Genome sequence of the haloarchaeon 
*Haloterrigena jeotgali* type strain A29^T^ isolated from salt-fermented food

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**Abstract**

*Haloterrigena jeotgali* is a halophilic archaeon within the family *Natrialbaceae* that was isolated from shrimp jeotgal, a traditional Korean salt-fermented food. A29^T^ is the type strain of *H. jeotgali*, and is a Gram-negative staining, non-motile, rod-shaped archaeon that grows in 10 %–30 % (w/v) NaCl. We present the annotated *H. jeotgali* A29^T^ genome sequence along with a summary of its features. The 4,131,621 bp genome with a GC content of 64.9 % comprises 4,215 protein-coding genes and 127 RNA genes. The sequence can provide useful information on genetic mechanisms that enable haloarchaea to endure a hypersaline environment.

**Keywords:** Haloarchaeon, *Haloterrigena jeotgali*, Genome sequence, Salt-fermented food, Jeotgal

**Introduction**

An extremely halophilic archaeon, called a haloarchaeon, that is a member of the family *Natrialbaceae* [1] was isolated from various hypersaline environments such as soda and salt lakes, solar salterns, salt mines, salted soils, deep-sea brine, and various salt-fermented foods. Although high salinity is toxic to most cells, extreme halophiles are adapted to their hypersaline environments [2]. Most haloarchaeal require at least 1.5 M NaCl for growth and optimum growth occurs in the range of 3.1 to 3.4 M NaCl [3]. Since haloarchaeal enzymes from the haloarchaea are generally considered to be active and stable at high salt concentrations, they have potential for biotechnological applications such as engineering for salt-resistant plants in agriculture, environmental bioremediation of organic pollutants and production of fermented foods. The genus *Haloterrigena* was first proposed by Ventosa et al. [4] with the reclassification of *Halococcus turkmenicus* as *Haloterrigena turkmenicus* [4], and presently includes nine species: *H. turkmenica* [4], *H. thermotolerans* [5], *H. longa*, *H. limicola* [6], *H. saccharivortans* [7], *H. hispanica* [8], *H. jeotgali* [9], *H. salina* [10], and *H. daqingensis* [11], all of which are pleomorphic, Gram-negative staining, and red- or light pink-pigmented. However, the genus *Haloterrigena* is poorly characterized at the genome level.

A29^T^ (= KCTC 4020^T^ = DSM 18794^T^ = JCM 14585^T^ = CECT 7218^T^) is the type strain of *H. jeotgali* and was isolated from shrimp jeotgal, a traditional Korean salt-fermented food [9]. Although little is known about the roles of the haloarchaea during the fermentation process, the increasing genome information is expected to contribute to expansion of the understanding of their roles and halotolerant features. Here, we present a summary of the classification and features of *H. jeotgali* A29^T^ along with the annotated genome sequence.

**Organism information**

**Classification and features**

A taxonomic analysis was conducted by comparing the *H. jeotgali* A29^T^ 16S rRNA gene sequence with the most recent release of the EzTaxon-e database [12]. Phylogenetic relationships between strain A29^T^ and closely related species were evaluated using MEGA6 program [13],
and dendrograms were generated by the neighbor-joining [14], minimum evolution [15], and maximum likelihood [16] methods. A bootstrap analysis investigating the stability of the dendrogram was performed by obtaining a consensus tree based on 1,000 randomly generated trees. Strain A29\textsuperscript{T} showed the highest level of the 16S rRNA gene similarity to \textit{H. thermotolerans} PR5\textsuperscript{T} (99.0 %), \textit{H. saccharavitans} AB14\textsuperscript{T} (98.3 %), \textit{H. limicola} AX-7\textsuperscript{T} (97.1 %), \textit{H. turkmenica} 4k\textsuperscript{T} (96.8 %), \textit{H. salina} XH-65\textsuperscript{T} (96.6 %), \textit{H. hispanica} FP1\textsuperscript{T} (96.1 %), \textit{H. longa} ABH32\textsuperscript{T} (94.9 %), and \textit{H. daqingensis} JX313\textsuperscript{T} (94.6 %). The DNA-DNA relatedness between strain A29\textsuperscript{T} and the related strains \textit{H. thermotolerans} PR5\textsuperscript{T}, \textit{H. saccharavitans} AB14\textsuperscript{T}, and \textit{H. limicola} AX-7\textsuperscript{T} was 23.2 %, 22.0 %, and 17.9 %, respectively. The 16S rRNA gene sequence similarity data and DNA–DNA relatedness values less than \textit{70 %} [17] suggested that strain A29\textsuperscript{T} represents a distinct genospecies [9] (Table 1).

