Thiohalospira halophila gen. nov., sp. nov. and *Thiohalospira alkaliphila* sp. nov., novel obligately chemolithoautotrophic, halophilic, sulfur-oxidizing gammaproteobacteria from hypersaline habitats

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A previously unknown ecotype of obligately chemolithoautotrophic, sulfur-oxidizing bacteria was discovered in sediments of various inland hypersaline lakes and a solar saltern. The salt requirements for these bacteria were similar to those of haloarchaea, representing the first example of extreme halophiles occurring among the chemolithoautotrophs. They were enriched and isolated at 4 M NaCl under aerobic conditions with thiosulfate or tetrathionate as the electron donor or under micro-oxic conditions with sulfide. In total, 20 strains were obtained from hypersaline inland lakes in central Asia, central Russia and Crimea and a sea saltern of the Adriatic Sea. The isolates were thin, motile spirilla, some of which possessed a yellow, membrane-bound pigment. They were obligately aerobic, chemolithoautotrophic, sulfur-oxidizing bacteria that used thiosulfate, sulfide, sulfur and tetrathionate as electron donors. The characteristic feature of the group was the production of large amounts of tetrathionate as an intermediate during the oxidation of thiosulfate to sulfate. All but one of the strains grew within the pH range 6.5–8.2 (optimally at pH 7.3–7.8) and at NaCl concentrations from 2.0 to 5 M (optimally at 3.0 M). A single strain, designated ALgr 6sp^T, obtained (by enrichment) from the hypersaline alkaline lakes of the Wadi Natrun valley, was found to be moderately halophilic and facultatively alkaliphilic (capable of growth at pH 10). The predominant cellular fatty acids were quite unusual, with 10-methyl C_{16:0} and C_{16:0} predominating. Cells grown at 4 M NaCl accumulated extremely high concentrations of glycine betaine as a compatible solute. The 20 neutrophilic isolates contained three genospecies (on the basis of DNA–DNA relatedness data) but could not be discriminated phenotypically. On the basis of the phenotypic and genotypic analyses, the isolates constitute a novel genus and species, for which the name *Thiohalospira halophila* gen. nov., sp. nov. is proposed. The type strain of *Thiohalospira halophila* is HL 3^T (=DSM 15071^T=UNIQEM U219^T). The haloalkaliphilic strain ALgr 6sp^T represents a second species of the new genus, for which the name *Thiohalospira alkaliphila* sp. nov. is proposed. The type strain of *Thiohalospira alkaliphila* is ALgr 6sp^T (=DSM 17116^T=UNIQEM U372^T).

Hypersaline habitats, such as inland salt lakes and solar salterns, are extreme habitats traditionally regarded as low-diversity environments dominated by heterotrophic haloarchaea (Oren, 2002). However, this must be regarded as being true only of the brines; in the sediments, extreme

and moderate halophiles with more versatile metabolisms replace the haloarchaea. In particular, the latter largely include representatives of the *Gammaproteobacteria*, such as moderately halophilic, heterotrophic members of the genera *Halomonas* and *Marinobacter*, which are better adapted to lower and fluctuating salinities (Ventosa *et al.*, 1998), moderately halophilic sulfate-reducing bacteria (Kjeldsen *et al.*, 2007) and the recently discovered extremely halophilic heterotrophic bacteria that form a phylogenetic cluster around the genus *Halovibrio* (former

Abbreviation: SOB, sulfur-oxidizing bacteria.

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Pseudomonas halophila) (Sorokin *et al.*, 2006a; Maturrano *et al.*, 2006; Kharroub *et al.*, 2006). Furthermore, chemolithoautotrophic sulfur-oxidizing bacteria (SOB) have the opportunity of adapting to extremely high-salt conditions, because they possess a very efficient energy metabolism (Oren, 1999). Recently, a large diversity of moderately, and even extremely, halophilic SOB have been detected in hypersaline habitats at neutral pH (Sorokin *et al.*, 2006b). Of the six different types of halophilic SOB discovered, two groups of aerobic moderate halophiles were found to belong to the existing genera *Thiomicrospira* (Sorokin *et al.*, 2006c) and *Halothiobacillus*. The other two groups of moderate halophiles included novel genera of denitrifying SOB, i.e. *Thiohalophilus* (Sorokin *et al.*, 2007a) and *Thiohalomonas* (Sorokin *et al.*, 2007b). The moderately halophilic SOB grew best at low salinities around 0.5–1.0 M NaCl but could tolerate quite high salinities (up to saturation). Previously, only a single species of SOB, *Halothiobacillus halophilus*, was known to be able to grow at 4 M NaCl (Wood & Kelly, 1991). Furthermore, apart from moderately halophilic SOB, two novel, previously unknown chemolithoautotrophs, extremely halophilic SOB groups have been discovered in sediments from hypersaline habitats. One group was obligately aerobic and the other one was thiodenitrifying (Sorokin *et al.*, 2006b).

