Transfer of *Halomonas canadensis* and *Halomonas israelensis* to the genus *Chromohalobacter* as *Chromohalobacter canadensis* comb. nov. and *Chromohalobacter israelensis* comb. nov.

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16S rRNA gene sequence comparisons and DNA–DNA hybridization data support the conclusion that two species previously described as members of the genus *Halomonas*, *Halomonas israelensis* and *Halomonas canadensis*, should be placed in the genus *Chromohalobacter*. Both *H. israelensis* ATCC 43985^T (= Ba₁^T) and *H. canadensis* ATCC 43984^T (= NRCC 41227^T) have been used extensively for physiological studies for many years; nevertheless, they were not named and classified taxonomically until quite recently. Their phenotypic resemblance (at least 65% Jaccard similarity) to some members of the genus *Halomonas* and the degree of DNA–DNA relatedness (lower than 60%) to other described species of this genus permitted the conclusion that they were distinct species belonging to the genus *Halomonas*. In this study, the 16S rDNA of both species has been sequenced completely and found to share higher similarity to the available sequences of the moderately halophilic bacterium *Chromohalobacter marismortui* than to sequences of members of the genus *Halomonas*. *C. marismortui* is the sole species of the genus *Chromohalobacter*, also included in the family *Halomonadaceae*, and shares many phenotypic features with *H. canadensis* and *H. israelensis*. It is proposed that the two species should be renamed as *Chromohalobacter canadensis* comb. nov. and *Chromohalobacter israelensis* comb. nov. An emended description of the genus *Chromohalobacter* is given in order to include the features of these two species.

Keywords: *Halomonas*, *Chromohalobacter canadensis*, *Chromohalobacter israelensis*, moderately halophilic bacteria, 16S rRNA sequence

INTRODUCTION

Strain Ba₁^T (= ATCC 43985^T) was isolated from the Dead Sea by Rafaeli-Eshkol (1968) and was the subject of several physiological and biochemical studies dealing mainly with the effects of NaCl on respiratory enzymes, osmoregulatory mechanisms and ion transporters (Ken-Dror & Avi-Dor, 1985; Ken-Dror *et al.*,

1984; Rafaeli-Eshkol, 1968). Strain NRCC 41227^T was reported as a medium contaminant by Matheson *et al.* (1976) and served as a model for some physiological studies (Falkenberg *et al.*, 1976; Ken-Dror *et al.*, 1984). A summary of these studies conducted on the two strains can be found in a recent review (Ventosa *et al.*, 1998) about moderately halophilic bacteria, which are defined as those micro-organisms able to grow optimally in media containing 3–15% (w/v) NaCl (Kushner & Kamekura, 1988). During all this time, they were referred to simply as strains Ba₁ and NRCC 41227. It was not until 27 and 19 years, respectively, after the reports of their isolation that

The EMBL accession numbers for the 16S rRNA gene sequences of *Halomonas canadensis* ATCC 43984^T, *Halomonas israelensis* ATCC 43985^T and *Halomonas salina* F8-11^T are AJ295143, AJ295144 and AJ295145, respectively.

they were classified as members of the genus *Halomonas* and named *Halomonas israelensis* and *Halomonas canadensis* (Huval *et al.*, 1995). The taxonomic study of Huval *et al.* (1995) was done by comparing these two strains with four other *Halomonas* strains and taking 125 phenotypic features into account. A further comparison, using a larger number of related reference strains, or a phylogenetic study has never been done, to our knowledge, and this led us to carry out a detailed study of these two *Halomonas* species.

METHODS

Strains and culture conditions. *H. israelensis* ATCC 43985^T, *H. canadensis* ATCC 43984^T, *Halomonas salina* F8-11^T, *Halomonas elongata* ATCC 33173^T, *H. elongata* DSM 3043, *Halomonas halodurans* ATCC 29686^T, *Chromohalobacter marismortui* ATCC 17056^T and *C. marismortui* A-492 were grown on SW-10 medium (Nieto *et al.*, 1989), which contained a final salt concentration of about 10% (w/v) and 0.5% (w/v) yeast extract (Difco). The pH was always adjusted to 7.2. Cultures were incubated at 37 °C in an orbital shaker (New Brunswick Scientific) at 200 strokes min⁻¹. Fresh mounts from exponentially growing cultures of *H. canadensis* and *H. israelensis* were examined by light microscopy (phase-contrast) to determine their cell size. Hydrolysis of casein, aesculin, gelatin, DNA and starch, as well as other biochemical and nutritional tests, were performed as reported previously (Ventosa *et al.*, 1982).

