenetic lineage within the genus *Alteromonas*. MLPA using five housekeeping genes (*dnaK*, *sucC*, *rpoB*, *gyrB* and *rpoD*) also demonstrated that strain SN2<sup>T</sup> forms a phylogenetic lineage with *A. stellipolaris* LMG 21861<sup>T</sup> and *A. addita* R105W13<sup>T</sup> with a bootstrap value of 100 % (Fig. 2). Sequence similarities of the concatenated sequences of the five housekeeping genes between strain SN2<sup>T</sup> and type strains of other species of the genus *Alteromonas* were less than 95.0 %, which is below the recommended threshold of 98.9 % for the genus *Alteromonas* (Ng et al., 2013). To support the taxonomic affiliation of strain SN2<sup>T</sup> further, a MALDI-TOF MS analysis was performed. The dendrogram based on the MALDI-TOF MS results confirmed that strain SN2<sup>T</sup> was closely related to *A. stellipolaris* LMG 21861<sup>T</sup> and *A. addita* R105W13<sup>T</sup> (Fig. 3), which is consistent with the topologies of phylogenetic trees based on the 16S rRNA gene and MLPA.

It has been suggested that between 98.65 and 98.7 % 16S rRNA gene sequence similarity may qualify in bacterial classification as a threshold for performing DNA–DNA hybridization (Stackebrandt & Ebers, 2006; Kim et al., 2014). Therefore, the type strains of only three species of *Alteromonas*, *A. stellipolaris*, *A. addita* and *A. macleodii*, showing more than 98.4 % sequence similarity, were selected for evaluation of DNA–DNA relatedness to strain SN2<sup>T</sup>, although the type strains of many other species of the genus *Alteromonas* displayed >97 % 16S rRNA gene sequence similarity. DNA–DNA hybridization was carried out reciprocally in triplicate using the DIG High Prime DNA Labelling kit (Roche Applied Science) according to previously described procedures (Lee et al., 2011). Hybridization signals were analysed using Adobe Photoshop CS6 (version 13.0; Adobe Systems). Hybridization signals produced by the hybridization of the probes to the homologous target DNA were evaluated at 100 %, and signal intensities derived from self-hybridizations of serial dilutions were used as a standard for the calculation of DNA–DNA relatedness. The DNA–DNA relatedness between strain SN2<sup>T</sup> and *A. stellipolaris* DSM 15691<sup>T</sup>, *A. addita* KCTC 12195<sup>T</sup> and *A. macleodii* LMG 2843<sup>T</sup> was 48.7 ± 6.6, 24.9 ± 7.5 and 27.9 ± 8.4 %, respectively, clearly below the 70 % threshold generally accepted for species delineation (Stackebrandt et al., 2002).

Growth of strain SN2<sup>T</sup> was assessed at 30 °C for 3 days on MA, R2A agar (BD), laboratory-prepared Luria–Bertani (LB) agar, nutrient agar (NA; BD) and tryptic soy agar (TSA; BD), which were supplemented with NaCl at approximately 2 % (w/v) final NaCl concentration. Growth of strain SN2<sup>T</sup> was tested in MB at 0, 4, 10, 15, 20, 25, 30, 35, 40 and 45 °C and pH 5.0–11.0 (at intervals of 0.5 pH units) for 3 days. MB below pH 8.0 and at pH 8.0–11.0 was prepared using Na<sub>2</sub>HPO<sub>4</sub>/NaH<sub>2</sub>PO<sub>4</sub> and Tris/HCl buffers, respectively (Gomori, 1955), and the pH was adjusted again, if necessary, after sterilization (121 °C for 15 min). Growth in the absence of NaCl and in the presence of 0.5 % and 1–15 % (w/v) NaCl
(at intervals of 1%) was assessed in MB, which was prepared in the laboratory according to the BD formula except that NaCl was omitted. Gram staining was tested using the bioMérieux Gram Stain kit according to the manufacturer’s instructions. Cell morphology and motility of strain SN2T were investigated using transmission electron microscopy (JEM-1010; JEOL) and phase-contrast microscopy with cells grown on MA at 30°C for 36 h.

Nitrate reduction was evaluated based on the method described by Lányi (1987). Catalase and oxidase activities of strain SN2T were tested based on the production of oxygen bubbles in 3% (v/v) aqueous hydrogen peroxide solution and the oxidation of 1% (w/v) tetramethyl p-phenylenediamine (Merck), respectively (Smibert & Krieg, 1994). Anaerobic growth was assessed on MA and MA containing nitrate (0.2% NaNO₃) or nitrite (0.2% KNO₂) at 30°C for 20 days under anaerobic conditions (with 4–10% CO₂) using the BBL GasPak Plus System (BD).