The aerobic halophilic SOB described in this paper were obtained from samples of sediments from hypersaline lakes in NE Mongolia, SW Siberia and Crimea (Ukraine), from Lake Baskunchak (South Russia) and from the Sečovlje solar saltern (Slovenia) of the Adriatic Sea (Sorokin *et al.*, 2006b). In general, the salt content of the brines varied from 10 to 38 % (w/v) and the pH ranged from 6.5 to 8.2; the predominant ions were Na^+ , Mg^{2+} , Cl^- and SO_4^{2-} . One of the enrichments was also made with sediment samples from eight hypersaline alkaline lakes at Wadi El Natrun in Egypt. The lake brines there were predominantly of the chloride-sulfate type but also contained a fraction of sodium carbonates, which raised the pH to 9.0–10.0 (Taher, 1999).

The mineral base medium used for the enrichment and growth experiments contained the following: NaCl (4.0 M), K_2HPO_4 (10 mM) and NH_4Cl (5 mM). The pH was adjusted to 7.2 with 10 % KH_2PO_4 . After sterilization, the medium was supplemented with 2 mM $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$ and 1 ml trace metal solution l^{-1} (Pfennig & Lippert, 1966). Thiosulfate (5–20 mM) or tetrathionate (5 mM) was added as an electron donor from filter-sterilized 1 M solutions. Filter-sterilized NaHCO_3 (10–40 mM, pH 8.0) was used as the carbon source and as the pH buffer. Routine incubation was performed in closed bottles with a liquid/gas ratio of 10:90 to prevent loss of CO_2 from the NaHCO_3 , leading to spontaneous alkalization of the medium during the initial growth phase. With sulfide as the substrate, the principle of gradient cultivation (Nelson & Jannasch, 1983) was employed using 50 ml glass cylinders, with sulfide diffusing upward from the bottom 2 % (w/v) agar layer (10 ml, 0.1 mmol Na_2S) overlaid by

30 ml of the above-mentioned mineral medium with 3 M NaCl containing five-times less trace elements (to slow down spontaneous oxidation) and 0.15 % (w/v) Noble agar (Difco). For the Wadi Natrun enrichments, the pH was brought to 9.2 by the addition of 10 % Na_2CO_3 . Oxygen diffused downwards from the 10 ml headspace. The SOB usually developed within a thin layer of 1–2 mm, 1 cm below the surface of the top layer of medium. Cultivation was performed at 28 °C. Growth was monitored by following the optical density at 600 nm and the consumption of substrate. Pure cultures were obtained after several rounds of serial dilution to extinction in liquid media, as neither of the isolates formed colonies on solid medium. The serial dilutions from sulfide gradient enrichments were done with thiosulfate in liquid medium but at 2 % oxygen and with a liquid/gas ratio of 1:20. Culture purity was checked on rich organic medium in which the inorganic electron donor was replaced with yeast extract. Sulfur (sulfide, sulfur, thiosulfate, tetrathionate and sulfate) compounds were analysed as described previously (Sorokin *et al.*, 2001). Cell protein was measured by using the Lowry method after the removal of interfering sulfur compounds either by washing (thiosulfate, tetrathionate) or by overnight extraction with acetone (sulfur). Phase-contrast microphotographs were obtained using Axioplan Imaging 2 (Zeiss). For electron microscopy, the cells were pre-fixed in glutaraldehyde (final concentration 3 %, v/v) at pH 7.0 in the presence of 2 M NaCl, then post-fixed in 1 % (w/v) OsO_4 /2.0 M NaCl for 12 h at room temperature, washed and stained overnight with 1 % (w/v) uranyl acetate, dehydrated in an ethanol series and then embedded in Epon resin. Lead citrate (1 %, w/v) was used to provide contrast for thin sections.

