Classification of “*Chromobacterium marismortui*” in a New Genus, *Chromohalobacter* gen. nov., as *Chromohalobacter marismortui* comb. nov., nom. rev.

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Phenotypic and chemotaxonomic characteristics of seven moderately halophilic isolates from a mediterranean saltern showed that they were very closely related to “*Chromobacterium marismortui*.” This species, which was originally described on the basis of strains isolated from the Dead Sea, was not included on the Approved Lists of Bacterial Names and is not accepted as a member of the genus *Chromobacterium* since it produces a pigment that is not violacein, does not possess the characteristic flagellar arrangement, and is not genotypically related to this genus as determined by deoxyribonucleic acid-ribosomal ribonucleic acid hybridization experiments. On the basis of the special features of these strains, we propose that they should be placed in a new genus, *Chromohalobacter*, which includes a single species, *Chromohalobacter marismortui* comb. nov., nom. rev. The deoxyribonucleic acid base composition is 62.1 to 64.9 mol% guanine plus cytosine. The type strain is strain ATCC 17056 (= CCM 3518).

Moderately halophilic bacteria are organisms that are able to grow optimally in media containing between 3 and 15% (wt/vol) NaCl (22). This physiological group of microorganisms includes several gram-negative eubacteria (10, 12, 14, 16, 20, 28, 29, 34, 41, 43; B. Elazari-Volcani, Ph.D. thesis, Hebrew University, Jerusalem, Israel, 1940) and gram-positive eubacteria (5, 15, 27), as well as some archaeobacteria (26, 33, 42).

In 1940, Elazari-Volcani (Ph.D. thesis) described a moderately halophilic bacterium, “*Chromobacterium marismortui*,” that was isolated from the Dead Sea. This species was described in *Bergey's Manual of Determinative Bacteriology*, 7th ed. (2), and in *Bergey's Manual*, 8th ed. (3). It was included in the genus *Chromobacterium* as a species incertae sedis since it did not produce violacein and lacked the typical flagellar arrangement of the genus *Chromobacterium*. It was not included on the Approved Lists of Bacterial Names (36).

In a previous study we isolated from a saltern seven strains with some morphophysiological and biochemical characteristics similar to those of this species (40). The purpose of this study was to compare our isolates with the original species “*Chromobacterium marismortui*” and to determine their taxonomic position.

MATERIALS AND METHODS

Bacterial strains. We studied seven strains (strains A-56, A-65, A-100, A-102, A-429, A-431, and A-492) which were isolated from water samples collected from ponds with salinities between 22.2 and 29.0% (wt/vol) total salts of a commercial solar saltern located near Alicante, Spain, between February 1979 and January 1980 (40). We also studied “*Chromobacterium marismortui*” ATCC 17056^T (T = type strain) and one subculture of the original strain, which was kindly provided by B. Elazari-Volcani, Scripps Institution of Oceanography, La Jolla, Calif. For comparative purposes the following strains were also used: *Chromobacterium violaceum* ATCC 12472^T, *Janthinobacterium lividum* ATCC 12473^T, *Alteromonas luteoviolacea* ATCC 33492^T, *Vibrio costicola* NCMB 701^T, *Deleya halophila* CCM 3662^T, *Flavobacterium halmephilum* CCM 2833^T, *Halomonas elon-*

gata ATCC 33173^T, and “*Pseudomonas halosaccharolytica*” CCM 2851.

Strains were maintained on agar slants containing 10% (wt/vol) salts with the following composition: 8.1% (wt/vol) NaCl, 0.7% (wt/vol) MgCl₂, 0.96% (wt/vol) MgSO₄, 0.036% (wt/vol) CaCl₂, 0.2% (wt/vol) KCl, 0.006% (wt/vol) NaHCO₃, and 0.0026% (wt/vol) NaBr. This preparation was supplemented with 0.5% (wt/vol) Proteose Peptone no. 3 (Difco Laboratories, Detroit, Mich.), 1% (wt/vol) yeast extract (Difco), and 0.1% (wt/vol) glucose (12). The pH was adjusted to 7.5 with 1 M KOH. When required, agar (Difco) was added to a concentration of 2% (wt/vol).

Phenotypic characterization. Tests for 107 characteristics, including morphological, physiological, biochemical, and nutritional features, were carried out. The methodology used has been described previously (12, 34, 40). Unless otherwise indicated, all tests were performed in media containing 10% (wt/vol) salts and with a pH of 7.5, and incubation was at 37°C in sealed containers.