The following properties of strain SN2T and the reference strains were investigated in parallel under the same conditions at 30°C: (i) naphthalene degradation was evaluated in serum bottles containing naphthalene and seawater as

**Fig. 1.** NJ tree based on 16S rRNA gene sequences showing phylogenetic relationships between strain SN2T and related taxa. Bootstrap values >70% are shown at nodes as percentages of 1000 replicates. Filled circles indicate that the corresponding nodes were also recovered in trees generated using the maximum-likelihood and maximum-parsimony algorithms. *Lonsdalea quercina* subsp. *iberica* LMG 26264T (GenBank accession no. JF311441) was used as an outgroup (not shown). Bar, 0.01 changes per nucleotide position.

**Fig. 2.** MLPA showing the phylogenetic position of strain SN2T based on concatenated sequences of five housekeeping genes (*dnaK, sucC, rpoB, gyrB* and *rpoD*). Numbers at branching points are percentage bootstrap values >70% based on 1000 replications. Bar, 0.01 substitutions per nucleotide position.
Cells of strain SN2T were Gram-staining-negative in 2 % NaCl, but did not grow on NA containing 2 % NaCl. Characteristics of strain SN2T are presented in the species description (Jin et al., 2012); (ii) hydrolysis of Tweens 20 and 80, casein, starch, tyrosine and agar was checked on MA according to previously described methods (Lanyi, 1987; Smibert & Krieg, 1994); and (iii) additional enzymic activities, biochemical features and oxidation of carbon sources were tested using the API ZYM and API 20NE kits (bioMérieux) and the GN2 MicroPlate System (Biologa) according to the manufacturers’ instructions, with the exception that cells resuspended in artificial seawater (20 g NaCl, 2.9 g MgSO4, 4.53 g MgCl2.6 H2O, 0.64 g KCl and 1.75 g CaCl2.2H2O per litre) were used as the inocula.

Strain SN2T grew well on MA, TSA and R2A agar containing 2 % NaCl, but did not grow on NA containing 2 % NaCl. Cells of strain SN2T were Gram-staining-negative and presented as motile rods with a single polar flagellum (0.7–1.0 μm wide and 1.6–2.7 μm long) (Fig. S1, available in the online Supplementary Material). Strain SN2T was able to degrade naphthalene, while the reference strains were not. Strain SN2T did not grow anaerobically on MA or on MA containing nitrate or nitrite. Phenotypic characteristics of strain SN2T are presented in the species description and compared with those of closely related type strains of the genus Alteromonas in Tables 1 and S1. Most properties, such as strictly aerobic growth, ranges of NaCl, pH and temperature for growth, motility and oxidase- and catalase-positive properties of strain SN2T, were similar to those of related members of the genus Alteromonas, while nitrate reduction and naphthalene degradation capacity differentiated strain SN2T from other members of the genus Alteromonas (Table 1).

The isoprenoid quinone composition of strain SN2T was analysed with an HPLC system (model LC-20A; Shimadzu) equipped with a reversed-phase column (250 × 4.6 mm, Kromasil; Akzo Nobel) and a diode array detector (SPDM20A; Shimadzu) using methanol/2-propanol (2 : 1, v/v) as the eluent (1 ml min⁻¹) as described previously (Koma-gata & Suzuki, 1987). For cellular fatty acid analysis, strain SN2T and the type strains of five species of the genus Alteromonas were cultivated in MB at 30 °C and microbial cells were harvested at 36 h, showing the same growth phase (exponential phase, OD600 = 0.8). The fatty acids were saponified, methylated and extracted using the standard MIDI protocol. Fatty acid methyl esters were analysed using gas chromatography (Hewlett Packard 6890; Agilent Technologies) and identified by using the TSBA6 database of the Microbial Identification System (Sherlock version 6.0B; Sasser, 1990). The polar lipids of strain SN2T were analysed by TLC using cells harvested during the exponential growth phase as described by Minnikin et al. (1977). The following reagents were sprayed to detect different polar lipids: 10 % ethanolic molybdatophosphoric acid (for total polar lipids), ninyhydrin (for aminolipids), Dittmer–Lester reagent (for phospholipids) and α-naphthol sulfonic acid (for glycolipids). The DNA G+C content of strain SN2T was obtained from the whole-genome sequence, available in GenBank (Jin et al., 2011).