Growth in enrichment cultures at 4 M NaCl was very slow, with full consumption of 20 mM thiosulfate after 1 month. Because of this, initial attempts to find extremely halophilic SOB failed. Only after the prevention of an initial rise in the pH (above 8.0), through the use of static cultures in closed bottles, did it become possible to obtain positive results for most of the samples from the different geographical areas. This indicated the presence of indigenous SOB populations able to develop at saturating salt concentrations. In total, 14 strains were obtained from the aerobic enrichments with thiosulfate and tetrathionate and 6 strains were obtained from the sulfide–oxygen gradient cultures. A single strain was isolated on alkaline medium from a sulfide–oxygen gradient enrichment inoculated with sediments from the Wadi Natrun lakes. All 21 isolates were thin, motile spirilla with single bipolar flagella and Gram-negative type cell walls (Fig. 1). Some of the strains contained a membrane-bound yellow pigment that was extractable with methanol and had a spectrum (max. at 440 nm) similar to those of natronochromes (xanthine-like polyenes found recently in extremely natronophilic SOB of the genus *Thioalkalivibrio*; Takaichi *et al.*, 2004).

Cellular fatty acids were analysed using cells grown at 30 °C with 4 M NaCl and thiosulfate. Freeze-dried biomass was

Fig. 1. Cell morphology of representative strains of the genus *Thiohalospira* grown at 2–4 M NaCl. (a–d) Phase-contrast microphotographs of strain HL 3^T (a), strain HL 4 (b), strain HL 25 (c) and strain ALgr 6sp^T (d); (e and f) electron microphotographs of total preparation of strain HL 3^T (e) and thin section of strain HL 3^T (f). Bars, 10 μ m (a–d), 1 μ m (e and f).

extracted with a methanol/chloroform mixture and was analysed by GC-MS according to the method described by Zhilina *et al.* (1997). Analysis of strains HL 3^T and HL 4 demonstrated the complete predominance of saturated species: 10-methyl $C_{16:0}$, $C_{16:0}$ and $C_{18:0}$ constituted more than 85 % of the total and $C_{16:1\omega7}$ and $C_{18:1\omega7}$ made up the rest. Whereas $C_{16:0}$ often predominates in halophilic bacteria, the presence of 10-methyl $C_{16:0}$ as a predominant fatty acid of polar lipids is certainly unusual and may be unique to the novel bacteria. A spectroscopic analysis of cell fractions obtained from strains HL 3^T and HL 4 identified cytochrome c_{554} as the major cytochrome, both in the membranes and in the soluble fractions, and revealed the presence of cytochrome b_{561} in the membranes.

Organic compatible solutes were extracted from the freeze-dried cells grown at 4 M NaCl on mineral medium with thiosulfate (see above) and analysed using HPLC as described previously (Banciu *et al.*, 2004). Analysis of strain HL 3^T grown at 4 M NaCl on mineral medium with thiosulfate demonstrated the accumulation of a single compound, identified as glycine betaine, at an extremely high specific concentration (33 % of total cell mass). As no organic compounds were included in the medium, these results indicated the potential of the extremely halophilic SOB for *de novo* synthesis of glycine betaine.

The novel bacteria were obligately chemolithoautotrophic and obligately aerobic SOB, although the strains enriched

with sulfide in gradient culture grew optimally at low oxygen (2 % of the gas phase) and did not tolerate more than 10 % O₂. In addition to growth with thiosulfate and sulfide, growth with tetrathionate and elemental sulfur was also possible. In all strains except ALgr 6sp^T, growth with thiosulfate occurred in two phases: during the initial phase more than 60 % of the thiosulfate was converted to tetrathionate, which was eventually oxidized to sulfate: $2S_2O_3^{2-} \rightarrow S_4O_6^{2-} \rightarrow 4SO_4^{2-}$.

