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A report of 7 unrecorded haloarchaea species isolated from solar salterns in Yellow Sea

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Solar saltern samples were collected from diverse regions near Yellow Sea to obtain unrecorded haloarchaea in Korea, including Siheung in Gyeonggi-do, Taean in Chungcheongnam-do, and Buan, Jeollabuk-do. Samples were suspended in a 20% (w/v) NaCl solution and enriched for one month at 37°C in freshly prepared DB Characterization Medium No. 2 broth with minor modifications. The enriched cultures were then spread onto agar plates to isolate single colonies of halophilic archaea. Phylogenetic analysis of the 16S rRNA gene revealed that the isolates exhibited at least 98.7% sequence similarity to previously described species. In total, seven haloarchaeal species, previously unreported in Korea but validly published under the International Code of Nomenclature of Prokaryotes, were obtained. These isolates were classified into the order *Halobacteriales*. The 7 *Halobacteriales* species were further categorized into the 6 species of the family *Haloferacaceae* and 1 species of the family *Halobacteriaceae*, comprising 4 genera, including *Halobellus* (4 species), *Haloplanus* (1 species), *Salinigranum* (1 species), and *Natronomonas* (1 species). Collectively, these unrecorded haloarchaeal species spanned 1 order, 2 families, and 3 genera. This research shows the potential for discovering previously unreported species within domestic solar saltern environments. Comprehensive analyses, including Gram staining, cell morphology, physiological characteristics, basic biochemical profiling, and phylogenetic analysis, were performed and presented for each species.

Keywords: comprehensive analyses, haloarchaea, solar saltern, unrecorded species

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Introduction

Archaea possess distinctive biological characteristics that set them apart from bacteria and eukaryotes. In 1977, Carl Woese employed 16S rRNA sequence data to infer phylogenetic relationships among diverse prokaryotic groups, revealing that a cluster of aerobic, red-pigmented extreme thermophiles constituted a newly defined lineage now recognized as the Archaea (Woese and Fox, 1977). This group encompassed methanogens as well as thermophilic and hyperthermophilic prokaryotes, including organisms later classified within the *Halobacteria* (Oren, 2014). A seminal study published in 1978 examined the small-subunit rRNA of *Halobacterium halobium* and *Halobacterium cuticulumbrum*. These species were later reclassified as strains of *Halobacterium salinarum*, providing critical evidence that extreme halophiles were phylogenetically distinct from bacteria (Ventosa and Oren, 1996).

Haloarchaea are renowned for their exceptional tol-

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erance to high-salt environments, a capability achieved through the regulation of osmotic balance via the production of compatible solutes (DasSarma and DasSarma, 2015). They are typically small in size and display diverse cellular morphologies, including rods, cocci, and spirals (Hezayen *et al*., 2001). Haloarchaea generate energy through multiple metabolic pathways, encompassing aerobic and anaerobic respiration, fermentation, and phototrophic ATP production mediated by bacteriorhodopsin (Bickel-Sandkötter *et al*., 1996). Their vibrant pigmentation derives largely from carotenoids, which also protect against UV-induced cellular damage (Oren and Rodriguez-Valera, 2001). Additional adaptations, including specialized transport proteins and membrane structures composed of ether-linked lipids, enable these organisms to endure extreme salinity (van de Vossenberg *et al*., 2000). In high-salt environments, halophilic archaea depend on Na^+ ions to stabilize their cell walls, ribosomes, and enzymes. Unlike non-halophilic bacteria, which possess robust cross-linked peptidoglycan cell walls, halophilic archaea feature thick, rigid cell walls and cytoplasmic membranes that require high salt concentrations for structural integrity and survival (Kandler and König, 1993; DasSarma and DasSarma, 2015). These cells are further protected by envelopes containing highly glycosylated S-layers composed of negatively charged saccharides, contributing to surface stability under hypersaline conditions (Kandler and König, 1993).

The kingdom *Halobacteria* currently comprises 9 families, 82 genera, and 357 species with validly published names, representing an approximately 50% increase from the 6 families, 57 genera, and 233 species reported in 2017 (Arahal *et al*., 2017; Cui *et al*., 2023). This expansion is largely attributable to major taxonomic revisions informed by comprehensive phylogenomic analyses based on single-copy marker proteins. These analyses prompted the reorganization of orders within the kingdom *Halobacteria*, including the merger of the former orders *Haloferacales* and *Natrialbales* into *Halobacteriales* (Cui *et al*., 2023). As global diversity continues to be redefined, efforts to document regional microbial resources have become increasingly important.

