EXPERIMENTAL ARTICLES

Ectothiorhodosinus mongolicum gen. nov., sp. nov., a New Purple Bacterium from a Soda Lake in Mongolia

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Abstract—A new nonmotile purple sulfur bacterium (strain M9) was isolated from the steppe soda lake Lake Dzun Uldziin Nur (pH 9.4; mineralization, 3.3%) situated in southeastern Mongolia. Individual cells appear as vibrios $0.3-0.5\times0.7-1~\mu m$ in size. The dividing cells often do not separate from each other, forming an almost closed ring. The internal photosynthetic membranes are represented by concentric lamellae lining the cell wall. Photosynthetic pigments are bacteriochlorophyll a and carotenoids of the spirilloxanthin series. The main carotenoid (>96%) is spirilloxanthin. Two typical light-harvesting complexes (LH1 and LH2) are present in the membranes in a 1:1 ratio. The bacterium is an anaerobe and facultative photoorganoheterotroph. Photolithoautotrophic growth on sulfide is scarce. Thiosulfate is utilized as an electron donor only in the presence of organic matter. Globules of elemental sulfur are formed as an intermediary product of sulfide and thiosulfate oxidation and are deposited outside the cells. The end product of oxidation is sulfate. In the presence of sulfide and carbonates, acetate, lactate, malate, pyruvate, propionate, succinate, and fumarate are used as additional sources of carbon in anoxygenic photosynthesis. Vitamins are not required. The bacterium is an alkaliphile, the pH optimum is at 8.3–9.1, the pH range is 7.6–10.1. The optimum NaCl concentration in the medium is 1 to 7%; the range is 0.5 to 0.9%. The optimum carbonate content in the medium is 2%; the range is 1 to 10%. The best growth occurs at 30-35°C. The DNA G+C content is 57.5 mol %. According to the results of analysis of the 16S rRNA gene sequences, the new isolate M9 belongs to the phylogenetic cluster containing representatives of the family Ectothiorhodospiraceae within the class "Gammaproteobacteria." In this class, the new isolate forms a new branch, which occupies an intermediate position between the representatives of the genera Ectothiorhodospira and Thiorhodospira. Based on the phenotypic and genetic characteristics, the new purple sulfur bacterium was assigned to a new species of a new genus of the family Ectothiorhodospiraceae, Ectothiorhodosinus mongolicum gen. nov., sp. nov.

Key words: alkaliphiles, purple sulfur bacteria, the family Ectothiorhodospiraceae, Ectothiorhodosinus mongolicum gen. nov., sp. nov., soda lakes.

Purple sulfur bacteria are included in the Phylum BXII Proteobacteria, Class III "Gammaproteobacteria" [1] of the order "Chromatiales." The order is subdivided into two families: Chromatiaceae and Ectothiorhodospiraceae. This subdivision is supported by both genetic and phenotypic differences between the members of these two families. The representatives of the family Ectothiorhodospiraceae are characterized by extracellular deposition of sulfur globules in the process of oxidation of the reduced sulfur compounds sulfide or thiosulfate. The family has long been represented by moderately halophilic species of the genus Ectothiorhodospira and extremely halophilic species of the genus *Halorhodospira* [2]. Some species belonging to these two genera are alkaliphiles. Both the red species containing bacteriochlorophyll a and the green species containing bacteriochlorophyll b were described among the extremely halophilic isolates. The diagnosis of the family Ectothiorhodospiraceae specifies that all its members have intracellular membrane structures in the form of stacks of lamellae [3]. Later, this family was supplemented by the new genus and species *Thiorhodospira sibirica* [4]. The bacteria of the genus Thiorhodospira possess a number of distinctive properties, including unusual photosynthetic membranes represented by strands of lamellae which pierce the whole cell, leaving cytoplasm islets, and are never arranged as stacks of lamellae as in the rest of the Ectothiorhodospiraceae strains. In addition, these bacteria deposit sulfur not only outside the cells but also in the periplasm, so that sulfur deposits appear as intracellular.