The rationale for thiosulfate conversion to tetrathionate is not clear for these neutrophilic SOB, in contrast to the mechanism in acidophiles, which use this method to protect the substrate from spontaneous degradation at low pH (Pronk *et al.*, 1990). This reaction is catalysed by tetrathionate synthase (thiosulfate dehydrogenase) (Kelly & Wood, 1994). High activity for this enzyme was found in cell-free extracts of strains HL 3^T and HL 4 with ferricyanide as an artificial acceptor [up to 5 µmol (mg protein)⁻¹ min⁻¹]. The activity was located in the soluble fraction, most probably in the periplasm, as it was maximal at 3–4 M NaCl and dependent on both Na⁺ and Cl⁻ ions. The mechanism for tetrathionate conversion to sulfate was not so clear. In acidophiles, tetrathionate hydrolase has been found to convert tetrathionate to a mixture of thiosulfate, sulfur and sulfate (Pronk *et al.*, 1990). In experiments with washed cells of strains HL 3^T and HL 4, anaerobic incubation with tetrathionate yielded only thiosulfate and sulfate, suggesting disproportionation as opposed to hydrolysis. This requires further investigation. Strain ALgr 6sp^T did not form tetrathionate from thiosulfate and showed very low levels of tetrathionate oxidation.

The most striking feature of the novel SOB was their extreme halophilism (except in the case of strain ALgr 6sp^T), which was evident from their dependence on salt for growth (Fig. 2a). In four of the strains tested, the NaCl range for growth was from 2–2.5 to 4–5 M, with an optimum at 3 M. Such a salt range for growth has never before been observed in chemolithoautotrophic bacteria. Strain ALgr 6sp^T had a profile typical of that of a moderate halophile. In contrast to growing cultures, washed cells of extremely halophilic strains were still active at salinities below 2 M, but the cells lysed rapidly at NaCl concentrations below 1 M (Fig. 2b). The pH values suitable for growth of strains HL 3^T, HL 4 and HL 25 (from pH-neutral habitats) were found to be within the range 6.5–8.2, with an optimum between 7.3 and 7.8. In contrast, strain ALgr 6sp^T (from Wadi Natrun) was able to grow at pH values up to 10.2, with half of the NaCl being replaced by NaHCO₃/Na₂CO₃ on the basis of total [Na]. However, it still grew at neutral pH (down to 7.0) and had an optimum at pH 8.5. This identified the Wadi Natrun isolate as a facultatively alkaliphilic halophile (Fig. 2c).

Both the sodium ion and chloride were essential for growth of the novel SOB. Growth of strains HL 3^T and HL 4 was arrested at just 25–30 % replacement of the NaCl with KCl

Fig. 2. Influence of NaCl on growth (a) of strain HL 3^T at pH 7.5 and strain ALgr 6sp^T at pH 8.5 with thiosulfate and on activity (b) of sulfur-compound oxidation by washed cells of strain HL 3^T at pH 7.5. (c) pH profile for growth of strain HL 3^T at 3 M NaCl and strain ALgr 6sp^T at 2 M NaCl with thiosulfate. Symbols in (a) and (c): ○, strain HL 3^T; ●, strain ALgr 6sp^T. Symbols in (b): ●, thiosulfate oxidation to tetrathionate; ○, tetrathionate oxidation to sulfate; △, sulfide oxidation. 100 % specific growth rates for strains HL 3^T and ALgr 6sp^T were 0.04 and 0.07 h⁻¹, respectively. 100 % activities for thiosulfate, tetrathionate and sulfide oxidation were 650, 340 and 620 nmol O₂ (mg protein)⁻¹ min⁻¹, respectively.

at 3 M total salt (i.e. 2 M NaCl/1 M KCl). The minimum requirement for K⁺ was very low (1 mM). Sodium chloride substitution by sodium sulfate had a less dramatic result, with full growth occurring at up to 50 % chloride

substitution (by charge, $2\text{Cl}^- = 1\text{SO}_4^{2-}$; i.e. 1.5 M NaCl/0.75 M Na_2SO_4). The minimum chloride requirement (at 3 M Na^+) for initiating growth was 1 M. However, the activity of washed cells was much less sensitive to sodium replacement with potassium (50 % activity at 50 % substitution) and chloride substitution by sulfate (100 % activity at up to 70 % substitution by charge). In the case of high potassium, however, almost all of the cells had lysed by the end of a 2 h experiment.