To contribute to the understanding of domestic biodiversity for haloarchaea, this study focuses on unrecorded haloarchaeal species that have not yet been reported in Korea. Based on 16S rRNA gene sequence analysis, seven species from the order *Halobacteriales*, belonging to four genera (*Halobellus*, *Haloplanus*, *Natronomonas*, and *Salinigranum*) and the families *Haloferacaceae* and *Halobacteriaceae*, were identified. Their phenotypic characteristics and phylogenetic analyses further confirmed their status as previously unrecorded haloarchaea in Korea.

Materials and Methods

Samples were collected from solar salterns located in Siheung (July 2018), Taean (January 2024), and Buan (January 2024). Each sample (1 g) was suspended in 10 mL of 20% (v/v) NaCl solution and thoroughly vortexed. The resulting suspensions were inoculated directly into DB Characterization Medium No. 2 (DBCM2) agar plates or into 100 mL of modified DBCM2 broth in 500 mL shaking flasks. The modified DBCM2 broth contained the following components (per liter): 833 mL MDS salt water (7 g of KCl, 35 g of $MgSO_4 \cdot 7H_2O$, 30 g of $MgCl_2 \cdot 6H_2O$, 240 g of NaCl, and 5 mL of 1 M $CaCl_2$ solution), 1 mL of $FeCl_2$ solution, 0.05 g of peptone (Oxoid, Hampshire, UK), 0.25 g of yeast extract (BD, Franklin Lakes, NJ, USA), 5 mL of 1 M NH_4Cl, 2 mL of potassium phosphate buffer, 1 mL of trace element solution (2.0 mg of $FeSO_4 \cdot 7H_2O$, 141.5 mg of $ZnSO_4 \cdot 7H_2O$, 57.6 mg of $MnSO_4 \cdot H_2O$, 6.0 mg of H_3BO_3, 190.0 mg of $CoCl_2 \cdot 6H_2O$, 2.0 mg of $CuCl_2 \cdot 2H_2O$, 24.0 mg of $NiCl_2 \cdot 6H_2O$, and 36.0 mg of $Na_2MoO_4 \cdot 2H_2O$ per liter), 3 mL of vitamin solution (3.0 mg of biotin, 4.0 mg of folic acid, 50.0 mg of pyridoxine·HCl, 33.0 mg of thiamine·HCl, 10.0 mg of riboflavin, 33.0 mg of nicotinic acid, 17.0 mg of DL-calcium pantothenate, 17.0 mg of vitamin B_{12}, 13.0 mg of *p*-aminobenzoic acid, and 10 mg of lipoic acid per liter), 10 mL of 1 M sodium pyruvate solution. The medium was further supplemented with 0.25 g of fish peptone (HiMedia, Maharashtra, India), 1 g of D-glucose (Samchun Chemical, Pyeongtaek, Korea), and 1 g of sucrose (Samchun Chemical, Pyeongtaek, Korea), and the pH was adjusted to 7.0–7.3 with 1 M Tris-base. DBCM2 agar plates were solidified with 2% (w/v) agarose (KisanBio, Seoul, Korea). Agar cultures were incubated at 37°C for one month, while broth cultures were incubated at 37°C with shaking at 200 rpm. Subsequently, agar and broth cultures were serially diluted and spread onto fresh DBCM2 agar plates. Distinct colonies were selected and repeatedly subcultured onto fresh media every 3–7 days. After at least three successive subculturing steps, pure isolates were obtained and preserved at −80°C in a cryoprotectant solution containing 20% (w/v) glycerol and 20% (w/v) NaCl.

Phenotypic characterization was performed using cultures grown at 37°C on DBCM2 agar plates. Cell morphology was examined by light microscopy (CX23; Olympus, Tokyo, Japan) and scanning electron microscopy (SUPRA 55VP; Carl Zeiss, Oberkochen, Germany). Gram staining was carried out using a commercial Gram stain kit (BioWORLD, Dublin, OH, USA) following the manufacturer's instructions. To assess salinity tolerance, each species was cultivated in DBCM2 broth containing NaCl concentrations ranging from 5% to 30% (w/v) in 5% increments and incubated for 3–7 days at 37°C and 200