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An alkaliphilic purple sulfur bacterium, strain M9, with characteristics atypical of other *Ectothiorhodospiraceae* representatives, was isolated from a steppe soda lake in southeastern Mongolia. It has small nonmotile curved cells containing photosynthetic membranes in the form of peripheral circular lamellae and deposits extracellular sulfur in the course of oxidation of reduced sulfur compounds. According to the results of analysis of the 16S rDNA gene nucleotide sequences, this bacterium belongs to the *Ectothiorhodospiraceae* cluster, being, however, remote from the known representatives of this family. In this paper, this bacterium, strain M9, is described as the new genus and species *Ectothiorhodosinus mongolicum* gen. nov., sp. nov.

MATERIALS AND METHODS

Source of isolation. The purple sulfur bacterium, strain M9, was isolated from a sample of decomposing near-shore algae and cyanobacteria driven by the wind to the shore of the steppe soda lake Lake Dzun Uldziin Nur located not far from the town of Choybalsan. The total mineralization of the lake water in the sampling period was 3.3%; the sulfate content was 0.08%; alkalinity equaled 180 mM (bicarbonates, 85 mM; carbonates, 95 mM); pH 9.4. The water had a characteristic sulfide odor.

Isolation and cultivation. Medium of the following composition (per 1 l of distilled water) was used for the cultivation of the purple sulfur bacterium, strain M9: KH₂PO₄, 0.5 g; NH₄Cl, 0.5 g; NaCl, 30 g; MgCl₂ · 6H₂O, 0.2 g; CaCl₂, 0.1g; NaHCO₃, 5 g; Na₂CO₃, 5 g; Na-acetate, 1 g; yeast extract, 0.1 g; Na₂S₂O₃ · 5H₂O, 0.5 g; Na₂S · 9H₂O, 0.3 g; vitamin B₁₂, 20 µg; trace element solution, 1 ml [5]; pH 9. The culture purification was carried out on agarized (0.7%) medium of the same composition by repeatedly inoculating the medium with colonies from end-point dilutions. The culture purity was checked by microscopy and inoculation of agarized medium under anaerobic and aerobic conditions. In liquid media, the bacterium was cultivated in 50-ml flasks with screw caps. The cultures were incubated at 2000 lx and 30 to 35°C.

Study of cell morphology and fine structure. The morphology of the bacterium was studied by means of light phase-contrast microscopy and electron transmission microscopy. Specimens of whole cells for electron microscopy were negatively stained with 1% phosphotungstic acid. The microorganism ultrastructure was studied as described earlier [4]. The sections and specimens of whole cells were examined under a Jeol JEM 100C electron microscope (Japan) at an accelerating voltage of 80 kV.

Study of the cell pigment composition. The pigment composition of the bacterium was studied in crude chromatophore fraction, in the supernatant fluid after centrifugation of cells destroyed by ultrasound, as well as in acetone—methanol extracts. The absorption

spectra were recorded using an SF 56 spectrophotometer (LOMO, Russia) at 350–1000 nm or a UV-160 spectrophotometer (Shimadzu, Japan) at 200–1100 nm. The absorption spectra of the light-harvesting complexes were recorded directly in the gel. The chromatophores were isolated after cell destruction with ultrasound by differential centrifugation. The technique of polyacrylamide gel electrophoresis for the isolation of the complexes was described in detail earlier [6]. One modification was made in it: instead of the strong nonionic detergent Triton X-100, a milder detergent, dodecyl maltoside, was used.

To extract carotenoids, 1 ml of the bacterium chromatophores with an optical density of 40 to 50 units at 850 nm was added to 10 ml of an acetone–methanol mixture (7:2) under constant stirring. Petroleum ether (2–4 ml) and water (20–25 ml) were sequentially added to the resulting extract and mixed. The extracted pigments occurred in the petroleum ether at the top of the mixture. They were sampled with a pipette, transferred to a small glass vial, and dried in a nitrogen flow. The resulting pigment film was dissolved in methylene chloride, and 25 μ l of the extract was applied onto an HPLC column.

