Draft genome sequence of *Dethiobacter alkaliphilus* strain AHT1<sup>T</sup>, a gram-positive sulfidogenic polyextremophile

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**Abstract**

*Dethiobacter alkaliphilus* strain AHT1<sup>T</sup> is an anaerobic, sulfidogenic, moderately salt-tolerant alkaliphilic chemolithotroph isolated from hypersaline soda lake sediments in northeastern Mongolia. It is a Gram-positive bacterium with low GC content, within the phylum Firmicutes. Here we report its draft genome sequence, which consists of 34 contigs with a total sequence length of 3.12 Mbp. *D. alkaliphilus* strain AHT1<sup>T</sup> was sequenced by the Joint Genome Institute (JGI) as part of the Community Science Program due to its relevance to bioremediation and biotechnological applications.

**Keywords:** Extreme environment, Soda lake, Sediment, Haloalkaliphilic, Gram-positive, Firmicutes

**Introduction**

Soda lakes are formed in environments where high rates of evaporation lead to the accumulation of soluble carbonate salts due to the lack of dissolved divalent cations. Consequently, soda lakes are defined by their high salinity and stable highly alkaline pH conditions, making them dually extreme environments. Soda lakes occur throughout the American, European, African, Asian and Australian continents and host a wide variety of Archaea and Bacteria, specialized at surviving under such high salt and high pH conditions [1]. These haloalkaliphiles drive a number of biogeochemical cycles essential to their survival, most notably; the sulfur cycle is very active in these unique habitats [2–4]. The most noteworthy taxa associated with the reductive sulfur cycle are the *Deltaproteobacteria* and the *Firmicutes*. Recently, a number of Gram-positive *Firmicutes* genomes have been analyzed and published describing their metabolic potential and environmental adaptations, including the polyextremophile *Natronarabius thermophilus* [5], and species belonging to the *Desulfotomaculum* spp. [6–8] and the *Desulfosporosinus* spp. [9]. Here we give an extended insight into the first known genome of a haloalkaliphilic Gram-positive sulfur disproportionator within the phylum *Firmicutes: Dethiobacter alkaliphilus* AHT1<sup>T</sup>.

**Organism information**

**Classification and features**

The haloalkaliphilic anaerobe *D. alkaliphilus* AHT1<sup>T</sup> was isolated from hypersaline soda lake sediments in northeastern Mongolia [10]. *D. alkaliphilus* AHT1<sup>T</sup> cells are Gram-positive and the motile rod-shaped cells form terminal ellipsoid endospores (Fig. 1). The strain tolerates salt concentrations ranging from 0.2–0.8 M Na<sup>+</sup> with an optimum at 0.4 M and is an obligate alkaliphile, growing within a pH range from 8.5–10.3 with an optimum at 9.5 [10]. Phylogenetic analysis showed that strain AHT1<sup>T</sup> is a member of the phylum *Firmicutes* and the order *Clostridiales* (Fig. 2). Its closest relative is an acetate-oxidizing syntrophic alkaliphile, described as “*Candidatus Contubernalis alkalaceticum*” which was isolated from a soda lake [11] (Fig. 2). The 16S ribosomal RNA of *D. alkaliphilus* AHT1<sup>T</sup> (EF422412) is 88% identical to the 16S rRNA of “*Candidatus Contubernalis alkalaceticum*” (DQ124682) [12].

**Extended feature descriptions**

*D. alkaliphilus* AHT1<sup>T</sup> is an obligate anaerobe that can produce sulfide by using elemental sulfur and polysulfides...
as electron acceptor [10]. Additionally, it has been shown to incompletely reduce thiosulfate to sulfide and sulfite with hydrogen or formate as electron donor [10]. Strain AHT1T is the first representative from the *Firmicutes* with the metabolic capacity to grow by elemental sulfur disproportionation [13] and, therefore, is a very interesting organism to compare to the typical sulfur disproportionators from the *Deltaproteobacteria*. This species may play an important role in the reductive sulfur cycle in soda lake environments [2] and possibly also in other alkaline anaerobic habitats, such as serpentinization “cement springs”, where sequences closely related to *Dethiobacter* have been found [14, 15]. Also, its affiliation with the syntrophic *Clostridia* “Candidatus Contubernalis alkaleticum” (Fig. 2) implies that *D. alkaliphilus* AHT1T could be involved in syntrophic anaerobic metabolic activity. More classifications and features of this species are listed in Table 1.

