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Marinobacter santoriniensis sp. nov., an arsenate-respiring and arsenite-oxidizing bacterium isolated from hydrothermal sediment

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A Gram-negative, arsenate-respiring and arsenite-oxidizing marine bacterium, NKSG1^T, was isolated from hydrothermal sediment at Santorini, Greece. Strain NKSG1^T was a facultatively anaerobic, motile, non-spore-forming, rod-shaped bacterium. Growth occurred optimally at 35–40 °C, between pH 5.5 and 9.0 and with 0.5–16 % NaCl. Energy was conserved by the aerobic oxidation of a range of complex substrates, carbohydrates and organic acids, or anaerobically by arsenate reduction, nitrate reduction coupled to the oxidation of organic carbon or lactate fermentation. Oxidation of arsenite and anaerobic nitrate-dependent oxidation of Fe(II) were facilitated by the presence of an organic carbon source. The DNA G+C content was 58.1 mol%. The major respiratory quinone was Q-9. The significant fatty acids were 16 : 1ω9*c*, summed feature 3 (iso-15 : 0 2-OH/16 : 1ω7*c*), 16 : 0 and 18 : 1ω9*c*. Analysis of 16S rRNA gene sequences showed that strain NKSG1^T fits within the phylogenetic cluster of the genus *Marinobacter* and is most closely related to *Marinobacter koreensis* DD-M3^T (99.3 % similarity). The degree of relatedness with *M. koreensis* DSM 17924^T based on DNA–DNA hybridization was 56 %. The results of a polyphasic study indicated that strain NKSG1^T is a representative of a novel species within the genus *Marinobacter*, for which the name *Marinobacter santoriniensis* sp. nov. is proposed. The type strain is NKSG1^T (=DSM 21262^T =NCIMB 14441^T=ATCC BAA-1649^T). The capacity for arsenic reduction or oxidation has not been demonstrated previously for this genus.

The genus *Marinobacter* was designated by Gauthier *et al.* (1992) based on the type species *Marinobacter hydrocarbonoclasticus*. A further 19 species with validly published names have subsequently been included within the genus (Antunes *et al.*, 2007; Gorshkova *et al.*, 2003; Green *et al.*, 2006; Gu *et al.*, 2007; Guo *et al.*, 2007; Kim *et al.*, 2006; Liebgott *et al.*, 2006; Martin *et al.*, 2003; Romanenko *et al.*, 2005; Shieh *et al.*, 2003; Shivaji *et al.*, 2005; Xu *et al.*, 2008; Yoon *et al.*, 2003, 2004, 2007); *Marinobacter aquaeolei* (Huu *et al.*, 1999) has been proposed to be a synonym of *Marinobacter hydrocarbonoclasticus* (Marquez & Ventosa, 2005). These species are motile, halophilic, Gram-negative gammaproteobacteria isolated from saline terrestrial or, more typically, marine environments. Commonly, they are flagellate and rod-shaped, with ubiquinone-9 as the major respiratory quinone. In terms of metabolism, they are either facultatively anaerobic or strictly aerobic heterotrophs. Often, they are capable of dissimilatory nitrate reduction and, for some species, hydrocarbon degradation and/or fermentation have also been demonstrated.

Strain NKSG1^T was isolated from the ninth subculture of an arsenate-reducing enrichment culture on *Marinobacter* medium (DSMZ medium 970) agar plates (at 25 °C). The enrichment culture inoculum (10 % v/v) comprised hydrothermal sediment from a shallow bay along the coast of Nea Kameni, situated within the flooded caldera of the Greek island of Santorini in the Aegean Volcanic Arc. Sediment at the site is actively deposited from numerous underlying vents and has a reported temperature range of 20–40 °C (Bostrom & Widenfalk, 1984). At the time of collection, the sediment had a temperature of 25 °C and was significantly enriched in both iron and arsenic, with concentrations of approximately 50 % and 400 p.p.m., respectively (unpublished data).