Extraction of genomic DNA and determination of DNA base composition. DNA was extracted and purified by the method of Marmur (1961). Purity was assessed from the A_{260}/A_{280} and A_{230}/A_{260} ratios (Johnson, 1994). The G + C content of the DNA was determined from the mid-point value (T_m) of the thermal denaturation profile (Marmur & Doty, 1962) obtained with a Perkin-Elmer UV-Vis 551S spectrophotometer at 260 nm; this instrument was programmed for temperature increases of 1 °C min⁻¹. The T_m was determined by a graphical method described by Ferragut & Leclerc (1976) and the G + C content was calculated from this temperature by using the equation of Owen & Hill (1979), in 0.1 × SSC buffer (0.15 M NaCl buffered with 0.015 M trisodium citrate, pH 7.0). The T_m value of reference DNA from *Escherichia coli* NCTC 9001 was taken as 74.6 °C in 0.1 × SSC (Owen & Pitcher, 1985).

Preparation of labelled DNA and DNA-DNA hybridization experiments. DNA was labelled by the multiprime system with a commercial kit (RPN 1601Y; Amersham) that employs deoxy-[1',2',5'-³H]cytidine 5'-triphosphate. The mean specific activity obtained with this procedure was 8.4×10^6 c.p.m. µg⁻¹ DNA. The labelled DNA was denatured before hybridization by heating at 100 °C for 5 min and then placed on ice.

DNA-DNA hybridization studies were performed by the competition procedure of the membrane method described by Johnson (1994). Competitor DNAs were sonicated (Braun Melsungen) at 50 W for two periods of 15 s. Membrane filters (HAHY; Millipore), 0.5 cm in diameter, containing reference DNA (25 µg cm⁻²) were placed in 5 ml screw-capped vials (Greiner) that contained the labelled, sheared, denatured DNA and the denatured, sheared competitor DNA. The ratio of the concentrations of competitor to labelled DNA was at least 150:1. The final volume and

concentration were adjusted to 140 µl, 2 × SSC and 30% formamide. The optimal hybridization temperatures were 56.9 °C for *H. canadensis* and 58.2 °C for *H. israelensis*, which are within the limits of validity for the filter method (De Ley & Tijtgat, 1970). The vials were shaken gently for 18 h in a water bath (Grant Instruments); these procedures were done in triplicate. After hybridization, the filters were washed in 2 × SSC at the optimal renaturation temperatures reported above. The radioactivity bound to the filters was measured in a liquid scintillation counter (Beckman Instruments) and the percentage similarity was calculated according to Johnson (1994). At least two independent determinations were carried out for each experiment and the reported results are the mean values.

Phylogenetic analysis. Isolation of genomic DNA from *H. israelensis* ATCC 43985^T, *H. canadensis* ATCC 43984^T and *H. salina* F8-11^T, *in vitro* amplification of the 16S rRNA genes and direct sequencing of the PCR-amplified 16S rDNA fragments were carried out by using methods that have been described previously (Springer *et al.*, 1993).

Data analyses, including more than 20000 complete or almost complete 16S rRNA sequences (at least 1400 bases) available from rRNA sequence databases, were performed by using the ARB software package (Ludwig & Strunk, 1996). The most closely related sequences were used, together with a large number of outgroup sequences, to construct a similarity matrix. A tree was derived from the corrected distance values by using the neighbour-joining method (Saitou & Nei, 1987). Maximum-parsimony- and maximum-likelihood-based trees, respectively using the full dataset or a selection of about 50 sequences, were obtained and compared in order to make an estimate of the confidence. The effects on the results of a base-frequency filter in the sequence comparison analysis were also evaluated.

RESULTS AND DISCUSSION

We determined the cell size of *H. canadensis* and *H. israelensis* and some biochemical features that were not reported in the descriptions of these two species or in subsequent publications. Both strains were negative for the hydrolysis of casein, gelatin, DNA, aesculin and starch. The G + C contents of the DNA of these two strains were also estimated by the thermal denaturation method (Table 1). Our values, 62 and 65 mol% for *H. canadensis* and *H. israelensis*, differ slightly from the previously published values (57 and 64 mol%, respectively), probably due to the fact that a different method (buoyancy) was used. Several tests allowed the differentiation of *H. canadensis* and *H. israelensis* from each other as well as from *C. marismortui* (Table 2) or species of the genus *Halomonas*. In the original proposal (Huval *et al.*, 1995), *H. canadensis* and *H. israelensis* were classified within the genus *Halomonas* according to their phenotypic characteristics and DNA-DNA hybridization experiments, but only four *Halomonas* strains (representing three species) were used for comparison. However, the phylogenetic relationships of these two species were not determined. In this study, the almost complete 16S rDNA sequences (ca. 1530 bases) of *H. canadensis* and *H. israelensis* were obtained and their phylogenetic position was determined. We found that