### Genome sequencing and assembly

The size of the assembled *D. alkaliphilus* AHT1T genome sequence was 3.12 Mbp. The draft genome was generated at the JGI using a combination of Sanger, Solexa/Illumina [20] and 454 DNA sequencing technologies [21]. An 8 Kb Sanger library was constructed that provided 2.5 x coverage of the genome (15,321 reads generated) and a Solexa shotgun library and a 454 Titanium standard library, which provided 25× genome coverage totalling 110.0 Mbp of 454 data. The 454 Titanium data were assembled with Newbler. The Newbler consensus sequences were computationally shredded into 2 Kb overlapping fake reads (shreds). Illumina sequencing data was assembled with VELVET, version 1.0.13 [22], and the consensus sequences were computationally shredded into 1.5 Kb overlapping fake reads (shreds). We then integrated Sanger reads, the 454 Newbler
Table 1 Classification and general features of *D. alkaliphilus* AHT1T

| MIGS ID | Property                              | Term                                           | Evidence code |
|---------|---------------------------------------|------------------------------------------------|---------------|
|         | Classification                        | Domain: *Bacteria*                              | TAS [51]      |
|         |                                       | Phylum: *Firmicutes*                            | TAS [52–54]   |
|         |                                       | Class: *Clostridia*                             | TAS [55–56]   |
|         |                                       | Order: *Clostridiales*                         | TAS [57, 58]  |
|         |                                       | Family: *Syntrophomonaecae*                    | TAS [59]      |
|         |                                       | Genus: *Dethiobacter*                          | TAS [10, 60]  |
|         |                                       | Species: *Dethiobacter alkaliphilus*           | TAS [10, 60]  |
|         |                                       | Type strain: AHT1T                             | TAS [10]      |
|         | Gram stain                            | positive                                       | TAS [10]      |
|         | Cell shape                            | rod-shaped                                     | TAS [10]      |
|         | Motility                              | motile                                         | TAS [10]      |
|         | Sporulation                           | endospore-forming                              | TAS [10]      |
|         | Temperature range                     | mesophile                                      | TAS [10]      |
|         | Optimum temperature                   | 33                                             |               |
|         | pH range; Optimum                     | 8.5–10.3; 9.5                                  | TAS [10]      |
|         | Carbon source                         | CO₂, acetate                                   | TAS [10]      |
| MIGS-6  | Habitat                               | hypersaline soda lakes, sediments             |               |
| MIGS-6.3| Salinity                              | moderately salt-tolerant                       |               |
| MIGS-22 | Oxygen requirement                    | anaerobe                                       |               |
| MIGS-15 | Biotic relationship                   | free-living                                    |               |
| MIGS-14 | Pathogenicity                         | none                                           |               |
| MIGS-4  | Geographic location                   | northeastern Mongolia; lakes Hotontyn and Shar-Burdiin | TAS [2] |
| MIGS-5  | Sample collection                     | September 1999                                 |               |
| MIGS-4.1| Latitude                              | 48° 19′ 40″                                    | TAS [2]       |
| MIGS-4.2| Longitude                            | 114° 30′ 16″                                   | TAS [2]       |
| MIGS-4.4| Altitude                             | 1000 m                                         |               |

Evidence codes - IDA Inferred from Direct Assay, 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 [Cite ontology project]
consensus shreds and the Illumina VELVET consensus shreds using the PGA assembler [23], to combine sequence data from all three platforms for a most contiguous assembly. The software Consed [24] was used in the computational finishing process as described previously [25]. The final draft assembly contained 34 contigs in 5 scaffolds.