The enrichment medium consisted of a marine minimal medium (MMM) supplemented with 5 mM As(V) (as $Na_2HAsO_4 . 7H_2O$) and 10 mM lactate. The basal solution of MMM was modified from Caccavo *et al.* (1994) comprising (per litre): 2.5g $NaHCO_3$, 0.25 g NH_4Cl, 0.6

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The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain NKSG1^T is EU496088.

A supplementary table showing the electron donors that facilitate nitrate reduction by strain NKSG1^T and the type strains of phylogenetically related *Marinobacter* species is available with the online version of this paper.

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g $NaH_2PO_4.H_2O$, 0.1 g KCl, 10 ml vitamin solution and 10 ml mineral solution. The composition of the vitamin solution was described by Balch *et al.* (1979) and Wolin *et al.*, (1963). The mineral solution is modified from Balch *et al.* (1979) and Lovley *et al.* (1984) using $CoCl_2 . 6H_2O$, with the addition of 0.025 g $Na_2WO_4 . 2H_2O$ l^{-1} (from 10× stock). The basal solution was then amended with 20 g NaCl l^{-1} and 3 g $MgCl_2 . 6H_2O$ l^{-1} to emulate marine conditions, aliquoted into serum bottles and sparged with $N_2 : CO_2$ (80 : 20), attaining a final pH of 6.8–7.0. Bottles were sealed with butyl rubber stoppers prior to autoclaving. Enrichments were incubated in the dark at 25 °C. Isolates formed brownish-red colonies with a diamond morphology on *Marinobacter* medium within 72 h, and were tested for growth in defined media containing As(V) or As(III) (described below). Strain NKSG1^T was selected for its ability to both reduce and oxidize arsenic.

Cell morphology was determined after 24 h growth in marine broth 2216 (MB; Difco) at 30 °C, staining with 2 % uranyl acetate and imaging with a Philips CM200 FEG transmission electron microscope (FEI). Colonies were described following 3–4 days growth on spread and streak plates with marine broth agar (MA) and Miller's Luria–Bertani (LB) agar (Sigma) at 30 °C. Spore-forming ability was tested by staining with malachite green (Pro-Lab Diagnostics) and steaming (heating) for 5 min, and counterstaining with Safranin O solution (Sigma) for 1 min. Gram stain reactivity was determined using a Gram stain kit (Sigma). Motility was ascertained by light microscopy of cells grown in BBL trypticase soy broth (TSB; BD) with 10 % NaCl for 46 h at 30 °C without shaking. Flagella were determined by TEM and by light microscopy of stained cells (Flagella Stain Droppers; BD) grown for 24 h in MB at 30 °C without shaking.

The range of pH that supports growth was established using LB broth adjusted to pH 4.0–10.0 (in 0.5–1.0 unit increments) with NaOH and HCl. The pH was confirmed after autoclaving. Incubations were at 25 °C for 2–6 days. Growth response to NaCl was demonstrated using TYE medium [10 g tryptone l^{-1} (Fisher), 5 g select yeast extract (YE) l^{-1} (Sigma)] supplemented with NaCl at 0, 0.5, 1, 3, 8, 10, 12, 15, 16, 17, 18, 19 and 20 % at 30 °C for 7 days. Temperature experiments were conducted using TSB amended with 8 or 10 % NaCl. Cultures were incubated for 40 h at 4 °C or 10–50 °C in 5 °C increments.

Carbohydrate and organic acid utilization, nitrate reduction, indole production, glucose fermentation, arginine dihydrolase activity, urease activity, aesculin hydrolysis, gelatin hydrolysis and β-galactosidase activity were determined using API 20NE strips with AUX media (bioMérieux) (see Table 1). Strips were incubated at 30 °C for 2 weeks. API ZYM strips (bioMérieux) were used according to manufacturer's specifications to test enzyme activity. Results are given in the species description.

