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EXPERIMENTAL ARTICLES

Phylogenetic Position of the Purple Sulfur Bacterium *Lamprobacter modestohalophilus* Determined Based on the Data on New Strains of the Species

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Abstract—*Lamprobacter*, the genus of halophilic purple sulfur bacteria (PSB) with the single species *Lpb. modestohalophilus* was described in 1979. Rod-shaped *Lamprobacter* cells contained gas vesicles during the nonmotile growth phase; motile cells without gas vesicles were sometimes formed. Bacteria contained bacteriochlorophyll *a* and a carotenoid okenone. The names of this genus and species were included in the list of approved microbial names in 1988. Since the type strain *Lpb. modestohalophilus* RO1^T has been lost, its 16S rRNA gene sequences have not been obtained. Based on analysis of the 16S rRNA genes, a new genus *Halochromatium* comprising the motile extremely halophilic *Chromatium*-like species was proposed in 1998. Members of this genus never contain gas vesicles. In spite of the phenotypic differences between the genera *Lamprobacter* and *Halochromatium*, phylogenetic boundaries between these taxa remained undetermined. Description of a marine bacteria formerly belonging to *Lamprobacter* according to its morphological and physiological properties as a new *Halochromatium* species, *Hch. roseum*, resulted in additional complication of the taxonomic situation. The present work provides evidence for the preservation of two phenotypically and phylogenetically different genera, *Lamprobacter* and *Halochromatium*, *Lpb. modestohalophilus* is proposed as the type species of the genus *Lamprobacter*. Characteristics of two *Lpb. modestohalophilus* strains were extensively investigated, and one of them (strain Sivash) was proposed as the neotype strain of the species. It was suggested to retain the genus *Halochromatium* as containing extremely halophilic species *Hch. salexigens* and *Hch. glycolicum*, while transfer of the weakly halophilic species *Hch. roseum* to the genus *Lamprobacter* is proposed, resulting in a new combination *Lamprobacter roseus* comb. nov.

Keywords: halophilic purple sulfur bacteria, phylogeny, taxonomy, *Lamprobacter modestohalophilus*, *Halochromatium roseum*, *Lamprobacter roseus* comb. nov.

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Lamprobacter modestohalophilus, a new genus and species of purple sulfur bacteria, was described in 1979. Strains of this species, RO-1^T and WS-1, were isolated from saline lakes Rozovyi Porsugel' (Cheleken Peninsula, Turkmenia) and Veisovo (Slavyansk, Ukraine) [1]. The cells of this bacterium were rod-shaped or oval and possessed a complex life cycle with two alternating morphological forms: motile flagellated cells without gas vesicles during active growth and nonmotile cells with gas vesicles in the late exponential phase. Bacteriochlorophyll (Bchl) *a* and the carotenoid okenone were the photosynthetic pigments. Bacteria required NaCl for growth, with the optimal salinity at 1–2%. *Lpb. modestohalophilus* was described based on its morphological and physiological properties [1–3] and was included in the approved list of bacterial names [4, 5]. Since the type strain RO-1^T was lost, the strain *Lpb. modestohalophilus* Sivash was proposed as a neotype [6]. For this strain, the pigment–protein complexes of the photosynthetic apparatus, hydrogenase and the RuBisCO-encoding genes were studied [7–9]. Since the 16S rRNA gene sequence of strain Sivash remained undetermined for a long time, it could not be formally used as a neotype. Another strain of purple sulfur bacteria, ShN*Lb*02, isolated from a Siberian meromictic Lake Shunet in 2002, was phenotypically similar to *Lpb. modestohalophilus* [10].

The present work presents the results of phylogenetic, morphological, and physiological investigation of two strains, *Lpb. modestohalophilus* Sivash and ShN*Lb*02, one of which (Sivash) is proposed as a neotype for the species and genus.

MATERIALS AND METHODS

Source of isolation. *Lpb. modestohalophilus* Sivash was isolated in 1987 from a cyanobacterial mat of a shallow saline Lake Sivash (Crimea) with pH 7.8 and salinity 40 g/L. *Lpb. modestohalophilus* strain

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ShN*Lb*02 was isolated in 2002 from the redox zone (4.5 m) of a saline eutrophic meromictic Lake Shunet (Khakassia, Russia). This lake has water of the sulfate–chloride–sodium–magnesium type with a pronounced salinity gradient (10–65 g/L) and considerable sulfide concentration at the bottom (over 500 mg/L).