The consensus phylogenetic tree based on the 16S rRNA gene sequences indicated that strain A29\textsuperscript{T} was clustered in a branch with other species of the genus \textit{Haloterrigena} (Fig. 1).

\textit{H. jeotgali} A29\textsuperscript{T} is Gram-negative staining, non-motile, rod-shaped (0.4 \textmu m wide and 1.0 \textmu m long) (Fig. 2), and grows in irregular clusters. Colonies cultured on complex agar medium were light red, circular, and measured 0.5 mm in diameter after 7 days at 37 °C. Growth occurred in the presence of 10–30 % (w/v) NaCl at temperatures ranging from 17–50 °C and in the pH range of 6.5–8.5. Optimal conditions for growth were; a NaCl concentration of 15–20 % (w/v), a temperature ranging from 37–45 °C, and a pH of 7.0–7.5. The isolate was catalase-positive and oxidase-negative and did not reduce nitrate to nitrite. Mg\textsuperscript{2+} was not required for growth. Cell lysis occurred in distilled water. This strain was able to hydrolyze casein and Tween 80 but not

### Table 1 Classification and general features of \textit{Haloterrigena jeotgali} A29\textsuperscript{T} [19]

| MIGS ID | Property       | Term                                      | Evidence code° |
|---------|----------------|-------------------------------------------|----------------|
|         | Classification| Domain \textit{Archa}e                      | TAS [25]       |
|         |                | Phylum \textit{Euryarchaeota}              | TAS [26]       |
|         |                | Class \textit{Halobacteria}                | TAS [27, 28]   |
|         |                | Order \textit{Natrialbales}                | TAS [1]        |
|         |                | Family \textit{Natrialbaceae}              | TAS [1]        |
|         |                | Genus \textit{Haloterrigena}               | TAS [4]        |
|         |                | Species \textit{Haloterrigena jeotgali}    | TAS [9]        |
|         |                | (Type) strain A29\textsuperscript{T} | KCTC 4020, DSM 18794, JCM 14585, CECT 7218 | TAS [9] |
|         | Gram stain     | Negative                                   | TAS [9]        |
|         | Cell shape     | Rod                                        | TAS [9]        |
|         | Motility       | Non-motile                                 | TAS [9]        |
|         | Sporulation    | Not reported                               | TAS [9]        |
|         | Temperature range | 17–50 °C                           | TAS [9]        |
|         | Optimum temperature | 37–45 °C                       | TAS [9]        |
|         | pH range; Optimum | 6.5–8.5; 7.0–7.5                     | TAS [9]        |
|         | Carbon source  | Fructose, lactose, acetate                | TAS [9]        |
|         | Habitat        | Salt-fermented food                       | TAS [9]        |
|         | Salinity       | 35 % NaCl (w/v)                           | TAS [9]        |
|         | Oxygen requirement | Aerobic                                   | TAS [9]        |
|         | Biotic relationship | Free-living                        | TAS [9]        |
|         | Pathogenicity  | Not reported                               | TAS [9]        |
|         | Geographic location | South Korea                      | TAS [9]        |
|         | Sample collection | 2006                                      | NAS            |
|         | Latitude       | Not reported                               | NAS            |
|         | Longitude      | Not reported                               | NAS            |
|         | Altitude       | Not reported                               | NAS            |

°Evidence codes - TAS: Traceable Author Statement (i.e., a direct report exists in the literature); NAS: Non-traceable Author Statement (i.e., not directly observed for the living, isolated sample, but based on a generally accepted property for the species, or anecdotal evidence). These evidence codes are from the Gene Ontology project [29].
starch, gelatin, urea, or DNA. Anaerobic growth occurred in the presence of nitrate but not of sulfate, thiosulfate, dimethyl sulfoxide, or trimethylamine N-oxide. Fructose, lactose, and acetate—but not sucrose, glucose, citrate, or formate—were utilized as carbon and energy sources.

![Fig. 1](image1.png) **Fig. 1** Phylogenetic tree based on the neighbor-joining (NJ) algorithm for the 16S rRNA gene sequences of strain A29T and closely related taxa. Numbers at the nodes indicate bootstrap values calculated using NJ/minimum evolution (ME)/maximum likelihood (ML) probabilities. Filled and open circles represent nodes recovered by both ME and ML methods or by either method, respectively. *Methanospillum hungatei* JF-1T served as an outgroup.