Oxidase was determined by the Kovacs (21) and Gaby-Hadley methods (11). The benzidine test (6) was used to detect porphyrin-containing enzyme systems. Utilization of carbohydrates was determined by using modified marine oxidation-fermentation medium (23) supplemented with 10% (wt/vol) total salts and the following sugars: D-glucose, D-galactose, glycerol, D-arabinose, trehalose, maltose, D-mannitol, lactose, sucrose, and D-xylose. We also used the conventional oxidation-fermentation medium of Hugh and Leifson (17) supplemented with 8% (wt/vol) NaCl and glucose, as well as standard medium (18) supplemented with 10% (wt/vol) salts and different sugars.

DNA base composition. Exponential-phase cells of strains were ruptured, and the deoxyribonucleic acid (DNA) was purified by using the method of Marmur (24). The guanine-plus-cytosine (G+C) content of the DNA was determined from the midpoint value of the thermal denaturation profile (25), which was obtained with a model UV-Vis 551S spectrophotometer (The Perkin-Elmer Corp., Norwalk, Conn.) at 260 nm; this instrument was programmed for temperature increases of 1.0°C/min. The midpoint of the thermal denaturation profile was determined by a graphic method as described by Ferragut and Leclerc (9), and the G+C content

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was calculated from this temperature by using the equation of Owen and Hill (30) in $0.1 \times \text{SSC}$ ($1 \times \text{SSC}$ is 0.15 M NaCl plus $0.015 \text{ M trisodium citrate}$, pH 7.0). The midpoint of the thermal denaturation profile for reference DNA from *Escherichia coli* NCTC 9001 was taken to be 74.6°C in $0.1 \times \text{SSC}$ (31).

Preparation of labeled DNA. DNA was labeled by using the multiprime system, a commercial kit (kit RPN 1601Y; Amersham International, Amersham, England), and [^3H] deoxy(1',2',5')cytidine 5'-triphosphate (Amersham). The average specific activity obtained with this procedure was $8.4 \times 10^6 \text{ cpm}/\mu\text{g}$ of DNA. The labeled DNA was denatured before hybridization by heating at 100°C for 5 min and was then placed on ice.

DNA homology experiments. DNA-DNA homology studies were performed by using the competition procedure of the membrane filter method described by Johnson (19). Competitor DNAs were sonicated (Braun Melsungen, Melsungen, Federal Republic of Germany) at 50 W for two 15-s intervals. Membrane filters (type HAHY; Millipore Corp., Bedford, Mass.) containing reference DNA (ca. $25 \mu\text{g}/\text{cm}^2$) were placed in 5-ml screw cap vials which contained the labeled, sheared, denatured DNA and the denatured and sheared competitor DNA. The ratio of the concentrations of competitor DNA to labeled DNA was at least 150:1. The final volume and concentration was adjusted to $140 \mu\text{l}$, $2 \times \text{SSC}$, and 30% formamide solution. The hybridization temperature ranged between 55 and 58°C , which is below the limit for the validity of the filter method (8). The vials were shaken slightly for 18 h in a water bath (Grant Instruments, Cambridge, England); these procedures were done in triplicate. After hybridization the filters were washed in $2 \times \text{SSC}$ at the optimal renaturation temperature. The radioactivity bound to the filters was measured with a liquid scintillation counter (Beckman Instruments, Inc., Palo Alto, Calif.), and the percentage of homology was calculated by using the method of Johnson (19). At least two independent determinations were carried out for each experiment, and the results reported below are the mean values.

RESULTS

Morphology. All of the strains examined were gram-negative rods, 0.6 to 1.0 by 1.5 to $4.0 \mu\text{m}$. The cells were motile by means of peritrichous flagella. No spores were observed.

Cultural characteristics. The colonies of all strains were circular, smooth, entire, and pigmented characteristically with dark brown centers followed by bluish brown, grayish brown, and yellow rings. They produced a yellow pigment and a violet blue pigment which was not violacein (37). The nature of these pigments is being studied currently.

On liquid medium containing 10% total salts all of the strains produced turbidity and pellicles and were usually brown.