The pigments were analyzed by HPLC as described in [7], on a Spherisorb ODS2 column (5 μ m \times 250 mm, Waters, England). The HPLC unit consisted of an LC 10ADvp pump with an FCV 10Alvp module (Shimadzu, Japan), which allowed a solvent gradient to be created at a low pressure, a UV160 spectrophotometer (Shimadzu, Japan) with an HPLC cell, a 2000 integrator (Merck, Germany), and a 201 fraction collector (Gilson, France). The solvent supply rate was 1 ml/min. The column was equilibrated with a 77% acetonitrile water (9:1) and 23% ethyl acetate mixture, which was passed through the column during the first 3 min. This mixture was then linearly replaced with ethyl acetate for 37 min, and pure ethyl acetate was passed through it for 3 min. The pigment fractions were collected by an collector operating in an automatic mode. The absorption spectra were recorded with a UV-160 spectrophotometer. The carotenoids concentration was calculated on the basis of the corresponding extinction coefficients and the volume of the fraction obtained, as described in [8].

Determination of the composition of the cellular isoprenoid quinones. The mass spectra of quinones were recorded using a Finnigan MAT 8430 mass spectrometer (Bremen, Germany) with an SS-300 data processing system at an accelerating voltage of 3 kV, an energy of ionizing electrons of 70 eV, an ion source temperature of 25°C, and a sample evaporation temperature of 150 to 170°C, using the system of direct introduction of substance into the ionization zone [9].

The study of physiology. To determine the spectrum of the organic substrates used, a nutrient mineral medium with sulfide (0.3 g/l), thiosulfate (0.5 g/l), and yeast extract (0.05 g/l) as a growth factor was used as a

basic one. The organic substances to be tested were added to a concentration of 0.5 g/l. To elucidate the requirements of the bacterium studied in H-donors, carbon and sulfur sources, and vitamins, as well as its reaction to different pH values and carbonate and NaCl concentrations, the basic medium was used in which the parameters studied were varied. The degree of favorableness of the cultivation conditions was judged from the biomass yield assessed from the optical density of the culture measured on a KFK-3 photometer (Russia) at 650 nm in the stationary growth phase, when the culture did not contain elemental sulfur.

Growth under microaerobic conditions was tested on agarized (0.7%) medium containing acetate and yeast extract in tubes with cotton plugs [10].

Utilization of sulfur compounds and their oxidation products were determined according to the standard techniques as described earlier [4].

Methods of genosystemics. DNA was isolated using the Marmur method [11]. The content of G+C pairs in DNA was determined according to the procedure described by Owen [12].

The 16S rRNA gene amplification and sequencing was carried out using primers universal for most prokaryotes [13]. Buffer of the following composition was used for the amplification: MgCl₂, 1.5 mM; KCl, 50 mM; Tris-HCl, 10 mM; pH 8.3; gelatin, 0.001%. The volume of the reaction mixtures was 100 µl, and they contained standard dNTP concentration and equimolar amounts of the primers pA and pH'. Thirty amplification cycles of the following temperature profile were carried out: DNA denaturation at 94°C for 30 s; primer annealing at 40°C for 1 min; elongation at 72°C for 2 min 30 s. After purification on low-gellingpoint agarose and on Promega columns, the 16S rRNA gene was sequenced in both directions with the use of forward and reverse universal primers and Sequenase (Biochemicals, Cleveland, Ohio, USA).

The primary analysis of similarities of the 16S rRNA gene nucleotide sequences of the strains studied was carried out using the BLASTA server. The sequences were aligned with the corresponding sequences of the closest bacterial species by means of the CLUSTALX software. Unrooted phylogenetic trees of the bacteria were constructed using the methods realized in the TREECON software package [14]. The 16S rRNA gene sequence of strain M9 was deposited in GenBank (accession number AY299804).

RESULTS AND DISCUSSION

Cultural properties. The cell suspension of the bacterial strain M9 grown under anaerobic conditions was red-colored. Homogeneous growth was observed on a liquid medium in flasks with screw caps under favorable conditions. In the exponential growth phase, the medium became turbid as a result of the deposition of elemental sulfur, observed under a microscope as

light-refracting extracellular drops. At the beginning of the stationary growth phase, no traces of elemental sulfur could be seen, and the culture got slimy. In the light, the bacterium formed small spherical colonies in the depth of the agarized medium.

Morphology and fine structure. The cells of the new bacterium are nonmotile and appear as vibrios $0.3-0.5\times0.7-1~\mu m$ in size (Fig. 1). They are surrounded by a diffuse slimy layer. When dividing by an asymmetrically ingrowing septum, the cells often do not separate from each other, forming a semicircle or an almost closed ring (Figs. 1b, 1c).