rpm. The pH range for growth was evaluated by cultivating cells for 3−7 days at 37°C and 200 rpm in buffer-adjusted media with pH values from 4.0 to 11.0 in 1.0 unit increments. The following 100 mM buffer systems were used: 100 mM of CH_3COOH/CH_3COONa buffer (pH 4.0−6.0), 100 mM of NaH_2PO_4/Na_2HPO_4 buffer (pH 7.0−8.0), 100 mM $NaHCO_3/Na2CO_3$ buffer (pH 9.0−10.0), and 100 mM of Na_2CO_3/NaOH buffer (pH 11.0−12.0). Growth temperature was assessed by incubating cultures on DBCM2 agar at 4, 10, 15, 20, 25, 30, 35, 37, 40, 45, and 55°C for 3−7 days. Catalase and oxidase activities were tested using 3% (v/v) H_2O_2 and 1% (w/v) tetramethyl-p-phenylenediamine, respectively.

Carbon and nitrogen source utilization was examined in modified DBCM2 broth lacking all carbon and nitrogen sources, supplemented individually (0.1%, w/v) with one of the following substrates: D-glucose, D-mannose, D-galactose, D-maltose, D-sucrose, D-lactose, D-fructose, D-ribose, D-arabinose, L-rhamnose, D-xylose, trehalose, raffinose, glycerol, L-sorbose, pyruvate, D-mannitol, succinate, DL-lactate, L-malate, fumarate, citrate, acetate, L-glycine, L-histidine, L-alanine, L-glutamate, L-glutamic acid, L-arginine, L-lysine, and L-ornithine.

Genomic DNA was extracted using the LaboPass™ Tissue Genomic DNA Isolation Kit (Cosmogenetech, Seoul, Korea). The partial 16S rRNA gene was amplified by polymerase chain reaction (PCR) using archaeal-specific primers described by Cui *et al.* (2009). PCR products were purified with the LaboPass™ PCR Purification Kit (Cosmogenetech, Seoul, Korea) and submitted to Macrogen Co., Ltd. (Seoul, Korea) for sequencing. Sequencing was performed using archaeal universal primers, including 18F (5′-ATTCCGGTTGATCCTGCC-3′), 344F (5′-CGGGYGCASCAGGCGCGAA-3′), 520R (5′-GWATTACCGCGGCKGCTG-3′), 787F (5′-ATTAGATACCCSBGTAGTCC-3′), and 1518R (5′-AGGAGGTGATCCAGCCGC-3′) (Abdallah *et al.*, 2018). Raw sequences were assembled using the SeqMan™ II expert sequence analysis software (Thombre *et al.*, 2016). Taxonomic identification of the assembled sequences was performed using the EzBioCloud 16S-based ID service (https://www.ezbiocloud.net/identify), and the closest related taxa were retrieved from the EzTaxon-e database (http://www.ezbiocloud.net/eztaxon) (Yoon *et al.*, 2017). Multiple sequence alignments were generated using the ClustalW algorithm implemented in BioEdit 7.2.6.1 (Thompson *et al.*, 1994; Hall, 1999).

Phylogenetic trees were constructed in MEGA 12 based on the aligned 16S rRNA gene sequences (Kumar *et al.*, 2024). Sequence relatedness was inferred using the maximum likelihood (ML) method (Felsenstein, 1981), and tree robustness was evaluated with 1,000 bootstrap replications. Evolutionary distances were calculated using the Kimura two-parameter model (Kimura, 1980).

Results and Discussion

The 16S rRNA gene sequence analyses revealed that all seven isolates represented species not previously reported in Korea. Detailed strain information, including taxonomic assignment from species to class level, identification results, isolation sources, and sequence accession numbers from both the National Institute of Biological Resources (NIBR) in Korea and GenBank, is provided in Table 1. Seven species were classified within the order *Halobacteriales*. Among them, six species belonged to the family *Haloferacaceae*, and one species belonged to the family *Halobacteriaceae*. The *Haloferacaceae* species comprised members of the genera *Halobellus* (4 species), *Haloplanus* (1 species), and *Salinigranum* (1 species). The single species assigned to the *Halobacteriaceae* was identified as *Natronomonas*. The isolated unrecorded haloarchaeal species exhibited various morphologies, including pleomorphic and rod-shaped (Fig. 1). All seven species were Gram-stain-negative and lysed in distilled water. Some species required Mg^{2+} for growth, and most exhibited mesophilic (20−40°C) and neutrophilic (pH 7.0) growth characteristics. All isolates grew at NaCl concentrations above 10% (w/v). Catalase activity was detected in all species, whereas oxidase activity varied among them. Growth was supported in all isolates when D-glucose or pyruvate was provided as the sole energy source. However, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, starch, L-lysine, and L-ornithine were not utilized as sole substrates.