Growth on a range of electron acceptors in anaerobic MMM containing 10 mM lactate as the electron donor was ascertained in triplicate by supplementing the medium with one of the following: 10 mM KNO_3; 5 mM As(V); 20 mM Mn(IV) (δ-MnO_2; Tebo *et al.*, 2007) with or without 1 g YE l^{-1}; 20 mM Fe(III) (amorphous FeOOH; Lovley & Phillips, 1986) with or without 1 g YE l^{-1} or 0.75 g Fe(III) nitrilotriacetic acid l^{-1} (Fredrickson *et al.*, 2000); 10 mM Fe(III) nitrilotriacetic acid with or without 1 g YE l^{-1}; 10 mM sulfate (Na_2SO_4); 5 mM sulfite (Na_2SO_3); 5 mM thiosulfate ($Na_2S_2O_3$); 0.005 % colloidal S^0 (Blumentals *et al.*, 1990); 20 mM fumarate; 10 mM malate; and 5 mM Se(IV) (Na_2SeO_4) with or without 1 g YE l^{-1}.

Growth on a range of electron donors in anaerobic MMM containing 10 mM KNO_3 was ascertained in triplicate by supplementing the medium with one of the following: 1 atm H_2 with or without 10 mM acetate; 10 mM acetate; 10 mM formate; 5 mM propionate; 5 mM n-butyrate; 10 mM pyruvate; 10 mM DL-lactate; 10 mM fumarate; 1 mM succinate; 10 mM citrate; 1 mM L-malate; 1 mM benzoate; 5 mM glycerol; 10 mM ethanol; 1 g YE l^{-1}; and 10 mM Fe(II) ($FeSO_4 . 7H_2O$) plus 5 mM acetate. Fermentative growth on 20 mM lactate was also tested. The oxidation of 5 mM As(III) ($NaAsO_2$) with or without 1 mM lactate was tested in aerobic MMM.

Electron donor and acceptor consumption and fermentation were analysed as follows. Nitrate, nitrite, arsenate, sulfate, thiosulfate and selenate were measured using a Dionex DX600 ion chromatograph, fitted with a 4 mm ion exchange column (AS4A-SC) and AG4A-SC guard column (Dionex Corporation). Samples were eluted in 2.1 mM Na_2CO_3/4.9 mM $NaHCO_3$ (flow rate 1.7 ml min^{-1}; pressure 1.38×10^7 Pa). Organic acids were quantified with a Dionex DX120 ion chromatograph, fitted with a Dionex ICE AS1 ion-exclusion column. Samples were eluted in 1 mM octane sulfonic acid (0.6 ml min^{-1}; 1.034×10^7 Pa). As(V) and As(III) concentrations were determined by the molybdenum blue colorimetric method (Murphy & Riley, 1962; Strickland & Parsons, 1968). Prior to arseno-molybdenum complexation, samples were digested in 25 mM HCl for As(V), oxidized in 5 mM KIO_3 with 50 mM HCl for As(III) (Johnson & Pilson, 1972) or reduced to account for phosphate interference (Johnson, 1971). Absorbance was measured at 840 nm. The ferrozine colorimetric assay was used to determine bioavailable Fe(II) after 0.5 M HCl digestion (Lovley & Phillips, 1986) and bioavailable Fe(III) after reduction by 0.25 M hydroxylamine hydrochloride/0.5 M HCl (Anderson & Lovley, 1999; Lovley & Phillips, 1987). The concentration of Mn(II), in solution and associated with solid-phase MnO_2, was ascertained by the formaldoxime colorimetric method (Tebo *et al.*, 2007) following digestion in 0.5 M HCl (Lovley & Phillips, 1986). Mn(IV) was measured after reducing samples with 0.1 % hydroxylamine hydrochloride ($H_3NO . HCl$) (Tebo *et al.*, 2007). The methylene blue colorimetric assay was used for the quantitative detection of sulfide (H_2S, HS^-, S^{2-}) (Cline, 1969). Growth on electron donors and by fermentation was also determined by optical density measurements at 600 nm.