Isolation and purification. *Lpb. modestohalophilus* Sivash grown in the medium of the following composition (g/L distilled water) was used: KH_2PO_4, 0.5; NaCl, 20–40; $MgCl_2$, 0.2; NH_4Cl, 0.5; KCl, 0.33; $NaHCO_3$, 1,5; $CaCl_2 \cdot 6H_2O$, 0.1; $Na_2S \cdot 9H_2O$, 0.5; $Na_2S_2O_3 \cdot 5H_2O$, 0.5; $CH_3COONa \cdot 3H_2O$, 0.5; yeast extract, 0.1; vitamin B_{12}, 20 μg; trace element solution, 1 mL [11]; pH 7.5.

Strain ShN*Lb*02 was grown in a similar medium with the salt mixture simulating the chemical composition of Lake Shunet water (g/L distilled water): NaCl, 5.3; $MgSO_4 \cdot 7H_2O$, 0.5; NH_4Cl, 0.7; KCl, 0.33; Na_2SO_4, 21; $MgCl_2 \cdot 7H_2O$, 4.3.

Pure cultures were obtained by the serial dilutions method after repeated transfers of well-isolated colonies grown in agar (0.7%) medium. The bacteria were grown at 30°C under anoxic conditions in 30-mL screw-capped vials under illumination (2000 lx).

Absorption spectra of the pigments for live cells in 50% glycerol and for acetone–methanol extracts (7 : 2) were determined on an SF-56 spectrophotometer (LOMO, Russia).

Morphology of the cells was examined by light and electron microscopy. Total preparations for electron microscopy were stained with 2% uranyl acetate. Ultrathin sections were obtained as described previously [12].

The basal mineral medium with sulfide (0.5 g/L), thiosulfate (0.5 g/L), and yeast extract (0.05 g/L) was used to determine utilization of various organic substrates (0.5 g/L) and response to various pH levels and salt concentrations. Growth was assessed during the stationary growth phase by OD_{650} on a KFK-3 photometer (Russia). Thiosulfate, sulfide, and sulfite were determined by iodometric titration [13]. Sulfate was determined turbidimetrically [14]. Ability to utilize organic substrates was determined as the difference between photoautotrophic growth and growth in the presence of an organic substrate.

DNA extraction and amplification and sequencing of the 16S rRNA genes. DNA was extracted according to Marmur [15]. The DNA G+C content was determined by thermal denaturation [16]. DNA–DNA hybridization was carried out by the optical reassociation method [17].

DNA extraction and purification for analysis of the 16S rRNA genes was carried out as described previously [18]. Amplification of the 16S rRNA genes was carried out with the universal bacterial primers [19]. Amplification products were sequenced according to Sanger using the Big Dye Terminator v. 3.1 kit on an ABI 3730 automatic sequencer (Applied Biosystems, United States) according to the manufacturer's recommendations.

Phylogenetic analysis of the 16S rRNA sequences. The sequences were edited using BioEdit [http://jwbrown.mbio.ncsu.edu/BioEdit/bioedit.html]. Initial comparative analysis of the de novo obtained sequences with those from the GenBank database was carried out using NCBI BLAST [http://www.ncbi.nlm.nih.gov/blast]. The sequences were aligned with the relevant sequences of the most closely related bacterial species using the CLUSTALW v. 1.75 software package. The phylogenetic tree was constructed using the methods implemented in the TREECONW [http://bioc-www.uia.ac.be/u/yvdp/treeconw.html] and PHYLIP [http://evolution.genetics.washington.edu/phylip.html] software packages.

RESULTS

The isolates were morphologically similar, with oval or rod-shaped cells (2.0–2.5 × 4–5 μm). When grown in the medium with salinity exceeding the optimal value, the cells were slightly curved. The cells divided by binary fission. Both strains had a pronounced growth cycle. In young cultures, motile cells with irregularly located flagella were observed (Fig. 1a). Nonmotile cells with gas vesicles forming gas vacuoles visible under light microscope predominated in mature cultures (Fig. 1b). Droplets of elemental sulfur (Fig. 1c) observed during the early stage of growth were not revealed in older cultures.