The study of the fine structure of M9 cells showed that they had a cell wall of the gram-negative type (Figs. 1d, 1e). The internal photosynthetic membranes were represented in the bacterium by poorly developed concentric lamellae lining the cell wall (Fig. 1d, 1e). Often, no intracellular membranes could be revealed in the cells at all; thus, areas of compartmentalized cytoplasmic membrane may also be thought to perform the photosynthetic function in this bacterium. In all of the known Ectothiorhodospiraceae species, the lamellae are arranged into ordered stacks. The exception is Thiorhodospira sibirica [4], in which the lamellae appear as long strands piercing the whole cell and sometimes forming coils located at the periphery. The new bacterium, strain M9, formed only ring-shaped lamellae, similar to the membranes present in the halophilic nonsulfur purple bacterium Rhodothalassium salexigens [15, 16]. Structures of this type were not found earlier in representatives of the family Ectothiorhodospiraceae. Electron-dense round inclusions, likely polyphosphates, were infrequently present in the cytoplasm of the M9 cells (Fig. 1e).

Pigments. The absorption spectra of strain M9 whole cells (Fig. 2) and those of the membranes (chromatophores) isolated from them had three absorption maximums at 797, 854, and 873 nm (Fig. 2). The latter maximum belongs to the LH1 complex, which is a constituent of the complex core (the LH1-RC ensemble), and the other two belong to the LH2 peripheral lightharvesting complex. In the visible part of the absorption spectrum of these membranes, the absorption band with a maximum at 590 nm, corresponding to the Qx transition of the bacteriochlorophyll molecules, was present as in other bacteria. The aggregate of the spectral characteristics (the absorption spectra of cells, membranes, and acetone–methanol extract) testify to the presence of bacteriochlorophyll a in strain M9 cells. The peaks at 485, 514, and 550 nm indicate the presence of carotenoids of the normal spirilloxanthin series in the cells, which is confirmed by the spectrum of the acetonemethanol cell extract (Fig. 2) and the results of the HPLC analysis. The study of the carotenoid composition confirmed that the main pigment in this bacterium is spirilloxanthin, which accounts for 96 to 97% of the total amount of carotenoids. In addition, anhydror-

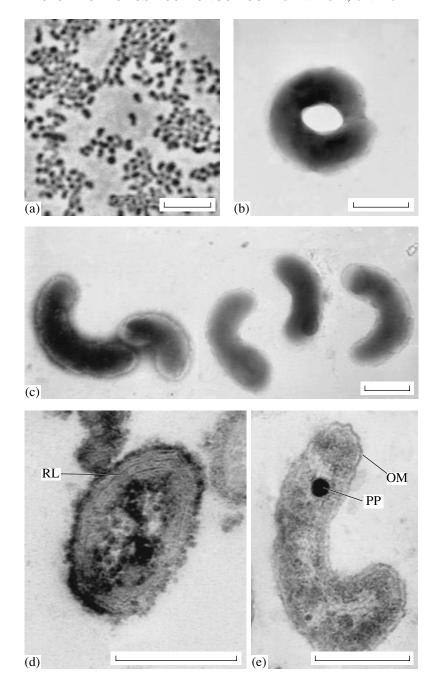


Fig. 1. Morphology and the fine structure of strain M9 cells: (a) phase contrast light microscopy and transmission electron microscopy of (b, c) total specimens contrasted with phosphotungstic acid and (d, e) ultrathin cell sections. RL, ring-shaped lamellae; PP, polyphosphates; OM, outer membrane. Scale bars: (a) 5 μm; (b–d) 0.5 μm.

hodovibrin (2 to 2.5%) and trace amounts of lycopene (<1%) were also revealed.

The presence in the absorption spectrum of the peak at 421 nm, which belongs to a membrane-bound cyto-chrome, is not quite typical. Such cytochromes are normally absent from most of the photosynthesizing bacteria studied [17].