The identification of the seven unrecorded species based on 16S rRNA gene sequence similarities was further supported by phylogenetic analysis using the ML algorithm (Fig. 2). Detailed morphological, physiological, and biochemical characteristics of the seven haloarchaeal species are presented in the following strain descriptions.

Description of *Salinigranum marinum* MBLA0167

Cells are Gram-stain-negative and rod-shaped. Colonies are red, circular, and flat after 7 days of incubation on DBCM2 agar at 37°C. Catalase activity is positive, whereas oxidase activity is negative. Growth occurs at 25−45°C (optimum, 37°C) in 10−25% NaCl (optimum, 15%), and at pH 5.0−10.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is required for growth. D-glucose, sucrose, lactose, D-sorbitol, pyruvate, L-malate, glycine, and L-alanine are utilized as sole energy sources. In contrast, D-mannose, D-galactose, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, starch, glycerol, D-mannitol, acetate, DL-lactate, succinate, fumarate, citrate, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PV549648. Strain MBLA0167

Table 1. Summary of all strains isolated in this study and their taxonomic affiliations.

Order	Family	Strain ID	Accession/ NIBRARC number	Closest species	Similarity (%)	Isolation source	Medium
Halobacteriales	*Haloferacaceae*	MBLA0167	PV549648 NIBRARC000513757	*Salinigranum marinum*	99.4	Solar saltern in Siheung	DBCM2
		MBLA0307	PP917501 NIBRARC000513548	*Halobellus clavatus*	99.7	Solar saltern in Taean	
		MBLA0308	PP916780 NIBRARC000513549	*Halobellus salinus*	100.00	Solar saltern in Taean	
		MBLA0309	PP917499 NIBRARC000513550	*Halobellus ramosii*	99.6	Solar saltern in Taean	
		MBLA0310	PP917500 NIBRARC000513551	*Halobellus inordinatus*	99.6	Solar saltern in Buan	
		MBLA0311	PP917502 NIBRARC000513552	*Haloplanus salinus*	99.0	Solar saltern in Buan	
	Halobacteriaceae	MBLA0186	PQ481849 NIBRARC000513553	*Natronomonas aquatica*	98.8	Solar saltern in Siheung	

(=NIBRARC000513757) was isolated from a solar saltern in Siheung, Gyeonggi-do, Korea (37°24′08.6″N 126° 45′22.7″E).

Description of *Natronomonas aquatica* MBLA0186

Cells are Gram-stain-negative rod-shaped. Colonies are red, circular, and flat after 7 days of incubation on DBCM2 at 37°C. Catalase activity is positive, whereas oxidase activity is negative. Growth occurs at 25−50°C (optimum, 37°C) in 15−30% NaCl (optimum, 25%), and at pH 7.0−9.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is not required for growth. D-glucose, glycerol, pyruvate, L-alanine, and L-glutamate are utilized as sole energy sources. In contrast, D-mannose, D-galactose, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, sucrose, lactose, starch, D-mannitol, D-sorbitol, acetate, DL-lactate, succinate, L-malate, fumarate, citrate, glycine, L-arginine, L-aspartate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PQ481849. Strain MBLA0186 (=NIBRARC000513553) was isolated from a solar saltern in Siheung, Gyeonggi-do, Korea (37°24′08.6″N 126°45′22.7″E).

Description of *Halobellus clavatus* MBLA0307

Cells are Gram-stain-negative and rod-shaped. Colonies are red, circular, and convex after 7 days of incubation on DBCM2 at 37°C. Catalase and oxidase activity are positive. Growth occurs at 25−50°C (optimum, 37°C) at 10−30% NaCl (optimum, 20%), and at pH 6.0−9.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is not required for growth. D-glucose, D-mannose, D-galactose, sucrose, lactose, glycerol, pyruvate, DL-lactate, succinate, L-malate, and fumarate are utilized as sole energy sources. In contrast, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, starch, D-mannitol, D-sorbitol, acetate, citrate, glycine, L-alanine, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PP917501. Strain MBLA0307 (=NIBRARC000513548) was isolated from a solar saltern in Taean, Chungcheongnam-do, Korea (36°25′14.5″N 126°22′37.1″E).