Cell suspensions of both strains were pinkish-purple. Absorption spectra of the strains mostly coincided with each other and with the spectrum of the previously described strain *Lpb. modestohalophilus* RO-1^T. The peaks at 395, 830, and 880 nm indicated the presence of Bchl *a*, while absorption maxima at 512 nm and shoulders at 485 and 540 nm suggested the presence of the carotenoid okenone (Fig. 2). Absorption spectra of the acetone–methanol extracts confirmed the presence of Bchl *a* (360 and 770 nm) and okenone (489 and 579 nm).

Ultrathin sections of the cells of both strains revealed the presence of a well-developed photosynthetic apparatus of vesicular type (Fig. 1c). The cell wall structure was of the gram-negative type with a pronounced bilayer outer membrane and visible periplasmic space. The outer cell wall layer was thickened.

Both strain Sivash and strain ShN*Lb*02 grew under photolithoautotrophic conditions with sulfide, thiosulfate, S^0, or hydrogen as electron donors and CO_2 as a carbon source. Sulfide and thiosulfate were oxidized to elemental sulfur, which was accumulated in the cells and subsequently oxidized to sulfate.

Apart from CO_2, strains Sivash and ShN*Lb*02 were able to use organic carbon sources, which were, however, fewer than the sources used by the previ-