Physiological, biochemical, and nutritional characteristics. All strains grew in solid media containing 2 to 30% (wt/vol) total salts and grew optimally in media containing about 10% total salts. They grew at temperatures between 5 and 45°C and over a pH range of 5 to 10, but none grew at pH 4. Production of acid from glucose in the oxidation-fermentation medium of Hugh and Leifson containing 8% NaCl (17), in marine oxidation-fermentation medium (23) containing 10% total salts, and in standard medium (18) containing 10% total salts was positive in all cases in aerobic tubes but negative under anaerobic conditions. The results of all of the

TABLE 1. Phenotypic characteristics in which the eight strains of *Chromohalobacter marismortui* differ from one another

Characteristic	No. of strains positive	Reaction of strain ATCC 17056 ^T
Nitrate reduction	7	— ^a
Growth on ^b :		
Caprylate	1	+
Propionate	7	—
Trehalose	6	+
Lactose	1	+
L-Rhamnose	6	+
Starch	1	+
Adonitol	1	+
Fumarate	7	—
Benzoate	7	—
DL-Glycerate	7	—
D-Saccharate	7	—
Quinate	1	+
Succinate	7	—
D-Fructose	7	—
Growth on ^c :		
Aspartic acid	1	+
Glutamic acid	5	—
Glycine	7	—
L-Histidine	1	+
DL-Lysine	7	—
L-Methionine	7	—

^a +, Positive; —, negative.

^b When supplied as the sole source of carbon and energy.

^c When supplied as the sole source of carbon, nitrogen, and energy.

physiological and biochemical tests except the nitrate reduction test were the same for all strains; the nitrate reduction test was negative in "*Chromobacterium marismortui*" ATCC 17056^T. "*Chromobacterium marismortui*" ATCC 17056^T and the "*Chromobacterium marismortui*" strain obtained from Elazari-Volcani were identical except in pigmentation, which was less pronounced in the latter. Other characteristics that were common to all of the strains studied are given below in the species description. Characteristics that varied among the eight strains which we studied are shown in Table 1.

DNA base compositions. The DNA base compositions of the strains which we tested are shown in Table 2 and ranged from 62.1 to 64.9 mol% G+C.

DNA-DNA hybridization. The DNA relatedness results obtained with labeled reference DNAs from "*Chromobacterium marismortui*" ATCC 17056^T and strain A-100 are shown in Table 2. The levels of similarity for DNAs from labeled strains to DNAs from the other isolates ranged from 66 to 100%. Low levels of relatedness were found between the two reference strains and the other species used for comparison.

DISCUSSION

The phenotypic and genotypic results showed that our seven isolates were very similar to "*Chromobacterium marismortui*" ATCC 17056^T. This species was originally described by Elazari-Volcani (Ph.D. thesis) and was included in *Bergey's Manual*, 7th ed. (2). Our results agree with the original description and with the data reported in *Bergey's Manual* (2), except that the nitrate reduction test was negative for "*Chromobacterium marismortui*" ATCC 17056^T. The differences found with respect to the nutritional features can be attributed to the different isolation habitats, since the salt composition and nutrient availability of the Dead Sea are unlike those of the Mediterranean salterns (35).

TABLE 2. G+C contents of DNAs and levels of DNA-DNA relatedness between *Chromohalobacter marismortui* and other related species^a

Unlabeled DNA from:	G+C content (mol%)	% Homology with ³ H-labeled DNA from:	
		Strain ATCC 17056 ^T	Strain A-100
<i>Chromohalobacter marismortui</i> strains			
ATCC 17056 ^T	62.3	100	91
Elazari-Volcani strain	62.1	100	97
A-100	62.5	87	100
A-56	63.3	91	84
A-65	62.4	71	100
A-102	63.7	66	97
A-429	64.1	71	100
A-431	64.9	68	91
A-492	63.9	83	98
<i>Chromobacterium violaceum</i> ATCC 12472 ^T	67.2 ^b	14	12
<i>Janthinobacterium lividum</i> ATCC 12473 ^T	65.5 ^b	11	22
<i>Alteromonas luteoviolacea</i> ATCC 33492 ^T	42.1 ^c	20	4
<i>Vibrio costicola</i> NCMB 701 ^T	49.9 ^d	9	13
<i>Deleya halophila</i> CCM 3662 ^T	66.7 ^e	2	3
<i>Flavobacterium halmephilum</i> CCM 2833 ^T	49.7 ^f	28	13
<i>Halomonas elongata</i> ATCC 33173 ^T	60.5 ^g	13	19
“ <i>Pseudomonas halosaccharolytica</i> ” CCM 2851	ND ^h	15	20

^a Hybridizations were performed under optimal conditions.^b Data from reference 7.^c Data from reference 13.^d Data from reference 12.^e Data from reference 34.^f Data from reference 4.^g Data from reference 41.^h ND, Not determined.