Description of *Haloferax namakaokahaiae* MBLA0308

Cells are Gram-stain-negative and pleomorphic shaped. Colonies are red, circular, and convex after 7 days of incubation on DBCM2 at 37°C. Catalase and oxidase activity are positive. Growth occurs at 25−50°C (optimum, 37°C) in 10−30% NaCl (optimum, 20%), and at pH 6.0−9.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is not required for growth. D-glucose, sucrose,

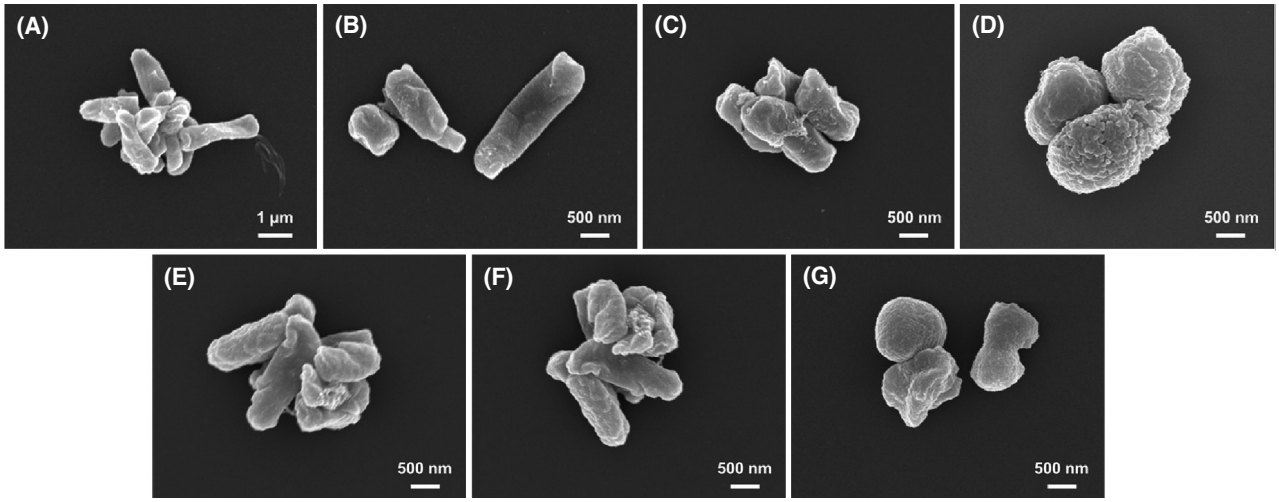


Fig. 1. Scanning electron micrographs of the 7 unrecorded species isolated in this study. Strains: A, MBLA0167; B, MBLA0186; C, MBLA0307; D, MBLA0308; E, MBLA0309; F, MBLA0310; G, MBLA0311.