The genomic DNA was extracted by using the phenol/chloroform method (Marmur, 1961). The G+C analysis and DNA–DNA hybridization were performed by using the thermal denaturation/reassociation technique (Marmur & Doty, 1962; De Ley *et al.*, 1970) with *Escherichia coli* as a standard. DNA–DNA hybridization showed that the isolates could be grouped into four genomic species (Table 1). Most of them clustered with strain HL 3^T, with DNA–DNA relatedness values above 70 %, whereas the isolates from Mongolia (HL 4) and the Adriatic Sea saltern had relatedness values of only 45–55 % with the main cluster, despite the absence of any significant phenotypic differences. Isolate ALgr 6sp^T from Wadi Natrun was genotypically most distant from the rest (showing no more than 40 % DNA–DNA relatedness).

The almost-complete 16S rRNA gene was amplified from pure cultures using bacterial primers GM3F and GM4R (Schäfer & Muyzer, 2001). The PCR products were purified from low-melting-point agarose by using a Wizard PCR-Prep kit (Promega) according to the manufacturer's instructions. Sequencing was performed using a BigDye Terminator version 3.1 sequencing reaction kit with an ABI 3730 DNA automatic sequencer (Applied Biosystems). The sequences were aligned with those from GenBank using

CLUSTAL W (Thompson *et al.*, 1994). Phylogenetic trees were reconstructed with four different algorithms by using the software packages TREECON W (van de Peer & De Wachter, 1994) and PHYLIP, version 3.5c (Felsenstein, 1993). Pair-wise evolutionary distances (expressed as estimated changes per 100 nt) were computed by using the Jukes–Cantor method (Jukes & Cantor, 1969). Because the topologies were very similar for all four types of phylogenetic tree (i.e. neighbour-joining, maximum-parsimony, distance matrix and maximum-likelihood), the final result is represented by a phylogenetic tree constructed using the neighbour-joining method (Fig. 3). Bootstrap analysis (1000 replications) was used to validate the reproducibility of the branching patterns of the trees. Analysis of the representative strains from four genomic species demonstrated that they indeed formed a compact group representing a novel lineage in the *Gammaproteobacteria* clustering with members of the family *Ectothiorhodospiraceae*. The sequence similarity between the extremely halophilic strains was 98.5–99.7 % and that between extremely halophilic strains and the moderately halophilic alkaliphilic strain ALgr 6sp^T was 93.5–94.6 %. The most closely related culturable representative of the halophilic SOB within the *Gammaproteobacteria* were members of the genus *Thioalkalivibrio* (90.0–93.1 % sequence similarity).

The data presented demonstrate the unique features of the novel group of SOB isolated from hypersaline habitats. On the basis of genetic properties, the 21 isolates can be separated into four genomic species. However, only two species could be clearly discriminated phenotypically and phylogenetically: one included extremely halophilic isolates isolated from neutral habitats and the other was repre-

Table 1. Pure cultures of halophilic aerobic SOB enriched and isolated at 3–4 M NaCl

Geographic region	Source of isolation	No. of strains	Strain designation(s)	DNA G+C content (mol%)	No. of strains in:			
					Genomic group* HL 3 ^T	Genomic group HL 4	Genomic group HL 25	Genomic group ALgr 6sp ^T
Kulunda Steppe (SW Siberia, Altai, Russia)	Salt lakes	15	HL 3 ^T , HL 9–HL 16, HL 18†, HL 22†, HLgr1–HLgr5‡	65.8–67.0	15			
NE Mongolia	Salt lakes	2	HL 4†, HL 21†	67.0	1	1		
Lake Baskunchak (South Russia)	Salt lakes	1	HL 23	65.8	1			
Crimea (Ukraine)	Salt lakes	1	HL 24	66.5	1			
Slovenia, Adriatic	Saltern	1	HL 25	66.0			1	
Wadi El Natrun (Egypt)	Salt lakes	1	ALgr 6sp ^T ‡	65.6				1

*Genetic groups HL 3^T, HL 4 and HL 25 shared DNA–DNA relatedness of around 50 % and showed less than 40 % DNA–DNA relatedness with respect to ALgr 6sp^T.

†Produces membrane-bound yellow pigment.

‡Enriched using sulfide–oxygen gradient culture.