Table 1. DNA G + C contents and levels of DNA–DNA relatedness for *H. canadensis*, *H. israelensis* and some related reference strains of the genera *Halomonas* and *Chromohalobacter*

Source of unlabelled DNA	G + C content (mol %)*	Similarity (%) to ³ H-labelled DNA from:	
		<i>H. canadensis</i> ATCC 43984 ^T	<i>H. israelensis</i> ATCC 43985 ^T
<i>H. canadensis</i> ATCC 43984 ^T	62.0	100	36
<i>H. israelensis</i> ATCC 43985 ^T	65.0	40	100
<i>C. marismortui</i> ATCC 17056 ^T	62.3 ^a	39	37
<i>C. marismortui</i> A-492	63.9 ^a	25	40
<i>H. elongata</i> ATCC 33173 ^T	60.5 ^b	0	0
<i>H. elongata</i> DSM 3043	64.2	35	50
<i>H. halodurans</i> ATCC 29686 ^T	63.2 ^c	0	0

* Data were taken from this study and from Ventosa *et al.* (1989) (a), Vreeland *et al.* (1980) (b) and Hebert & Vreeland (1987) (c).

Table 2. Phenotypic characteristics that differentiate *C. marismortui*, *H. canadensis* and *H. israelensis*

Data were taken from Huval *et al.* (1995), Ventosa *et al.* (1989) and this study. Characters are scored as: +, positive; –, negative.

Characteristic	<i>C. marismortui</i> ATCC 17056 ^T	<i>H. canadensis</i> ATCC 43984 ^T	<i>H. israelensis</i> ATCC 43985 ^T
Cell size (µm)	0.6–1.0 × 1.5–4.0	0.6–1.2 × 2.0–3.8	0.6–0.9 × 1.5–4.2
Pigmentation	Brown-yellow	White	Cream
NaCl concentration for growth (% w/v)			
Range	1.0–30	3–25	3.5–20
Optimum	10	8	8
Temperature range (°C)	5–45	15–45	15–45
pH range	5–10	5–9	5–9
Indole production	–	+	+
Nitrate reduction	–	+	+
Phosphatase	–	+	–
Simmons citrate	+	–	–
Lysine decarboxylase	–	+	+
Ornithine decarboxylase	–	+	+
Acid production from:			
Maltose	+	–	+
Sucrose	+	–	+
Trehalose	+	–	–
Growth on:			
Cellobiose	–	+	+
Aesculin	–	+	+
Starch	+	–	+

they share 97.1% overall similarity. The similarities between either of them and the available sequences of members of the genus *Halomonas* were significantly lower, ranging from 92.8 to 95.2%. In contrast, when compared with the sequences (U78719, X87219, X87220, X87221 and X87222) from five strains of *C. marismortui* (T1093, ATCC 17056^T, A-62, A-100 and A-492, respectively), higher overall similarity was found: *H. canadensis* and *H. israelensis* respectively showed 98.2 and 96.8% 16S rRNA similarity to the sequence of the type strain of *C. marismortui*.

In a preliminary phylogenetic tree (not shown) derived from the matrix distances, the new sequences from *H. canadensis* and *H. israelensis* did indeed group with the five sequences of *C. marismortui*, forming a cluster separated from the other species of the genus *Halomonas* with the exception only of *Halomonas marina*, which represents the deepest branching of the group. The 16S rRNA sequence of *H. salina* F8-11^T (AJ295145) determined in this study is almost identical to the sequences L42617 (from *H. salina* ATCC 49509^T), AJ243447 (from *H. salina* ATCC 49509^T) and

Fig. 1. Phylogenetic tree derived from analysis of the 16S rRNA sequences of *C. israelensis*, *C. canadensis*, *C. marismortui* and the type strains of species of the genus *Halomonas* (accession numbers in parentheses). Collapsed branches correspond to those whose topology was affected by the method applied. Bar, 5% sequence difference. The outgroup (not shown) consisted of a collection of more than 100 full sequences.

AJ243448 (from *H. salina* DSM 5928^T). In contrast, sequence X87217, although it apparently has the same origin (*H. salina* ATCC 49509^T), shares only approximately 96.3% similarity with any of the above sequences and could therefore represent a mislabelled sequence.

Regardless of the method applied or the set of sequences employed, *H. canadensis* and *H. israelensis* always clustered together with *C. marismortui*, as shown in the phylogenetic tree in Fig. 1. For its reconstruction, possible changes in the topology were evaluated, comparing the results from the three most accepted treeing methods: pairwise distances, maximum-parsimony and maximum-likelihood. Additionally, a filter, in which variable positions (less than 50% conservation in the sequences of the group that are the subject of this study) were removed, was used to test whether the more conservative part of the dataset yielded results similar to those for the complete dataset. Following the recommendations of Ludwig *et al.* (1998), the branches that were found to vary in relative order within a cluster depending on the method applied are indicated as multifurcations.