Table 1. Phenotypic comparisons between strain NKSG1^T and selected type strains of the genus *Marinobacter*

Strains: 1, strain NKSG1^T; 2, *M. koreensis* DSM 17924^T; 3, *M. pelagius* CGMCC 1.6775^T; 4, *M. hydrocarbonoclasticus* DSM 8798^T. Data were taken from the present study and from Gauthier *et al.* (1992), Spröer *et al.* (1998), Xu *et al.* (2008) and Kim *et al.* (2006), and from Yoon *et al.* (2003) for quinone data for *M. koreensis* and *M. aquaeolei*. +, Positive; −, negative; ND, no data available. The medium used for descriptions of colony growth was MA with the exception of *M. pelagius* CGMCC 1.6775^T, for which halophilic medium was used. All strains have rod-shaped cells and are negative for assimilation of glucose, arabinose, D-mannose and mannitol and for fermentation of D-glucose.

Characteristic	1	2	3	4
Cell size (μm)	0.5–1.3 × 1.2–4.5	0.3–0.5 × 1.5–3.0	0.4–0.8 × 2.0–4.0	0.3–0.6 × 2.0–3.0
Colony colour	Cream	Cream	Cream	White/rosy beige
Flagella	1 polar	1 polar	ND	None or 1 polar
Optimum growth temperature (°C)	35–40	28	25–30	32
NaCl concentration for growth (%)				
Range	0.5–16	0.5–20	0.5–15	0.5–20
Optimum	5–10	3–8	5.0	3–6
pH for growth				
Range	5.5–9	5–9	6–9	6–9.5
Optimum	7–8	6–8	7–8	7–7.5
Reduction of:				
Nitrate to nitrite	+	+	ND	+
Nitrite to N_2	−	ND	ND	+
Utilization of:				
Gluconate	+	−	−	−
Adipic acid	+	−	ND	+
Malic acid	+	+	+	ND
Phenylacetic acid	+	+	ND	ND
Maltose	−	−	−	ND
Capric acid	−	−	ND	ND
Citrate	−	−	−	+
Lactate	+	+	+	+
N-Acetylglucosamine	−	−	ND	−
Enzyme activities				
Urease	+	−	−	−
Arginine dihydrolase	−	−	ND	+
β-Galactosidase	−	−	ND	ND
Hydrolysis of:				
Aesculin	−	−	−	ND
Gelatin	−	−	−	ND
Indole production	−	−	−	ND
Lactate fermentation	+	ND	ND	ND
DNA G+C content (mol%)	58.1	54.1	59.0	57.5
Major respiratory quinone	Q-9	Q-9	ND	Q-9

Lactate or arsenite (with lactate supplementation) were oxidized in aerobic MMM. Arsenate and fumarate were respired anaerobically coupled with lactate consumption. Respiration of arsenate and oxidation of arsenite were further assessed by time-course growth experiments, demonstrating a positive correlation between cell growth with concentration of arsenate reduced to arsenite under anaerobic conditions, and with aerobic arsenite oxidation to arsenate in the presence of cells grown on lactate (Handley *et al.*, 2009). Alongside anaerobic lactate utilization, 10 mM Fe(III) nitrilotriacetic acid was partially reduced, yielding 20.6 % Fe(II) (SD 7.1 %) without YE and 25.2 % Fe(II) (SD 12.0 %) with YE. In comparison, FeOOH, sulfate, sulfite, thiosulfate, colloidal S^0, malate and Se(IV) with or without YE were not reduced. No significant increase of Mn(II) was detected, indicating no reduction of Mn(IV). The following substrates supported the anaerobic reduction of nitrate to nitrite: acetate, propionate, n-butyrate, pyruvate, DL-lactate, fumarate, YE and $FeSO_4 . 7H_2O$ (plus 5 mM acetate), but not H_2, citrate, benzoate, glycerol or ethanol. Partial nitrate reduction was achieved with weak utilization (32–55 % after 4 weeks incubation) of formate, succinate and L-malate. Similar organic substrate consumption and Fe(II) oxidation (coupled with nitrate reduction) was demonstrated by *M. koreensis* DSM 17924^T and *M. aquaeolei* DSM 11845^T (Supplementary Table S1, available in IJSEM Online). Complete fermentation of 20 mM lactate to acetate and

propionate in the absence of electron acceptors occurred within 2 months, but not before 2 weeks, of incubation.