![Fig. 2](image2.png) **Fig. 2** Transmission electron micrograph of *H. jeotgali* A29T. The scale bar represents 200 nm.

| MIGS ID | Property | Term |
|---------|----------|------|
| MIGS-31 | Finishing quality | Improved-high-quality draft |
| MIGS-28 | Libraries used | 300-bp paired end (Illumina); 400-bp single end (Ion Torrent); 10 kb (PacBio RS) |
| MIGS-29 | Sequencing platforms | Illumina MiSeq, Ion Torrent PGM, PacBio RS system |
| MIGS-31.2 | Fold coverage | 700x |
| MIGS-30 | Assemblers | CLC Genomics Workbench 6.5.1, SMRT Analysis 2.1 |
| MIGS-32 | Gene calling method | GLIMMER 3.02 |
|         | Locus Tag | HL44 |
|         | GenBank ID | JDTG00000000 |
|         | GenBank Date of Release | June 20, 2014 |
|         | GOLD ID | G00069863 |
|         | BIOPROJECT | PRJNA236631 |
| MIGS-13 | Source material identifier | A29T |
|         | Project relevance | Environmental and biotechnological |
sources. Acid was not produced from fructose, lactose, acetate, sucrose, glucose, citrate, or formate. Strain A29\textsuperscript{T} was resistant to bacitracin, penicillin, ampicillin, chloramphenicol, and erythromycin, but was sensitive to novobiocin, anisomycin, and aphidicolin. The major polar lipids were phosphatidylglycerol, phosphatidylglycerol phosphate methyl ester, and mannose-2,6-disulfate(1–2)-glucose glycerol diether [9].

**Genome sequencing and annotation**

**Genome project history**

*H. jeotgali* strain A29\textsuperscript{T} genome was sequenced to obtain information regarding mechanism(s) or molecule(s) that confer adaption to a hypersaline environment and to identify the primary structure of potentially novel halophilic enzymes with relatively low similarity to those in the sequence database. The genome project and sequence were

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![Graphical circular map of the *H. jeotgali* A29\textsuperscript{T} genome. RNA genes (red, tRNA and blue, rRNA) and genes on the reverse and forward strands (colored according to COG categories) are shown from the outside to the center. The inner circle shows the GC skew; yellow and blue indicate positive and negative values, respectively. GC content is indicated in red and green.](image-url)
deposited in the Genomes OnLine Database [18] and GenBank (JDTG000000000), respectively. Sequencing and annotation were performed by ChunLab Inc. (Seoul, Korea). Project information and associated MIGS version 2.0 compliance levels [19] are shown in Table 2.

**Growth conditions and genomic DNA preparation**

*H. jeotgali A29* was grown aerobically in DSM Medium 954 at 37°C. Genomic DNA was extracted and purified using a G-spin™ DNA extraction kit (iNtRON Biotechnology, Sungnam, Korea) according to the manufacturer's instructions.

**Genome sequencing and assembly**

The genome of *H. jeotgali A29* was sequenced from a total of 9,473,809 quality-trimmed sequencing reads (700.5-fold coverage) that combined 6,797,702 reads (473.8-fold coverage) from the Illumina MiSeq, 300 bp paired-end library (Illumina, San Diego, CA, USA); 2,617,102 reads (181.1-fold coverage) obtained using an Ion Torrent Personal Genome Machine (PGM) 318v2 chip (Life Technologies, Carlsbad, CA, USA); and 59,005 reads (45.7-fold coverage) from a PacBio RS 10 kb library (Pacific Biosciences, Menlo Park, CA, USA). Illumina and PGM data were assembled *de novo* with CLC Genomics Workbench 6.5.1 (CLC bio, Boston, MA, USA) and PacBio data were assembled with the HGAP2 algorithm in SMRT Analysis 2.1 (Pacific Biosciences). Resultant contigs were assembled with CodonCode Aligner 3.7 (CodonCode Corporation, Centerville, MA, USA). The final assembly yielded three scaffolds with 20 contigs spanning 4.1 Mb.

**Genome annotation**

Open reading frames of the assembled genome were predicted using the Integrated Microbial Genomes-Expert Review platform as part of the Joint Genome Institute genome annotation pipeline [20]. Additional gene prediction and functional annotation were achieved using the Rapid Annotation using Subsystem Technology pipeline. Predicted ORFs were compared during gene annotation using NCBI Clusters of Orthologous Groups [21], Pfam [22], and EzTaxon-e [12] databases. rRNA and tRNA genes were identified using RNAmmer 1.2 [23] and tRNAscan-SE 1.23 [24] tools, respectively. Genomic features were visualized with CLgenomics 1.06 (ChunLab Inc.).