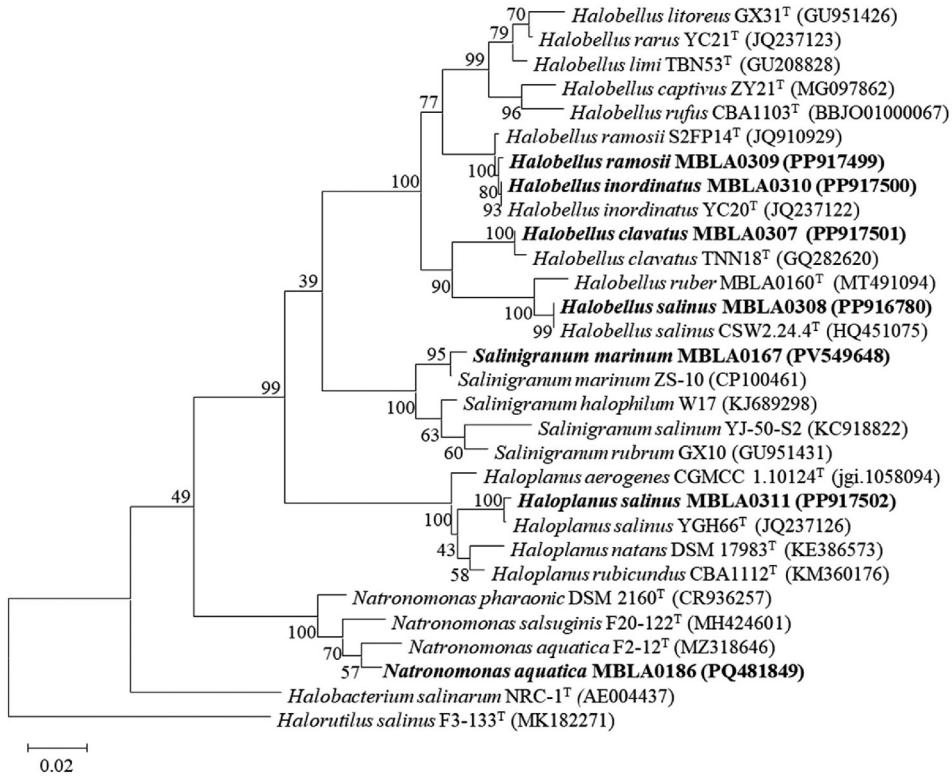


Fig. 2. Maximum likelihood (ML) phylogenetic tree based on the 16S rRNA gene sequences between the species isolated in this study. A phylogenetic tree was constructed with their relatives of the genera *Halobellus*, *Haloplanus*, *Natronomonas*, and *Salinigranum*. The numbers on the nodes indicate the bootstrap values. Bar, 0.02 accumulated changes per nucleotide, respectively.

glycerol, D-sorbitol, pyruvate, DL-lactate, fumarate, and citrate are utilized as sole energy sources. In contrast, D-mannose, D-galactose, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, lactose, starch, D-mannitol, acetate, succinate, L-malate, glycine, L-alanine, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PP916780. Strain MBLA0308

(=NIBRARC000513549) was isolated from a solar saltern in Taean, Chungcheongnam-do, Korea (36°25′14.5″N 126°22′37.1″E).

Description of *Halobellus ramosii* MBLA0309

Cells are Gram-stain-negative and rod-shaped. Colonies are red, circular, and convex after 7 days of incubation on DBCM2 at 37°C. Catalase activity is positive, whereas oxidase activity is negative. Growth occurs at 25−50°C (optimum, 37°C) in 15−30% NaCl (optimum, 25%), and at pH 7.0−9.0 (optimum, pH 7.0). Cell lyse in distilled water, and Mg^{2+} is not required for growth. D-glucose, glycerol, pyruvate, and succinate are utilized as sole energy sources. In contrast, D-mannose, D-galactose, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, sucrose, lactose, starch, D-mannitol, D-sorbitol, acetate, DL-lactate, L-malate, fumarate, citrate, glycine, L-alanine, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PP917499. Strain MBLA0309 (=NIBRARC000513550) was isolated from a solar saltern in Taean, Chungcheongnam-do, Korea (36°25′14.5″N 126°22′37.1″E).

Description of *Halobellus inordinatus* MBLA0310

Cells are Gram-stain-negative and rod-shaped. Colonies are red, circular, and convex after 7 days of incubation on DBCM2 at 37°C. Catalase activity is positive, whereas oxidase activity is negative. Growth occurs at 20−50°C (optimum, 37°C) in 10−30% NaCl (optimum, 20%), and at pH 6.0−9.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is required for growth. D-glucose, glycerol, acetate, pyruvate, DL-lactate, succinate, L-malate, and fumarate are utilized as sole energy sources. In contrast, D-mannose, D-galactose, D-fructose, L-sorbose, D-ribose, D-xylose, maltose, sucrose, lactose, starch, D-mannitol, D-sorbitol, citrate, glycine, L-alanine, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PP917500. Strain MBLA0310 (=NIBRARC000513551) was isolated from a solar saltern in Buan, Jeollabuk-do, Korea (35°35′50.7″N 126°36′46.8″E).

Description of *Haloplanus salinus* MBLA0311

Cells are Gram-stain-negative and pleomorphic shaped. Colonies are red, circular, and convex after 7 days of incubation on DBCM2 at 37°C. Catalase activity is positive, but oxidase activity is negative. Growth occurs at 20−50°C (optimum, 37°C) in 10−30% NaCl (optimum, 20%), and at pH 6.0−8.0 (optimum, pH 7.0). Cells lyse in distilled water, and Mg^{2+} is required for growth. D-glucose, D-mannose, pyruvate, and DL-lactate are utilized as sole energy sources. In contrast, D-galactose, D-fructose, L-sorbose, D-ribose, maltose, sucrose, lactose, starch, glycerol, D-mannitol, D-sorbitol, acetate, succinate, L-malate, fumarate, citrate, glycine, L-alanine, L-arginine, L-aspartate, L-glutamate, L-lysine, and L-ornithine are not utilized. The NCBI accession number for the 16S rRNA gene sequence is PP917502. Strain MBLA0311 (=NIBRARC000513552) was isolated from a solar saltern in Buan, Jeollabuk-do, Korea (35°35′50.7″N 126°36′46.8″E).

Conflicts of Interest

The author of this paper have no affiliation with any interests and are solely responsible for the paper.

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