The 16S rRNA gene was amplified directly from distinct colonies by PCR using the bacterial universal primers 8f (5′-AGAGTTTGATCCTGGCTCAG-3′) and 1492r (5′-TACGGYTACCTTGTTACGACTT-3′ (Lane, 1991) and the following protocol: 94 °C for 4 min; 35 cycles of 94 °C for 30 s, 57 °C for 30 s and 72 °C for 1 min; and 72 °C for 10 min. PCR products were purified using a QIAquick PCR Purification kit (Qiagen) and sequenced using primers 8f and 1492r, the internal primers 530f (5′-GTGCCAGCMGCCGCGG-3′) and 943r (5′-ACCGCTTG-TGCGGGCCC-3′) and an ABI Prism BigDye Terminator v3.1 cycle sequencing kit. Electrophoresis was performed with an ABI Prism 3100 Genetic Analyzer (Perkin Elmer Applied Biosystems). A consensus sequence was aligned with sequences from GenBank using MEGA 3.1 (Kumar *et al.*, 2004), and sequences were submitted to a BLAST search for analysis (Altschul *et al.*, 1990). A neighbour-joining phylogenetic tree was constructed using all type strains of *Marinobacter* species, with 1000 bootstrap replicates, based on evolutionary distances estimated using Kimura's correction (MEGA 3.1). According to phylogenetic analysis of almost-complete 16S rRNA gene sequences, the closest relative of strain NKSG1^T (1383 bp) was *M. koreensis* DD-M3^T, with 99.3 % sequence identity over 1380 bp. The 16S rRNA gene sequence identity of strain NKSG1^T with the type strains of other *Marinobacter* species ranged from 94.4 % (with *M. litoralis*) to 98.0 % (with *M. pelagius*). The phylogenetic tree shows that strain NKSG1^T forms a distinct cluster with *M. koreensis* and *M. pelagius* (Fig. 1). Comparable results were achieved with minimum-evolution or maximum-parsimony trees (data not shown).

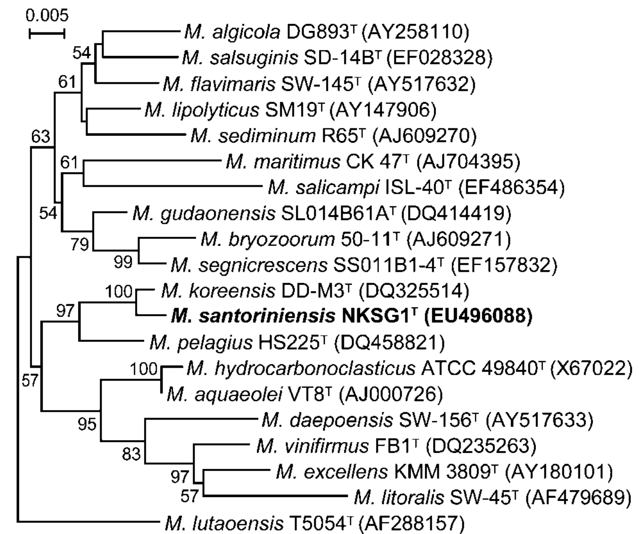

Fig. 1. Phylogenetic tree based on 16S rRNA gene sequences, showing the relationship of *Marinobacter santoriniensis* sp. nov. NKSG1^T to the type strains of other *Marinobacter* species. The outgroup is *Oceanospirillum linum* ATCC 11336^T (GenBank accession no. M22365.1) (not shown). Bootstrap values >50 % are shown. Bar, 5 substitutions per 1000 nucleotide positions.