Fig. 3. Neighbour-joining phylogenetic tree, based on 16S rRNA gene sequences, showing the position of halophilic aerobic SOB of the genus *Thiohalospira* from hypersaline habitats within the *Gammaproteobacteria*. Bootstrap percentages were derived from 1000 resamplings; values greater than 70 % were considered as significant. Names shown in bold belong to a group of moderately halophilic SOB isolated from the same habitats (Sorokin *et al.*, 2006b). Bar, 0.05 substitutions per nucleotide position.

sented by a moderately halophilic, facultative alkaliphile isolated from the alkaline hypersaline lakes of Wadi Natrun in Egypt. The extreme halophiles represent a novel genus and species, for which the name *Thiohalospira halophila* gen. nov., sp. nov. is proposed. A second novel species of this new genus, *Thiohalospira alkaliphila* sp. nov., is proposed for the facultatively alkaliphilic strain ALgr 6sp^T.

Description of *Thiohalospira* gen. nov.

Thiohalospira (Thi.o.ha'lo.spi'ra. Gr. n. *thion* sulfur; Gr. n. *hals*, *halos* salt of the sea; L. fem. n. *spira* spiral; N.L. fem. n. *Thiohalospira* halophilic sulfur spirillum).

Motile spirilla with Gram-negative type of cell wall. Obligately chemolithoautotrophic, aerobic, sulfur-oxidizing bacteria. Oxidize inorganic sulfur compounds to sulfate. Tetrathionate is the usual intermediate of thiosulfate oxidation. Includes extremely halophilic, neutrophilic and moderately halo(alkali)philic bacteria. Cellular fatty acids are dominated by saturated C₁₆–C₁₈ species. Isolated from hypersaline habitats. A member of the family *Ectothiorhodospiraceae* in the *Gammaproteobacteria*. The type species is *Thiohalospira halophila*.

Description of *Thiohalospira halophila* sp. nov.

Thiohalospira halophila (ha.lo'phi.la. Gr. n. *hals* salt; Gr. adj. *philos* loving; N.L. fem. adj. *halophila* salt-loving).

Exhibits the following properties in addition to those given in the genus description. Cells are spirilla of variable length, 0.4–0.5 × 2–8 µm, with single bipolar flagella. A membrane-bound yellow pigment can be present. Predominant cellular fatty acids are 10-methyl C_{16:0}, C_{16:0} and C_{18:0}. Accumulates glycine betaine as a compatible solute. Oxidizes thiosulfate to sulfate via tetrathionate. Also utilizes sulfide and elemental sulfur. Can be obligate microaerophiles. Extremely halophilic, with a salinity range for growth of 2.0–5.0 M NaCl and an optimum at 2.5–3.0 M. Requires high concentrations of both Na⁺ and Cl[−]. pH range for growth is between 6.5 and 8.2, with an optimum at pH 7.3–7.8. Optimum growth temperature is 32–35 °C. The DNA G+C content is 65.8–67.0 mol% (*T_m*) and that of the type strain is 65.8 mol% (*T_m*).

The type strain, HL 3^T (=DSM 15071^T=UNIQEM U219^T), was isolated from a hypersaline lake in SW Siberia (Russia). Includes another 19 strains isolated from sediments of hypersaline lakes and a solar saltern in Eurasia.

Description of *Thiohalospira alkaliphila* sp. nov.

Thiohalospira alkaliphila [al.ka.li.phi'la. M.L. n. *alkali* soda ash (from Arabic *al-qalyi* the ashes of saltwort); Gr. adj. *philos* loving; N.L. fem. adj. *alkaliphila* loving alkaline conditions].

Exhibits the following properties in addition to those given in the genus description. Cells are spirilla of variable length, 0.4–0.5 × 2–4 µm, with single polar flagella. Cells contain high concentrations of a yellow pigment in the membranes. Obligately microaerophilic; no growth occurs above 10 % O₂ in the gas phase, the optimum concentration being 2 %. Oxidizes thiosulfate and sulfide to sulfate with the occasional formation of elemental sulfur. Does not produce tetrathionate from thiosulfate. Moderately halophilic, with a salinity range for growth from 0.5 to 4.0 M NaCl and an optimum at 2.0 M. Requires high concentrations of both Na⁺ and Cl[−]. Facultatively alkaliphilic with a pH range for growth between 7.0 and 10.2 and an optimum at pH 8.5. Optimum growth temperature is 35 °C. The DNA G+C content of the type strain is 65.6 mol% (*T*_m).

The type strain, ALgr 6sp^T (=DSM 17116^T=UNIQEM U372^T), was isolated from sediments of hypersaline alkaline lakes at Wadi El Natrun in Egypt by means of sulfide–oxygen gradient cultivation.

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