Pigment–protein complexes. A preliminary assay of the composition of the pigment–protein complexes

performed by means of preparative electrophoresis showed that strain M9 membranes treated with dodecyl maltoside can be divided into three fractions: the LH1-RC ensemble, the LH2 complex, and the cytochrome fraction. The absorption spectra of both types of the complexes did not differ substantially from similar complexes from other photosynthesizing bacteria. The assay of carotenoids in these fractions showed that the LH1–RC ensemble contained only spirilloxanthin, and the LH2 complex, apart from spirolloxanthin, also

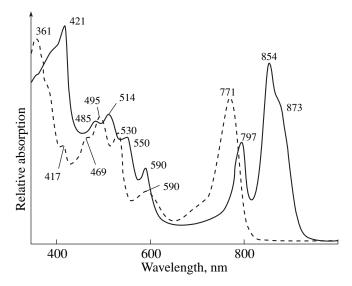


Fig. 2. Absorption spectra of whole cells (solid line) and acetone—methanol extract (broken line) of strain M9, cells.

contained anhydrorhodovibrin (3.5 to 4%) and trace amounts of lycopene. The analysis of the membrane absorption spectra and the results of the separation of the complexes allow a conclusion to be reached that one LH1–RC ensemble occurs per one LH2 complex. In other species of bacteria, this ratio is usually 1:2 or 1:3. This means that in the purple sulfur bacterium, strain M9, the size of the peripheral antenna and, hence, the size of the photosynthetic unit is two- to threefold less than in other bacterial species [18].

Composition of isoprenoid quinones. Mass spectra showed the presence in strain M9 of only one quinone, ubiquinone Q-8. Ubiquinone Q-8 had been found in most representatives of the family *Ectothiorhodospiraceae*, except *E. shaposhnikovii* and *E. vacuolata* [2]. It should be noted that *Ectothiorhodospiraceae* species usually also contain the menaquinones MK8, MK7, and MK4/5 purple bacteria. We did not

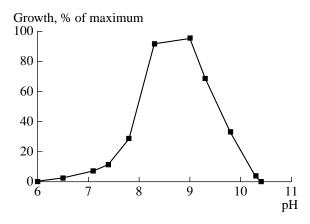


Fig. 3. Influence of pH on the growth of strain M9. The medium contained 1% carbonates and 3% NaCl.

succeed in revealing quinones other than Q-8 in strain M9 with the methods we used.

Physiological properties. Strain M9, exhibited weak photolithoautotrophic growth with sulfide as an electron donor and carbonate as the carbon source. The capacity for autotrophic growth was also evidenced by the presence of the gene determining "green" RuBPcarboxylase (our unpublished data), which has been detected in most purple sulfur bacteria. Good growth of the bacterium was possible only in the presence, along with bicarbonate, of acetate or some other organic compounds, including lactate, malate, pyruvate, propionate, succinate, and fumarate. Poorer growth, but more active than under photoautotrophic conditions, was maintained by casein hydrolysate, yeast extract, and fructose. Arginine, aspartate, benzoate, butyrate, valerate, glycolate, glycerin, glutamate, glucose, gluconate, caprylate, caproate, malonate, mannitol, methanol, sorbitol, tartrate, citrate, formate, and ethanol were not photoassimilated by strain M9. The bacterium showed good growth under photoheterotrophic conditions with acetate (1 g/l), lactate (1 g/l), and yeast extract (1 g/l) in the presence of 0.1 g/l sulfide as a source of reduced sulfur. The bacterium did not depend on vitamins, but the yeast extract appreciably stimulated growth.

In the presence of carbonates and acetate, sulfide or thiosulfate were oxidized to sulfur which resulted in the turbidity of the medium; subsequently, sulfur was oxidized to sulfates (data not shown).

Thus, the new bacterium showed a poor capacity for photolithoautotrophy, preferring photolithoheterotrophic or photoorganoheterotrophic growth.

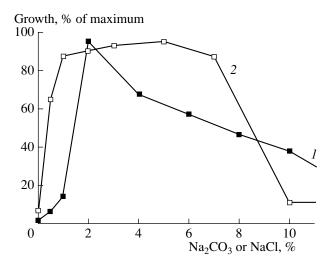


Fig. 4. Influence of (I) Na₂CO₃ and (2) NaCl concentrations on the growth of strain M9. The influence of the Na₂CO₃ concentrations was tested at pH 9 in the presence of 1% NaCl. pH was adjusted by the addition of 1 N HCl. On medium without Na₂CO₃, pH was adjusted to pH 9 by the addition of 1 N NaOH. The influence of NaCl concentrations was tested at pH 9 in the presence of 0.3% carbonates.