DNA G+C content, DNA–DNA hybridization and isoprenoid quinone and fatty acid methyl ester profiles were determined by the DSMZ Identification Service (Braunschweig, Germany). DNA for G+C content and DNA–DNA hybridization was extracted using a French pressure cell (Thermo Spectronic) and purified on a hydroxyapatite column (Cashion *et al.*, 1977). DNA G+C content was determined by reversed-phase HPLC (Shimadzu) analysis of deoxyribonucleosides with a Vydac 201SP54 (250 mm × 4.6 mm, 5 μm, C_{18}) column with 201GD54H guard column. Deoxyribonucleosides were obtained by hydrolysing DNA, nucleotides were dephosphorylated with bovine alkaline phosphatase (Mesbah *et al.*, 1989) and HPLC analysis was performed on a 10 μl sample at 45 °C with 0.3 M $(NH_4)H_2PO_4$ (pH 4.4) and acetonitrile (40 : 1, v/v) and a flow rate of 1.3 ml min^{-1} (adapted from Tamaoka & Komagata, 1984). The G+C content was calculated from the ratio of deoxyguanosine (dG) and thymidine (dT) (Mesbah *et al.*, 1989). DNA–DNA hybridization followed the method of De Ley *et al.* (1970) and modifications by Huß *et al.* (1983), utilizing a Cary 100 Bio UV/Vis spectrophotometer, fitted with a Peltier-thermostatted 6 × 6 multi-cell changer and temperature controller with an *in situ* temperature probe (Varian). Analysis of respiratory quinones was carried out according to methods described by Tindall (1990) using an LDC Analytical HPLC (Thermo Separation Products) fitted with a reversed-phase column (Macherey-Nagel; 2 × 125 mm, 3 μm, RP_{18}). Cellular fatty acids were analysed by gas chromatography (GC). Cell material was cultivated on TSB agar plates at 28 °C for 24 h. Fatty acids were obtained according to methods described by Kuykendall *et al.* (1988), except that saponification employed 1 ml of 3.75 M NaOH in 50 % methanol. Fatty acids were separated using a Hewlett Packard 5890 Series II gas chromatograph fitted with a phenylmethylsilicone-fused Ultra 2 column (25 m × 0.2 mm; Hewlett Packard) under conditions described in Kämpfer & Kroppenstedt (1996). The fatty acid composition of integrated peaks was assigned using the Sherlock Microbial Identification System (version 4.5, MIDI).

DNA–DNA hybridization of strain NKSG1^T was performed with *M. koreensis* DSM 17924^T owing to the high 16S rRNA gene sequence similarity – greater than the 98.5–99.0 % threshold recommended by Stackebrandt & Ebers (2006). Results indicated a DNA–DNA relatedness of 55.8–56.6 % (from duplicate measurements). The DNA G+C content of strain NKSG1^T was determined to be 58.1 mol%. The major respiratory quinone was ubiquinone 9 (Q-9). Q-8 and Q-10 were present in trace quantities. Significant fatty acids of strain NKSG1^T were 16 : 1ω9*c* (10.88 %), summed feature 3 (iso-15 : 0 2-OH and/or 16 : 1ω7*c*; 17.26 %), 16 : 0 (28.63 %) and 18 : 1ω9*c* (12.53 %) (Table 2). The G+C content is within the range

Table 2. Cellular fatty acid compositions of strain NKSG1^T and the type strains of selected *Marinobacter* species

Strains: 1, strain NKSG1^T; 2, *M. koreensis* DSM 17924^T; 3, *M. pelagius* CGMCC 1.6775^T; 4, *M. hydrocarbonoclasticus* DSM 8798^T. Data from this study, Kim *et al.* (2006) and Marquez & Ventosa (2005). Values shown are percentages of total fatty acids. Only components representing ≥1.0 % of the total are shown; −, less than 1.0%; NR, not reported.