The G+C content of "*Chromobacterium marismortui*" ATCC 17056^T was 62.3 mol%, a value in good agreement with the value reported previously (61.8 mol%) (7) and within the range obtained for the other seven strains studied. The DNA relatedness experiments showed that the seven isolates form a single DNA hybridization group with a high level of homology to "*Chromobacterium marismortui*" ATCC 17056^T. Low levels of homology were obtained between the two representative strains and the other gram-negative species studied. "*Chromobacterium marismortui*" was included as a species incertae sedis in the genus *Chromobacterium* in Bergey's Manual, 8th ed. (3), since the pigment produced is not violacein and the organism has a different flagellar arrangement. In an extensive study of the genera *Chromobacterium* and *Janthinobacterium*, De Ley et al. (7) concluded that "*Chromobacterium marismortui*" is not a member of either of these genera and that, on the basis of the ribosomal ribonucleic acid similarity maps obtained, "*Chromobacterium marismortui*" ATCC 17056^T "is either a border case of *Pseudomonas* section I or a member of a genus closely related to the latter taxon." However, clear differences were found between the strain studied and strains typical of the genus *Pseudomonas* (32).

Table 3 shows the characteristics that differentiate "*Chromobacterium marismortui*" from other related species. Since on the basis of phenotypic and genotypic criteria the

strains which we studied are not closely related to previously described bacteria, we formally propose that they should be classified in a new genus, *Chromohalobacter*, as *Chromohalobacter marismortui* comb. nov., nom. rev.

Description of *Chromohalobacter* gen. nov. The characteristics of *Chromohalobacter* (Chro.mo.hal.o.bac'ter. Gr. n. *chroma*, color; Gr. n. *halos*, the sea, salt; M.L. n. *bacter*, rod; M.L. masc. n. *Chromohalobacter*, colored salt rod). Cells are rods that are 0.6 to 1.0 by 1.5 to 4.0 µm when they are grown in the presence of 10% (wt/vol) salts; at higher and lower salt concentrations, the cells are longer. Gram negative. Motile by means of peritrichous flagella. Endospores are not formed. Colonies are violet blue to brown.

Chemoorganotrophs. Strictly aerobic. Catalase and benzidine tests are positive. Oxidase negative. Optimal growth occurs in media supplemented with 10% (wt/vol) salt. The optimal temperature is 37°C, and the optimal pH is 7.5. Acid is produced aerobically but not anaerobically from D-glucose and other sugars. Gelatin, casein, Tween 80, starch, esculin, and tyrosine are not hydrolyzed. Carbohydrates, amino acids, and some polyols can serve as sole carbon sources.

Habitat: Dead Sea and marine salterns.

The DNA base composition ranges from 62.1 to 64.9 mol% G+C, as determined by the thermal denaturation method.

The type species is *Chromohalobacter marismortui*.

Description of *Chromohalobacter marismortui* comb. nov., nom. rev. *Chromohalobacter marismortui* (ma.ris.mor'tu.i. L. gen. n. *maris*, of the sea; L. adj. *mortuus*, dead; M.L. gen. n. *marismortui*, of the Dead Sea). Gram-negative, nonsporeforming bacteria that are rod shaped (sometimes slightly curved); the length varies with the concentration of salt. At 10% (wt/vol) total salts, the cells are 0.6 to 1.0 by 1.5 to 4.0 µm; at higher and lower salts concentrations, the cells are longer. Cells occur singly or in pairs. Motile by means of peritrichous flagella.

On solid, complex media containing 10% (wt/vol) total salts, colonies are circular, convex, smooth, entire, and concentrically ringed with dark brown centers followed by bluish-brown, grayish brown, and yellow rings. They produce a yellow pigment and a violet blue pigment which is not violacein. Production of pigment is favored by suboptimal growth temperatures, glycerol, and a salt concentration of 10% (wt/vol). In liquid medium containing 10% (wt/vol) total salts turbidity and a pellicle are produced; usually brown to yellow pigments are also produced.

Growth occurs from pH 5 to 10 on solid media containing 10% total salts (optimal growth at pH 7.5) and between 5 and 45°C. The optimum temperature is 37°C. Growth occurs in media containing 1 to 30% (wt/vol) salt, with an optimum at about 10% (wt/vol).

Strictly aerobic. Catalase and benzidine tests are positive. Oxidase negative.

Acid is produced without gas under aerobic conditions in marine oxidation-fermentation medium supplemented with 10% (wt/vol) total salts and D-glucose, D-galactose, maltose, lactose, D-arabinose, D-xylose, sucrose, trehalose, glycerol, and D-mannitol. Acid is produced without gas in open Hugh-Leifson tubes with oxidation-fermentation glucose medium containing 8% NaCl.

Generally, nitrate is reduced to nitrite; nitrite is not reduced. Simmons citrate is utilized.