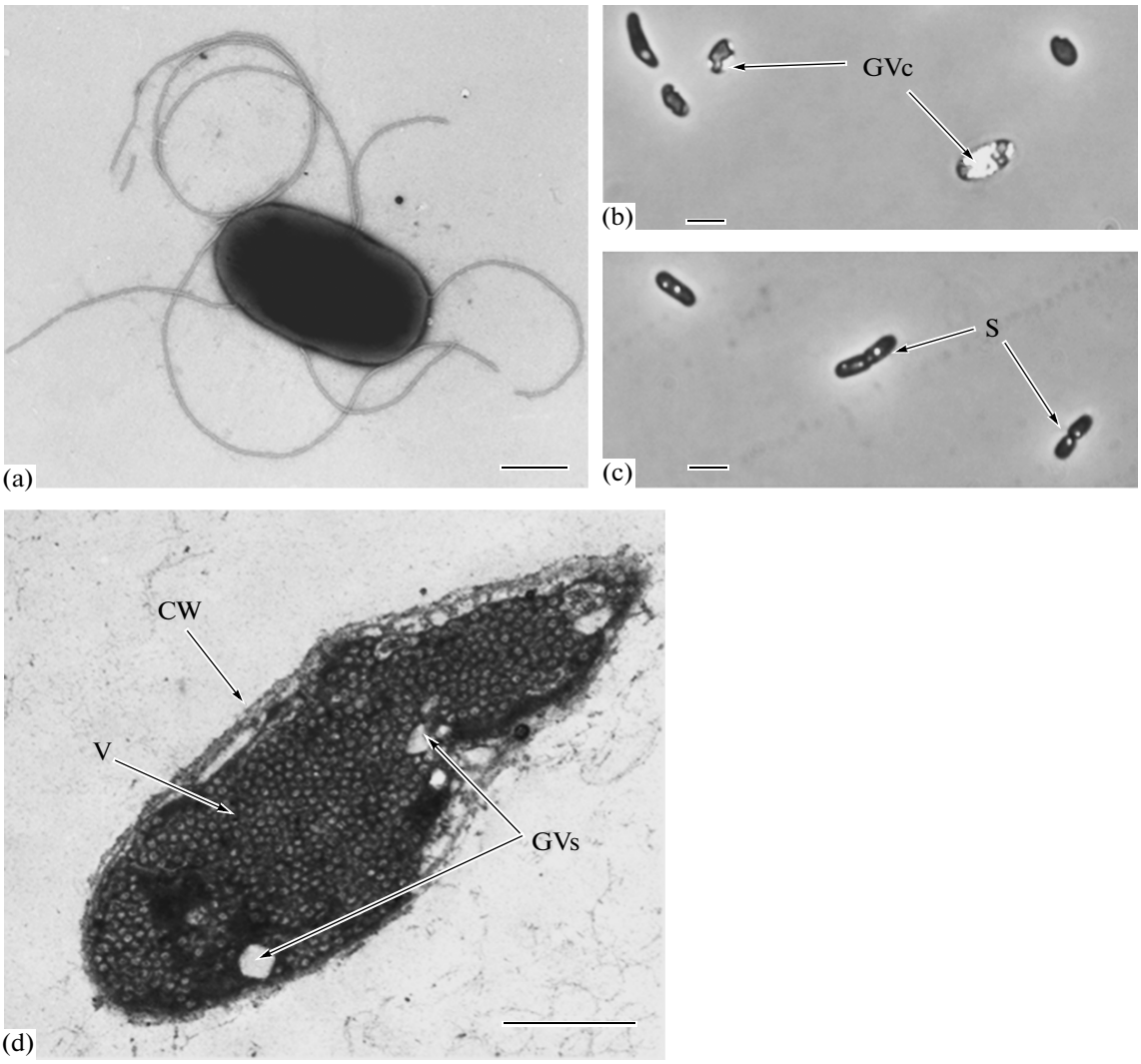

Fig. 1. Morphology (a, b, c) and ultrastructure (d) of *Lpb. modestohalophilus* strains Sivash (a, b) and ShN*Lb*02 (d). Scale bar, 1 μm (b) and 0.5 μm (b, c, d). Designations: CW, cell wall, V, vesicular photosynthetic structures, GVc, gas vacuoles, GVs, gas vesicles, S, intracellular sulfur.

ously described strain *Lpb. modestohalophilus* RO-1^T (Table 1). Strains Sivash and ShN*Lb*02 utilized acetate, pyruvate, lactate, glycerol, and yeast extract. Growth was most pronounced on glycerol, while only weak growth occurred in the presence of casein hydrolysate. The strains did not grow on arginine, aspartate, butanol, butyrate, benzoate, caprylate, caproate, citrate, ethanol, glucose, glutamate, formate, fructose, fumarate, malate, malonate, mannitol, methanol, propionate, propanol, sorbitol, tartrate, and valerate.

Since no assimilatory sulfate reduction was found in strain Sivash, reduced sulfur compounds were required for growth with organic substrates. Strain ShN*Lb*02 did not require reduced sulfur compounds for growth with the listed organic compounds. Unlike strains RO-1^T and Sivash, strain ShN*Lb*02 did not require vitamin B_{12} for growth.

Both strain Sivash and strain RO-1^T were capable of chemolithotrophic growth, while this capacity was not shown for strain ShN*Lb*02 (Table 2).

Similar to the previously described strain RO-1^T, strains Sivash and ShN*Lb*02 were obligate moderate halophiles. Growth occurred at NaCl concentrations from 1.5 to 9% with the optima at 4 and 2% NaCl for strains Sivash and ShN*Lb*02, respectively. Optimal growth of strains Sivash and ShN*Lb*02 occurred at pH 7.4–7.6 and 25–34°C.

The DNA G+C content for strains Sivash and ShN*Lb*02 was 62.5 and 62.4 mol %, respectively. DNA–DNA hybridization of strains Sivash and

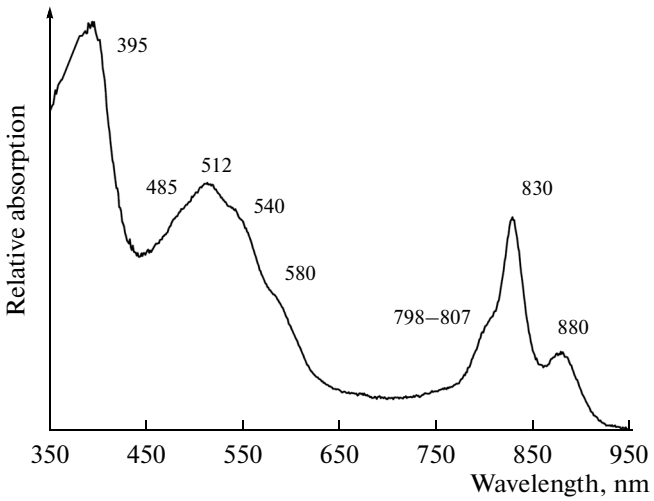

Fig. 2. Absorption spectrum of whole cells of *Lpb. modestohalophilus* strain Sivash.