Fatty acid	1	2	3	4
10 : 0	−	1.2	NR	1.0
12 : 0	7.29	8.6	NR	6.5
12 : 0 3-OH	7.03	8.3	8.3	10.3
14 : 0	2.14	2.1	4.7	2.8
15 : 0	−	−	NR	1.7
Summed feature 3*	17.26	20.5	NR	−
16 : 1ω9*c*	10.88	11.3	23.5	9.4
16 : 0	28.63	23.5	19.5	30.3
10-Methyl 16 : 0	2.19	1.6	NR	1.0
iso-17 : 0	−	−	NR	−
17 : 1ω8*c*	2.86	2.7	NR	2.8
17 : 0	1.65	1.0	1.2	3.5
18 : 1ω7*c*	2.22	2.6	NR	−
18 : 1ω9*c*	12.53	11.1	7.4	19.6
18 : 0	1.45	1.2	NR	1.8

*Summed feature 3 comprises iso-15 : 0 2-OH and/or 16 : 1ω7*c*.

reported for the genus *Marinobacter* (54.1–63.5 mol%). Q-9 is the common ubiquinone for the genus, and the fatty acid profile is similar to those of other *Marinobacter* species. The low degree of DNA–DNA relatedness (<70 %) indicates that strain NKSG1^T represents a species distinct from *M. koreensis* according to the recommendations of Wayne *et al.* (1987).

On the basis of the data presented here, strain NKSG1^T should be placed in the genus *Marinobacter* as the type strain of a novel species, for which the name *Marinobacter santoriniensis* sp. nov. is proposed.

Description of *Marinobacter santoriniensis* sp. nov.

Marinobacter santoriniensis (san.to.ri.ni.en′sis. N.L. masc. adj. *santoriniensis* from the island of Santorini, where the type strain was isolated).

Cells are Gram-negative, non-spore-forming, straight rods (0.5–1.3 × 1.2–4.5 μm) that are motile with a single polar flagellum. They are facultatively anaerobic, moderately halophilic, mesophilic and neutrophilic. Colonies on spread plates are slightly raised centrally, circular to irregular in form (7 mm mean diameter). On MA, colonies are translucent cream, whereas colonies have translucent to opaque brownish-red centres on LB. Streaked colonies tend to be opaque and slightly convex with a diamond-shaped morphology. The type strain grows well aerobically on MB, LB and TSB (supplemented with additional NaCl) agar. Growth occurs at pH 5.5–9.0 and 0.5–16 % NaCl, and is optimal at 35–40 °C, pH 7.0–8.0 and 5–10 % NaCl. Lactate supports aerobic growth, and anaerobic growth by fermentation (weak). Arsenite is oxidized aerobically in the presence of lactate. Carbon substrates assimilated are potassium gluconate, adipic acid, malic acid and phenylacetic acid, but not D-glucose, L-arabinose, D-mannose, D-mannitol, *N*-acetylglucosamine, maltose, capric acid or citrate. Reduction of nitrate (to nitrite) proceeds with the oxidation of formate, acetate, propionate, n-butyrate, pyruvate, lactate, fumarate, succinate, malate, yeast extract and $FeSO_4 . 7H_2O$ (plus 5 mM acetate). Lactate oxidation further supports the reduction of arsenate, Fe(III) nitrilotriacetic acid with or without yeast extract (weak) and fumarate. Enzymes expressed are alkaline phosphatase, esterase (C4), esterase lipase (C8), lipase (C14), leucine arylamidase, valine arylamidase, cystine arylamidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase and urease, but not trypsin, α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-glucosidase, β-glucosidase, *N*-acetyl-β-glucosaminidase, α-mannosidase or α-fucosidase. The DNA G+C content of the type strain is 58.1 mol%. Dominant cellular fatty acids are 16 : 1ω9*c*, summed feature 3 (iso-15 : 0 2-OH and/or 16 : 1ω7*c*), 16 : 0 and 18 : 1ω9*c*. The major isoprenoid quinone is Q-9.

The type strain, NKSG1^T (=DSM 21262^T =NCIMB 14441^T), was isolated from shallow marine hydrothermal sediment at Santorini, Greece.

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