Genome annotation
The assembled sequence was automatically annotated with the JGI prokaryotic annotation pipeline [26] with additional manual review using the IMG-ER platform [27]. Genes were predicted using Prodigal [28], ribosomal RNAs were detected using models built from SILVA [29] and tRNAs were predicted with tRNAScanSE [30]. The predicted CDs were translated and used to search the NCBI non-redundant database UniProt, TIGRFam, Pfam, KEGG, COG and InterPro databases. The final annotated genome is available from the IMG system [31]. We performed a CheckM analysis [32] and assessed that the genome is 95.8% complete.

Genome properties
The genome is 3,116,746 bp long with a GC content of 48.46%. A total of 3213 genes were found, of which 3163 coded for proteins and 50 genes encoded only RNA. From the total genes, 69.19% was assigned a putative function. The IMG taxon ID is 643,886,183. The different functional gene groups are summarized in Table 3. Furthermore, the number of genes assigned to functional COG categories is displayed in Table 4.

### Insights from the genome sequence

#### Extended insights: Metabolic potential
Hydrogen metabolism requires a number of hydrogenase operons, including the hyd operon, and a Ni-Fe metallo-center assembly (hyp) [33]. The first part of the hydrogenase hyd operon is the small hydrogenase subunit hydA located at DealDRAFT_1217, the closest NCBI BLAST hit [12] of this protein is the hydA gene in Desulfotomaculum gibsoniae (Desgi_1397) with 70.4% similarity in a pair-wise alignment [34]. Directly adjacent to hydA, is the large subunit hydB (DealDRAFT_1218) in the D. alkaliphilus AHT1T genome. This subunit is most similar (75.9%) to the hydB subunit in Dehalobacter sp. UNSWDHB (UNSWDHB_1527) [12, 34]. DealDRAFT_1219 is a cytochrome B561 of 198 amino acids and could therefore be the interacting partner and gamma subunit hydC in the hyd operon. The 6-gene hyp operon hypABCDEF is responsible for the assemblage of the Ni-Fe uptake hydrogenases [35]. The last 5 proteins of the hyp operon are annotated in the D. alkaliphilus AHT1T genome (DealDRAFT_0838-DealDRAFT_0842) and follow the organization hypBFCDE, as has been seen before in Rhizobium [36]. The first gene in the operon (DealDRAFT_0843) is a hypothetical protein of 88 nucleotides length and is assigned to pfam01155 hypA, which is 42.6% identical to the hypA gene in Moorella thermoacetica. Therefore, this hypothetical protein is most likely hypA in D. alkaliphilus AHT1T. Using hydrogen as electron donor, D. alkaliphilus AHT1T can grow autotrophically by fixing inorganic carbon through the Wood Ljungdahl pathway, the key genes are all present in the genome (Fig. 3a), including the acs gene.
cluster (Fig. 3b). Heterotrophic growth by *D. alkaliphilus* AHT1T can be achieved with glucose and fructose [10], the entire glycolysis pathway is present in the genome (Fig. 4). Carbohydrate metabolism in *D. alkaliphilus* AHT1T also includes oxidation of short chain organic acids; the tetrameric pyruvate oxidoreductase is present in the conformation *porBADC* (DealDRAFT_1244 – DealDRAFT_1247). Lactate dehydrogenases could not be found, although there is an L-lactate permease (DealDRAFT_0239), an L-lactate transport protein (DealDRAFT_1845) and a large and small subunit acetolactate synthase (DealDRAFT_2169 and 2170). For assimilation of acetate, strain AHT1T has an acetyl coenzyme A synthetase (DealDRAFT_1887).