ShN*Lb*02 revealed 92% homology, which corresponded to the intraspecific level.

Analysis of the 16S rRNA gene sequences of strains Sivash and ShN*Lb*02 revealed their high similarity (99.8%), confirming their classification as members of the same species. On the phylogenetic tree (Fig. 3), both strains fell into the cluster comprising marine and halophilic PSB of the genera *Halochromatium, Marichromatium*, and *Thiohalocapsa*. Type strains of the known *Halochromatium* species were most closely related to the strains under study. The highest similarity of the 16S rRNA gene sequences (99.0–99.1%) was found for *Hch. roseum* JA134^T. Homology with the species *Hch. salexigens* and *Hch. glycolicum* was 98.0–98.2%. The similarity between the 16S rRNA gene sequences of strains Sivash and ShN*Lb*02 and those of the type strains of *Marichromatium* and *Thiohalocapsa* species was considerably lower (95.2–96.7%), while homology to other members of the family *Chromatiaceae* was 89.1–95.4%, corresponding to the intrageneric level within this family.

DISCUSSION

The phenotypic characteristics of the PSB strains Sivash and ShN*Lb*02 agree with the previously published description of bacteria of the genus *Lamprobacter*. Results of DNA–DNA hybridization (92% homology) and analysis of the 16S rRNA gene sequences (99.8% similarity) support classification of strains Sivash and ShN*Lb*02 as members of the same species, namely, *Lpb. modestohalophilus*.

Phylogenetic investigation makes it possible to determine the boundaries between the genus *Lamprobacter* and closely related PSB genera. According to the 16S rRNA gene sequencing, *Lpb. modestohalophilus* strains revealed differences with other PSB genera within the family *Chromatiaceae*, including marine and halophilic PSB genera *Marichromatium* and *Thiohalocapsa* (Fig. 3). This was confirmed by analysis of RuBisCO genes in PSB [9]. Strains Sivash and ShN*Lb*02 were shown to possess identical *cbb*L genes encoding the "green" variant of form I RuBisCO with the similarity of 97.7% for nucleotides and 99.5% for amino acids. *Lpb. modestohalophilus* formed a separate branch on the *cbb*L tree comprising members of the family *Chromatiaceae*. Moreover, strain Sivash, unlike strain ShN*Lb*02, was shown to possess the *cbb*M gene encoding form II RuBisCO. This gene is not often found among autotrophs and probably explains capacity of strain Sivash for aerobic chemolithoautotrophic growth.

At the same time, phylogenetic similarity between *Lpb. modestohalophilus* and the type strains of *Halochromatium* species revealed by the 16S rRNA gene sequencing may indicate a need for elucidation of the taxonomic position of the latter.

The genus *Halochromatium*, established in the late 1990s, initially contained two extremely halophilic species, *Chromatium salexigens* [20] and *Chr. glycolicum* [21] under new names *Hch. salexigens* and *Hch. glycolicum* [22, 23]. These *Halochromatium* species had phenotypic characteristics differentiating them from the description of the genus *Lamprobacter*. The cells of *Halochromatium* spp. are rod-shaped, motile, and never form gas vesicles. Both *Halochromatium* species contain carotenoids of the spirilloxanthin series. NaCl concentrations from 2 to 20% are required for their growth, with the optimum at 4–11% (Table 2). Thus, in spite of the relative phylogenetic similarity between *Lpb. modestohalophilus* and the species *Hch. salexigens* and *Hch. glycolicum* (98.0–98.2% similarity between the 16S rRNA gene sequences), their pronounced morphological and physiological differences prevent combining them within one genus. *Hch. roseum*, which is similar to *Lpb. modestohalophilus* strains in morphology and physiology (presence of gas vesicles, okenone as the major carotenoid, and moderate halophily) [24] is exceptional in this respect (Table 2). According to our findings, *Hch. roseum* JA134^T exhibits the highest similarity (99.0–99.1%) with *Lpb. modestohalophilus* strains Sivash and ShN*Lb*02, which may suggest its classification within the genus *Lamprobacter*, rather than *Halochromatium*. Homology between the 16S rRNA gene sequences of *Hch. roseum* JA134^T and those of *Hch. salexigens* and *Hch. glycolicum* was lower (98.3 and 98.4%, respectively, of the previously reported 95.4 and 95.6% similarity [24]).