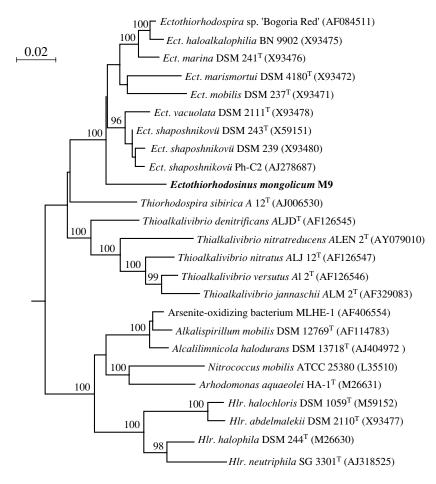


Fig. 5. Phylogenetic tree showing the position of strain M9 within the family *Ectothiorhodospiraceae*. The figures at the branching points are bootstrap values (values below 90 are not shown). The scale bar corresponds to five nucleotide substitutions per every 100 nucleotides (evolutionary distances).

The growth of strain M9 under photolithoheterotrophic conditions occurred in a pH range varying from 7.6 to 10.1, with an optimum pH 8.3–9.1 (Fig. 3). The microorganism did not grow at pH 7.0, and, thus, it may be considered to be an alkaliphile. The carbonate concentration most favorable for growth was 2% (0.24 M); the growth range varied from 1 to 10% (0.1–1.2 M) (Fig. 4). The new bacterium is a moderate halophile. It did not grow in the absence of sodium chloride. Growth was possible in the range of NaCl concentrations in the medium varying from 0.5 to 9%, with an optimum at 1–7% (Fig. 4). The best growth occurred at 30 to 35°C.

Phylogenetic position and taxonomy. According to the data of comparative analysis of the 16S rDNA gene sequences, strain M9 belongs to the family *Ectothiorhodospiraceae* (Fig. 5). In this family, it formed a new separate branch occupying an intermediate position between the cluster of species of the genus *Ectothiorhodospira* (93.9 to 96.3% of sequence similarity) and the separate branch made up by *Thiorhodospira sibirica* (93.2%).

The DNA G+C content of strain M9 was 57.5 mol %. This value is lower than that typical of the family *Ectothiorhodospiraceae*, where it varies within the range of 61.4–74.5 mol % (Table 1), with the exception of the extremely halophilic species *Halorhodospira halochloris* (50.5-52.9 mol %) and the recently described *Thiorhodospira sibirica* (56–57.4 mol %).

Thus, the separate position of the new isolate M9 in the phylogenetic tree of the purple bacteria of the family Ectothiorhodospiraceae, the low DNA G+C content, distinguishing it from most of the members of this family, as well as a number of unusual phenotypic features—unusual morphology; the absence of flagellumassisted motility; the ring-shaped lamellae serving as photosynthesizing membranes; the size of the peripheral antenna of the pigment-protein complex, which is 2 or 3 times smaller than in other species of purple bacteria; and poor photoautotrophic growth—lead us to propose that the purple sulfur bacterium, strain M9, be systematized in a new species of a new genus of the Ectothiorhodospiraceae family, for which we propose the name Ectothiorhodosinus mongolicum gen. nov., sp. nov.

Properties of four genera of the family Ectothiorhodospiraceae

Characteristic	Ectothiorhodosinus	Thiorhodospira [4]	Ectothiorhodospira [2]	Halorhodospira [2, 19]
Cell diameter, µm	0.3-0.5	3–4	0.7–1.5	0.5–1.2
Cell shape	Vibrio, toroid	Spirillum	Rod, vibrio, spirillum	Spirillum
Motility	_	+	+	+
Bacteriochlorophyll	a	a	a	a, b
IMS	Ring-shaped	Strands of lamellaer	Stacks of lamellae	Stacks of lamellae
Optimum NaCl, %	1–7	0.5–1	1–5	12–25
Optimum pH	8.3–9.1	8.5–9.5	7–9.5	8.3-9 (6.8-7)*
Reaction to oxygen	Anaerobes	Anaerobes	Anaerobes, microaerobes	Anaerobes
Thiosulfate consumption	+	_	+	+-
Photoautotrophic growth on sulfide	(+)	(+)	+	+
Photoorganotrophic growth	+	_	+	_
G+C in DNA, mol %	57.5 (Tm)	56–57.9 (Tm)	61.4–65 (Tm) 62.3–69.9 (Bd)	50.5–74.5 (Tm)

Note: +, the characteristic is positive; -, the characteristic is negative; and (+), the characteristic is poorly manifested. IMS, internal membrane structures. The DNA G+C content was determined by the thermal denaturation (Tm) or buoyant density (Bd) methods.