No hydrolysis of gelatin, casein, starch, esculin, tyrosine, and Tween 80. H₂S is not produced from cysteine.

No production of phosphatase, indole, urease, acetoin, deoxyribonuclease, or β-galactosidase.

No production of phenylalanine deaminase, arginine de-

TABLE 3. Characteristics useful in distinguishing strains of *Chromohalobacter marismortui* from other phenotypically similar species^a

Characteristic	<i>Chromohalobacter marismortui</i>	<i>Alteromonas luteoviolacea</i>	<i>Chromobacterium violaceum</i>	<i>Deleya halophila</i>	<i>Deleya cupida</i>	<i>Deleya marina</i>	<i>Halomonas elongata</i>	<i>Janthinobacterium lividum</i>	<i>Vibrio costicola</i>
Peritrichous flagella	+	—	+	+	+	—	+	+	—
Facultative anaerobe	—	—	+	—	—	—	+	—	+
Pigmentation	+	+	+	—	—	—	—	+	—
Oxidase	—	+	+	+	—	—	+	+	+
Na ⁺ requirement	+	+	—	+	+	+	+	—	+
Optimal growth at ca. 10% (wt/vol) salt	+	—	—	+	—	—	+	—	+
Acid production from:									
D-Glucose	+	d	+	+	ND	ND	+	+	+
Trehalose	+	+	+	—	ND	ND	ND	d	+
D-Arabinose	+	ND	—	ND	ND	ND	ND	+	—
D-Xylose	+	—	—	+	ND	ND	ND	+	—
Lactose	+	—	—	—	ND	ND	d	ND	—
Nitrate reduction	+	—	+	+	+	—	+	+	—
Nitrite reduction	—	—	+	—	—	—	+	+	—
Hydrolysis of:									
Gelatin	—	+	+	—	—	—	d	—	+
Casein	—	+	+	—	—	—	—	—	+
Starch	—	+	—	—	—	—	—	ND	—
Esculin	—	d	—	+	ND	ND	d	+	d
Tween 80	—	+	+	—	—	—	—	—	d
Growth on ^c :									
D-Fucose	+	ND	ND	ND	—	—	ND	ND	+
Butyrate	—	ND	ND	ND	+	+	ND	ND	d
Citrate	—	—	ND	+	+	+	ND	+	d
Malonate	—	—	ND	ND	+	+	ND	ND	—
Growth on ^d :									
Betaine	—	ND	ND	ND	+	+	ND	ND	—
L-Leucine	—	—	ND	ND	+	+	ND	ND	d
Sarcosine	—	ND	ND	ND	+	+	ND	ND	—
G+C content (mol%)	62.1–64.9	40–43	65–68	66.7	60–63	62–64	60.5	61–67	49.4–50.5

^a Data from this study and references 1, 12, 13, 34, 38, 39, and 41.^b +, Positive; —, negative; d, differs among strains; ND, not determined.^c When supplied as the sole source of carbon and energy.^d When supplied as the sole source of carbon, nitrogen, and energy.

hydrolase, lysine decarboxylase, or ornithine decarboxylase.

No hemolysis occurs on blood agar supplemented with 8% NaCl.

The following compounds are utilized as sole carbon and energy sources: dulcitol, D-fucose, D-galactose, D-glucuronate, D-glucose, glutamate, *meso*-inositol, maltose D-mannitol, D-mannose, pyruvate, D-ribose, sucrose, D-sorbitol, and D-xylose.

The following compounds are not utilized as sole carbon and energy sources: *N*-acetylglucosamine, amygdalin, DL- α -aminobutyrate, butyrate, cellobiose, citrate, esculin, *p*-hydroxybenzoate, hippurate, inulin, malonate, melibiose, oxalate, raffinose, salicylate, salicin, and D-tartrate.

The following compounds are utilized as sole carbon, nitrogen, and energy sources: L-alanine, DL-arginine, L-glutamine, L-ornithine, L-proline, putrescine, and L-serine.

The following compounds are not utilized as sole carbon, nitrogen, and energy sources: L-allantoin, betaine, creatine, ethionine, L-isoleucine, L-leucine, phenylalanine, sarcosine, L-threonine, and L-valine.

The G+C content of the DNA is 62.1 to 64.9 mol%, as determined by the thermal denaturation method.

Habitat: isolated from the Dead Sea and solar salterns.

The type strain is strain ATCC 17056 (= CCM 3518).

Description of the type strain. The description of the type strain is the same as that of the species. Nitrate is not reduced to nitrite. Other characteristics are listed in Table 1. The G+C content of the type strain is 62.3 mol%, as determined by the thermal denaturation method.

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