Thus, it is proposed to accept the previous name *Lamprobacter modestohalophilus* for rod-shaped PSB containing gas vesicles and forming a separate phylogenetic lineage within the halophilic PSB of the family *Chromatiaceae* according to the results of both the 16S rRNA and the RuBisCO gene sequencing.

According to the International Codex of Nomenclature of Bacteria (Principle 6, Section 5), priority of the generic and species name *Lamprobacter modestohalophilus* was established by publication in the list of validated taxa and by incorporation of the taxon in the last edition of the Bergey's Manual [4, 6, 25, 26]. It is proposed to preserve the genus *Halochromatium* with extremely halophilic species *Hch. salexigens* and *Hch. glycolicum*, while the subsequently described gas-vesiculated species *Hch. roseum* is proposed for transition to the genus *Lamprobacter* as a new combination *Lamprobacter roseus* comb. nov. It is proposed to retain *Lpb. modestohalophilus* as the type species of the genus *Lamprobacter*, with strain Sivash as the neotype strain of this species (Table 3).

Description of the genus *Lamprobacter* Gorlenko, Krasil'nikova, Kikina and Tatarinova 1988, 220^{VP} (effective publication: Gorlenko, Krasil'nikova, Kikina and Tatarinova 1979, 765)

Lamprobacter (Lam'pro.bac'ter. Gr. adj. *lampros* bright, brilliant; M.L. masc. n. *bacter* rod; M.L. masc. n. *Lamprobacter* brilliant rod).

The description is as given previously [6].

Emended description of *Lpb. modestohalophilus* Gorlenko, Krasil'nikova, Kikina and Tatarinova 1988, 220^{VP} (effective publication: Gorlenko, Krasil'nikova, Kikina and Tatarinova 1979, Gorlenko & Imhoff, 2005).

Lamprobacter modestohalophilus (mo.des'to.ha.lo'phi.lus. L. n. *modestus* moderate; Gr. n. *hals* salt; Gr. adj. *philos* loving; M.L. masc. adj. *modestohalophilus* moderate salt-loving). The description is as given previously [6] with the following modifications:

Neotype strain: Sivash, DSM 25653, VKM B-2538.

GenBank accession number (16S rRNA): HQ877095.

Description of *Lamprobacter roseus* comb. nov.

Lamprobacter roseus (*Halochromatium roseum* Kumar, Srinivas, Sasikala and Ramana 2007) (ro'se.us. L. neut. adj. roseus rose-colored, the color of the suspensions of the type strain). The description is the same as that for *Halochromatium roseum* [24].

Emended description of the genus *Halochromatium* Imhoff et al. 1998, 1139^{VP}.

Halochromatium (Ha'lo.chro.ma'ti.um. Gr gen. n. *halos* of the salt; *Chromatium* a genus name; M.L. neut n. *Halochromatium* the *Chromatium* of the salt).

The description was given previously [22, 27]. Additional description by Kumar et al., 2007 [24] should be considered invalid.

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Table 1. Utilization of organic compounds by *Lpb. modestohalophilus* strains

Organic compound	Strain Sivash	Strain ShN*Lb*02	Strain RO-1^T [1, 5]
Acetate	+	+	+
Arginine	–	–	ND
Aspartate	–	–	ND
Arabinose	–	–	–
Butyrate	–	–	–
Benzoate	–	–	–
Butanol	–	–	+
Valerate	–	–	ND
Galactose	–	–	–
Casein hydrolysate	(+)	(+)	ND
Glycerol	++	++	++
Glucose	–	–	–
Glutamate	–	–	ND
Yeast extract	+	+	ND
Caprylate	–	–	ND
Caproate	–	–	ND
Lactate	+	+	+
Lactose	–	–	–
Malonate	–	–	ND
Mannitol	–	–	–
Malate	–	–	–
Maltose	–	–	–
Methanol	–	–	–
Propionate	–	–	–
Pyruvate	+	+	+
Propanol	–	–	+
Sorbitol	–	–	–
Succinate	–	–	–
Tartrate	–	–	ND
Formate	–	–	–
Fructose	–	–	–
Fumarate	–	–	–
Citrate	–	–	ND
Ethanol	–	–	+

Designations: "++", "+", "(+)", and "–" stand for very good growth, growth, weak growth, and no growth, respectively. ND stands for no data.