The only respiratory lipoquinone detected in strain SN2T was ubiquinone 8 (Q-8). The major cellular fatty acids of strain SN2T (>5 %) were summed feature 3 (comprising C16:1ω7c and/or iso-C15:0 2-OH; 33.5 %), C16:0 (24.3 %), C18:1ω7c (9.6 %) and C12:0 (5.4 %). The overall fatty acid profile of strain SN2T was consistent with those of other species of the genus Alteromonas, although there were some differences in the proportions of some components (Van Trappen et al., 2004; Chiu et al., 2007) (Table S2). The polar lipids of strain SN2T consisted of phosphatidyethanolamine, phosphatidylglycerol, a glycolipid, an aminolipid and three unidentified lipids (Fig. S2). Although the polar lipid pattern containing phosphatidyethanolamine and phosphatidylglycerol as the major polar lipids was in accordance with those of other members of the genus Alteromonas, the presence of a glycolipid and an aminolipid differentiated strain SN2T from related species of the genus (Ivanova et al., 2005; Matsuyama et al., 2015). The DNA G+C content of strain SN2T was 43.5 mol%, which was near the range of DNA G+C of the genus Alteromonas.
content (44–48 mol%) of previously reported species of the genus *Alteromonas* (Table 1). In conclusion, the phylogenetic inference and the physiological and biochemical properties of strain SN2\(^T\) support its assignment to a novel species of the genus *Alteromonas*, for which the name *Alteromonas naphthalenivorans* sp. nov. is proposed.

### Description of *Alteromonas naphthalenivorans* sp. nov.


Cells are Gram-staining-negative, strictly aerobic, motile rods with a single polar flagellum (0.7–1.0 \(\mu\)m wide and 1.6–2.7 \(\mu\)m long). Colonies on MA are cream coloured, circular, convex and smooth. Growth occurs at 4–37 °C (optimum, 25–30 °C), pH 6.0–9.0 (optimum, pH 7.0–7.5) and 0.5–9.0 % (w/v) NaCl (optimum, 2 %). Oxidase- and catalase-positive. Hydrolyses Tweens 20 and 80, casein, starch, gelatin and aesculin, but not agar. Tyrosine-oxidizing (tyrosinase) activity is present, but tyrosine is not hydrolysed. Nitrate is reduced to nitrite, but does not

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*These analyses were conducted under the same conditions in this study.
†Taken from Jin et al. (2011).
produce nitrogen gas. Production of indole and H₂S is negative. Tests for alkaline phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, esterase (C4) and α-chymotrypsin activities are positive, but tests for urease, arginine dihydrolase, lipase (C14), cystine arylamidase, trypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-fucosidase and α-mannosidase activities are negative. Assimilates D-glucose, D-mannitol, malic acid and D-mannose, but not L-arabinose, N-acetylgalosamine, D-maltose, capric acid, adipic acid, trisodium citrate, phenylacetic acid or potassium gluconate. The following substrates are oxidized: α-cyclodextrin, dextrin, glyco- cogen, Tweens 40 and 80, L-arabinose, cellobiose, D-fructose, D-galactose, gentiobiose, α-D-glucose, lactose, lactulose, maltose, D-mannitol, melibiose, methyl β-D-glucoside, sucrose, D-trehalose, turanose, pyruvic acid methyl ester, D-galacturonic acid, γ-hydroxybutyric acid, DL-lactic acid, quinic acid, succinic acid, α-ketobutyric acid, succinamic acid, D- and L-alanine, L-alanyl glycine, L-asparagine, L-aspartic acid, L-glutamic acid, glycy1 L-glutamic acid, L-histidine, L-serine, urocanic acid, aspartate, isoleucine, thymidine, DL-α-glycerol phosphate, D-glucose 1-phosphate, D-glucose 6-phosphate, raffinose, D-sorbitol, D-gluconic acid, α-ketoglutaric acid, bromosuccinic acid and L-proline. The major cellular fatty acids (>5%) are summed feature 3 (comprising C₁₆:0ω7c and/or iso-C₁₅:0 2-OH), C₁₆:0, C₁₇:0ω7c and C₁₈:0. The only isoprenoid quinone is Q-8. Phosphatidylethanolamine, phosphatidylglycerol, a glycolipid, an aminolipid and three unidentified lipids are detected as the major polar lipids.

The type strain is SN2T (=KCTC 11700BP=JCM 17741T=KACC 18427T), isolated from tidal-flat sediment of the Taean coastal area in South Korea. The DNA G+C content of the type strain is 43.5 mol% (from the genome sequence).

Acknowledgements

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References