Although the genus *Halomonas* is not monophyletic and may undergo taxonomic changes in the future, the branch in which *C. marismortui* and the species *H. canadensis* and *H. israelensis* clustered was very stable across the different phylogenetic models that were applied, which can be taken as a strong evidence of the robustness of the topology presented in Fig. 1.

Recent comparative studies on 23S rRNA sequences (D. R. Arahal, W. Ludwig, K. H. Schleifer and A. Ventosa, unpublished data) carried out on species of the genera *Halomonas* and *Chromohalobacter* confirm this result and clearly support the placement of *H. canadensis* and *H. israelensis* in the genus *Chromohalobacter*. The close phylogenetic relationship with *C.*

marismortui could imply that they might be members of this species and we therefore conducted DNA–DNA hybridization experiments in order to clarify whether they represent different genospecies. Table 1 shows the results obtained from the DNA hybridization experiments. Low values of DNA–DNA relatedness (40% or less) were obtained between *H. canadensis* and *H. israelensis* and between both of them and the two *C. marismortui* strains used (the type strain and a reference strain). These data indicate clearly that they represent different species of the genus *Chromohalobacter*. It is noteworthy that they have high DNA relatedness to strain DSM 3043, a strain deposited as *Halomonas elongata* but which could be related more closely to the genus *Chromohalobacter* than to *Halomonas*. Its taxonomic placement is reconsidered in another study (Arahal *et al.*, 2001).

In summary, all of the different phylogenetic analyses performed are in good agreement and support the inclusion of *H. canadensis* and *H. israelensis* in the genus *Chromohalobacter*. Furthermore, other data presented in this article are consistent with this reclassification. Therefore, we propose the transfer of *H. canadensis* and *H. israelensis* to the genus *Chromohalobacter* as *Chromohalobacter canadensis* comb. nov. and *Chromohalobacter israelensis* comb. nov. Additionally, a redefinition of the genus *Chromohalobacter*, which previously comprised only a single species, is included.

Emended description of the genus *Chromohalobacter* (Ventosa *et al.* 1989) Arahal *et al.*

Cells are Gram-negative, straight or sometimes slightly curved, motile rods that are 0.6–1.2 × 1.5–4.2 µm and occur singly, in pairs and in short chains. Non-spore-forming. Colonies are pigmented cream to brown-yellow. Moderate halophiles. Salt is required for

growth. Optimal growth occurs in the presence of 8–10% (w/v) salt. May grow at salt concentrations up to 30% (w/v). The broader ranges of temperature and pH observed for growth are 5–45 °C and pH 5.0–10.0. Chemo-organotrophs. Aerobic. Catalase-positive. Most strains reduce nitrate, but H₂S is not produced. Negative for urease and phenylalanine deaminase. Casein, DNA, aesculin, gelatin, starch and Tween 80 are not hydrolysed. Acid is produced from arabinose, glucose, glycerol, lactose and xylose. Habitat: the Dead Sea and marine salterns. The DNA base composition ranges from 62 to 65 mol%, as determined by the thermal denaturation method. The type species is *Chromohalobacter marismortui*.

Description of *Chromohalobacter canadensis* (Huval et al. 1995) Arahal et al. comb. nov.

The description of *Chromohalobacter canadensis* comb. nov. is identical to that published for *H. canadensis* (Huval et al., 1995) with the addition that the cell size was determined to be 0.6–1.2 × 2.0–3.8 µm, it is not able to hydrolyse casein, DNA, aesculin, gelatin or starch and the G + C content of the DNA is 62 mol% (*T_m* method). The accession number of the 16S rDNA sequence is AJ295143.

The description is based on a single strain, the type strain NRCC 41227^T (= ATCC 43984^T = DSM 6769^T = CECT 5385^T = CCM 4919^T = CIP 105571^T = NCIMB 13767^T).

Description of *Chromohalobacter israelensis* (Huval et al. 1995) Arahal et al. comb. nov.

The description of *Chromohalobacter israelensis* comb. nov. is the same as that published for *H. israelensis* (Huval et al., 1995) with a few additions: the cell size was determined to be 0.6–0.9 × 1.5–4.2 µm, hydrolysis of casein, DNA, aesculin, gelatin and starch is negative and the G + C content of the DNA is 65 mol% (*T_m* method). The accession number of the 16S rDNA sequence is AJ295144.

The description is based on a single strain, the type strain ATCC 43985^T (= DSM 6768^T = CECT 5287^T = CCM 4920^T = CIP 106853^T = NCIMB 13766^T).

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