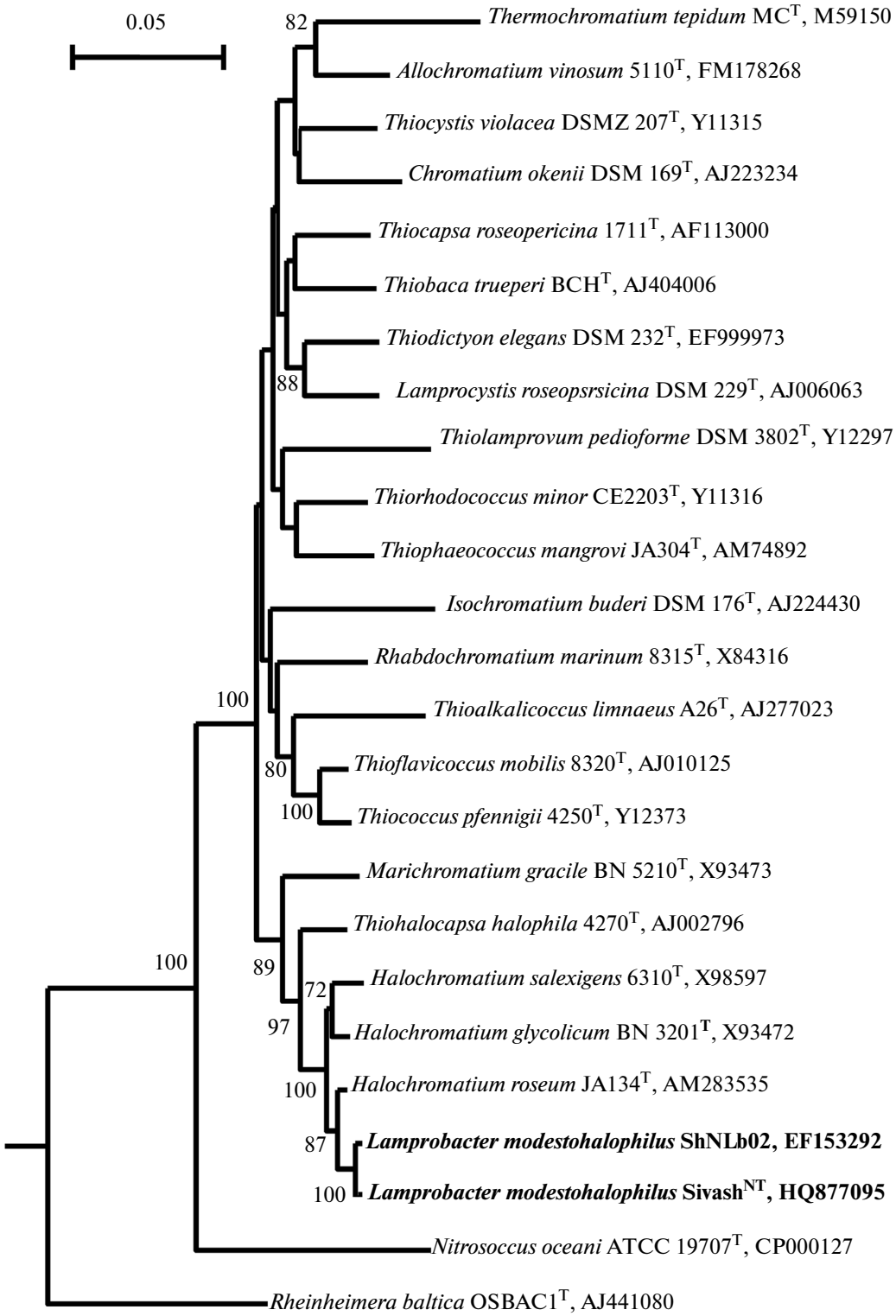

Fig. 3. Phylogenetic position of strains Sivash and ShN*Lb*02 among members of the family *Chromatiaceae* determined by comparative analysis of the 16S rRNA gene sequences. The tree was constructed using the neighbor-joining algorithm, with *E. coli* sequence used as an outgroup. The numerals indicate the branching order determined by bootstrap analysis, with the values exceeding 75 accepted as reliable. Scale bar corresponds to 5 nucleotide replacements per 100 nucleotides.