Description of *Ectothiorhodosinus* **gen. nov.** *Ectothiorhodosinus* (Ec.to.thi.o.rho.do.si'nus. Gr. prep. *ecto* meaning outside; Gr. n. *thios* meaning sulfur; Gr. n. *rhodon* meaning rose; L. n. *sinus* meaning bend; M.L. fem. n. *Ectothiorhodosinus*: red curved rod with extracellular sulfur).

The cells are vibrio-shaped or semicircular and nonmotile. The bacterium is gram-negative and belongs to phylum BXII Proteobacteria, class III Gammaproteobacteria, order Chromatiales, family Ectothiorhodospiraceae. Cells contain bacteriochlorophyll and carotenoids. The internal photosynthetic membranes have the form of concentric lamellae lining the cell wall. The metabolism is anaerobic, photolithoautotrophic, facultatively photolithoheterotrophic, or photoorganoheterotrophic. Sulfide is utilized as an electron donor. Globules of elemental sulfur are formed as an intermediary product of sulfide oxidation and are deposited outside the cells. The end product of sulfide oxidation is sulfate. In the presence of sulfide and carbonates, organic compounds are photoassimilated. Mesophile. Depends on medium salinity and alkalinity for growth.

The DNA G+C content is 57.5 mol % (Tm).

The habitat is subsaline soda lakes.

The type species of the genus is *Ectothiorhodosinus mongolicum* sp. nov.

Description of *Ectothiorhodosinus mongolicum* **sp. nov.** *Ectothiorhodosinus mongolicum* (mon'go'l.i.cum. M.L. fem. adj. *mongolicum*: related or belonging to Mongolia).

The cells are nonmotile, vibrio-shaped, semicircular, or toroid. The cell size is $0.3-0.5 \times 0.7-1$ µm. Cell

division occurs by means of a nonuniformly ingrowing cellular septum. The color of the cell suspension is pink to brownish red. Cells contain bacteriochlorophyll a and carotenoids of the spirilloxanthin series. The internal photosynthetic membranes have the form of concentric lamellae lining the cell wall. In some of the cells, no lamellae or any other intracytoplasmic membranes can be revealed. The size of the peripheral antenna of the pigment–protein complex is 2 or 3 times smaller (one LH1–RC ensemble per one LH2 complex) than in other species of purple bacteria. Electron-dense polyphosphate inclusions are present in the cells. Anaerobe. Photolithoautotrophic growth occuring in the presence of sulfide is scarce. Good growth under photolithoheterotrophic and photoorganoheterotrophic conditions. Sulfide and thiosulfate are utilized as electron donors. Globules of elemental sulfur are formed as an intermediate product of oxidation of reduced sulfur compounds and are deposited outside the cells. The end oxidation product is sulfate. In the presence of sulfide and carbonates, acetate, lactate, malate, pyruvate, propionate, succinate, and fumarate are utilized as additional sources of carbon. Alkaliphile, the pH optimum for growth is 8.3–9.1, and the growth range is 7.6–10.1. Moderate halophile. The optimum NaCl concentration in the medium is 1-7%; the growth range is 0.5-9%. The optimal carbonate content is 2% (0.24 M); the growth range is 1–10% (0.1–1.2 M). The temperature optimum for growth is 30–35°C.

The DNA G+C content is 57.5 mol % (Tm).

The habitat is near-shore sediments of subsaline soda lakes rich in organic matter and sulfide.

^{*} Characteristic of *H. neutriphila*.

The type strain is M9^T isolated from a sample of decomposing near-shore algae driven by the wind to the shoreline of the steppe soda lake Lake Dzun Uldziin Nur in southeastern Mongolia. Deposited with the German Culture Collection (DSMZ) under the number DSM 15479^T and with the Collection of Unique Cultures, Institute of Microbiology, Russian Academy of Sciences (UNIQEM) under the number U217^T.

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