**Table 3** Genomic statistics

| Attribute                | Value   | % of Total |
|--------------------------|---------|------------|
| Genome size (bp)         | 4,131,621 | 100.00     |
| DNA coding (bp)          | 3,538,864 | 85.65      |
| DNA G + C (bp)           | 2,682,192 | 64.92      |
| DNA scaffolds             | 20      | 100.00     |
| Total genes              | 4,342   | 100.00     |
| Protein-coding genes     | 4,215   | 97.08      |
| RNA genes                | 127     | 2.92       |
| Genes in internal clusters | 3,412 | 78.58      |
| Genes with function prediction | 2,636 | 60.71      |
| Genes assigned to COGs   | 2,144   | 49.38      |
| Genes with Pfam domains  | 2,638   | 60.76      |
| Genes with signal peptides | 79   | 1.82       |
| Genes with transmembrane helices | 984  | 22.66      |
| CRISPR repeats           | 1       |            |

**Table 4** Number of genes associated with general COG functional categories

| Code | Value | % of Total | Description                                      |
|------|-------|------------|-------------------------------------------------|
| J    | 154   | 6.53       | Translation, ribosomal structure, and biogenesis |
| A    | 1     | 0.04       | RNA processing and modification                  |
| K    | 107   | 4.54       | Transcription                                    |
| L    | 129   | 5.47       | Replication, recombination, and repair           |
| B    | 3     | 0.13       | Chromatin structure dynamics                     |
| D    | 19    | 0.81       | Cell cycle control, mitosis, and meiosis         |
| Y    | 0     | 0.00       | Nuclear structure                                |
| V    | 31    | 1.31       | Defense mechanisms                               |
| T    | 78    | 3.31       | Signal transduction mechanisms                   |
| M    | 69    | 2.93       | Cell wall/membrane biogenesis                    |
| N    | 17    | 0.72       | Cell motility                                    |
| Z    | 0     | 0.00       | Cytoskeleton                                     |
| W    | 0     | 0.00       | Extracellular structures                         |
| U    | 21    | 0.89       | Intracellular trafficking, secretion, and vesicular transport |
| O    | 101   | 4.28       | Posttranslational modification, protein turnover, chaperones |
| C    | 167   | 7.08       | Energy production conversion                     |
| G    | 88    | 3.73       | Carbohydrate transport metabolism                |
| E    | 217   | 9.20       | Amino acid transport metabolism                  |
| F    | 66    | 2.80       | Nucleotide transport metabolism                  |
| H    | 131   | 5.56       | Coenzyme transport metabolism                    |
| I    | 125   | 5.30       | Lipid transport metabolism                       |
| P    | 158   | 6.70       | Inorganic ion transport metabolism               |
| Q    | 50    | 2.12       | Secondary metabolites biosynthesis, transport catabolism |
| R    | 400   | 16.96      | General function prediction only                 |
| S    | 226   | 9.58       | Function unknown                                 |
| -    | 2198  | 50.62      | Not in COGs                                     |

The total is based on the total number of protein coding genes in the genome.
**Genome properties**

The draft genome sequence of *H. jeotgali A29T* was 4,131,621 bp and comprised three scaffolds including 20 contigs, and had a GC content of 64.9 % (Fig. 3 and Table 3). Of the 4,342 predicted genes, 4,215 were protein-coding and 2,636 ORFs (60.7 %) were assigned putative functions, whereas the remaining genes were annotated as hypothetical proteins. The genome contained 127 ORFs assigned to RNA genes, including 47 predicted for tRNA, 14 for rRNA (five 5S, two 16S, and seven 23S), and 66 for miscellaneous RNA (one archaeal signal recognition particle; five for the HgcC family; one archaeal RNA P; and 59 clustered regularly interspersed short palindromic direct repeat elements). The distribution of genes across COG functional categories is presented in Table 4.

**Conclusions**

*H. jeotgali A29T* encoded the genes associated with the mechanisms of salinity tolerance, biosynthesis and transport of compatible solutes such as glycine betaine (N,N,N-trimethylglycine) (choline sulfatase, choline dehydrogenase, betaine reductase, and glycine betaine transporter OpuD), ion exclusion using cation (Mg$^{2+}$ and Cu$^{2+}$) transport and K$^+$ transport and Na$^+/H^+$ antiporter systems. The sequences may contribute to expansion of our knowledge of complex osmoregulation mechanism of the haloarchaea that should facilitate biotechnological applications of the haloarchaea and provide useful information on genetic mechanisms that enable haloarchaea to endure hypersaline environments.

**Abbreviations**

ME: Minimum evolution; ML: Maximum likelihood; NJ: Neighbor-joining; PGM: Personal Genome Machine.

**Competing interests**

The authors declare that they have no competing interests.

**Authors’ contributions**

KJY and HSS carried out the microbial cultivation and DNA isolation. ITC, KJY and HSS participated in its design and coordination. All authors read and approved the final manuscript.

**Acknowledgments**

This research was supported by Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Science, ICT & Future Planning (2012R1A1A2040022 and 2014R1A1A1002980) and a Korea Basic Science Institute Nap grant (T34780).

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**Received:** 22 September 2014 **Accepted:** 21 July 2015

**Published online:** 05 August 2015

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