Table 2. Comparison of the properties of *Lpb. modestohalophilus* and related species

Feature	*Lpb. modestohalophilus*			*Hch. roseum* JA134^T [24]	*Hch. salexigens* [27]	*Hch. glicolicum* [27]
	strain RO-1^T [1, 5]	strain Sivash	strain ShN*Lb*02			
Cell shape	Rod-shaped or oval	Rod-shaped or oval	Rod-shaped or oval	Rods	Rods	Rods
Cell size, μm	2.0–2.5 × 4–5	2.0–2.5 × 4–5	2.0–2.5 × 4–5	2–3 × 3–5	2–2.5 × 4–7.5	0.8–1 × 2–4 auto 1.0–3.0 × 2–11 hetero
Motility	+	+	+	–	+	+
Gas vesicles	+	+	+	+	–	–
Color of cell suspension	Purple-red	Purple-red	Purple-red	Purple-red	Pink-red, slightly violet	Pink-red
Bacteriochlorophyll	*a*	*a*	*a*	*a*	*a*	*a*
Carotenoid group	Okenone	Okenone	Okenone	Okenone	Spirilloxanthin	Spirilloxanthin
pH optimum (range)	7.4–7.6	7.5 (6.5–8.5)	7.5 (6.5–8.5)	7.5 (7–8)	7.4–7.6 (7–8)	7.2–7.4 (6.2–9)
NaCl optimum, % (range)	1–2	3–4 (≤9)	2 (1.5–8)	1.5–2.5 (1–3)	8–11 (4–20)	4–6 (2–20)
Optimal temperature, °C	23–37	25–30	26–34	27	20–30	25–35
Growth factors required	B_{12}	B_{12}	–	B_{12}	B_{12}	–
Photoautotrophic growth	+	+	+	+	+	+
Assimilatory sulfate reduction	–	–	+	–	–	–
Chemolithotrophic growth	+	+	–	–	+	+
Utilized substrates	Hydrogen, sulfide, thiosulfate, sulfur, sulfite, glycerol, acetate, *n*-propanol, *n*-butanol, ethanol, *iso*-butanol, sec. butanol, *iso*-propanol, lactate, pyruvate	Hydrogen, sulfide, thiosulfate, sulfur, sulfite, glycerol, acetate, pyruvate, lactate, yeast extract, casein hydrolysate	Hydrogen, sulfide, thiosulfate, sulfur, sulfite, glycerol, acetate, pyruvate, lactate, yeast extract, casein hydrolysate	Sulfide, pyruvate, fumarate, succinate, malate, butanol, casein hydrolysate, peptone, glutamate	Hydrogen, sulfide, thiosulfate, sulfur, sulfite, acetate, pyruvate	Hydrogen, sulfide, thiosulfate, sulfur, sulfite, glycolate, glycerol, acetate, pyruvate, formate, fumarate, succinate, casein hydrolysate
DNA G+C content, mol %	64(T_m)	62.5 (T_m)	62.4 (T_m)	64 (HPLC)	64.6 (Bd)	66.1–66.5 (HPLC)

Designations: "+" and "–" stand for the presence or absence of a feature, respectively. G+C content was determined by thermal denaturation (T_m), buoyant density (Bd), and high-performance liquid chromatography (HPLC).

Table 3. Members of the genus *Lamprobacter*

Species name	Strain name	Previous species and strain name
Lpb. modestohalophilus	RO-1^T	*Lpb. modestohalophilus* RO-1^T
Lpb. modestohalophilus	Sivash^{NT}	*Lpb. modestohalophilus* Sivash^{NT}
Lpb. modestohalophilus	ShN*Lb*02	*Lpb. modestohalophilus* ShN*Lb*02
Lpb. roseus comb. nov.	JA134^T	*Halochromatium roseum* JA134^T

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