*D. alkaliphilus* AHT1T might play a role in the reductive sulfur cycle in alkaline habitats since it grows as a thiosulfate and sulfur/polysulfide reducer or by sulfur disproportionation in laboratory cultures [10]. The genome sequence contains a thiosulfate sulfurtransferase (DealDRAFT_1917), which is located directly adjacent to another sulfur transferase (Rhodanese domain DealDRAFT_1918). Both alpha and beta subunits of the adenyllylsulfate reductase *apr* operon were also found (DealDRAFT_1379, DealDRAFT_1380). The *qmo* electron transfer complex, which usually accompanies the

### Table 4

| Code | Value | % of total | Description                                                  |
|------|-------|------------|--------------------------------------------------------------|
| J    | 175   | 7.89       | Translation, ribosomal structure and biogenesis              |
| A    | not reported | not reported | RNA processing and modification                               |
| K    | 134   | 6.04       | Transcription                                                |
| L    | 83    | 3.74       | Replication, recombination and repair                         |
| B    | 1     | 0.05       | Chromatin structure and dynamics                              |
| D    | 45    | 2.03       | Cell cycle control, cell division, chromosome partitioning   |
| V    | 58    | 2.62       | Defense mechanisms                                            |
| T    | 131   | 5.91       | Signal transduction mechanisms                                |
| M    | 124   | 5.59       | Cell wall/membrane biogenesis                                 |
| N    | 52    | 2.35       | Cell motility                                                |
| U    | 34    | 1.53       | Intracellular trafficking and secretion                       |
| O    | 90    | 4.06       | Posttranslational modification, protein turnover, chaperones |
| C    | 178   | 8.03       | Energy production and conversion                              |
| G    | 81    | 3.65       | Carbohydrate transport and metabolism                         |
| E    | 227   | 10.24      | Amino acid transport and metabolism                           |
| F    | 69    | 3.11       | Nucleotide transport and metabolism                           |
| H    | 149   | 6.72       | Coenzyme transport and metabolism                             |
| I    | 80    | 3.61       | Lipid transport and metabolism                                |
| P    | 133   | 6.00       | Inorganic ion transport and metabolism                        |
| Q    | 24    | 1.08       | Secondary metabolites biosynthesis, transport and catabolism  |
| R    | 183   | 8.25       | General function prediction only                              |
| S    | 129   | 5.82       | Function unknown                                             |
| –    | 1242  | 38.66      | Not in COGs                                                  |

The total is based on the number of protein coding genes in the genome.
Genes in the Embden-Meyerhof pathway

| Reaction | Locus Tag |
|----------|-----------|
| Glucose  | not found |
| Glucose - 6P | 1542, 1576 |
| Fructose - 6P | 1891, 3046 |
| Fructose - 1,6P | 1713, 2869 |
| Glyceraldehyde -3P | 1171, 1544 |
| P - 1,3 biphosphoglycerate - P | 1172 |
| 3-phosphoglycerate - P | 2216, 1174, 0668 |
| 2-phosphoglycerate - P | 1175 |
| 2-phosphoenolpyruvate - P | 1892 |
| Pyruvate | 0082, 2280, 2780, 2781, 2783 |
| Acetyl CoA | 0020 - 0025, 1244 - 1247 |

Fig. 4 KEGG orthologs annotated in the Embden-Meyerhof pathway of organic carbon assimilation in *D. alkalophilus* strain AHT1T. The numbers of the locus tags of the genes catalyzing each reaction are indicated and must be preceded by DealDRAFT_

The absence of these genes is surprising. It is conceivable however, that the sequencing quality of the permanent draft is insufficient to recover complete pathways. Indeed, CheckM analysis revealed that the genome was only 95.8% complete. Unfortunately, we can therefore not explain the key dissipatory disproportionation mechanism from this genomic data. The genome also contains some assimilatory sulfate reduction genes, such as *cysND* (DealDRAFT_1193 and DealDRAFT_1192).

Extended insights: Haloalkaliphilic adaptations

In order to generate ATP, *D. alkalophilus* AHT1T has an *ntp* gene operon encoding a vacuolar ATP synthase (*V_oV_1*-type) (DealDRAFT_1677 – DealDRAFT_1685) (Fig. 5a). This operon structure is conserved among the *Clostridia* (Fig. 5b). The *ntp* operon encodes the ATP synthase for ATP generation and follows the GILEX-FABD organization in the *Deinococcus-Thermus* phylum [38]. In the *Firmicutes*, the gene organization is slightly different at GIKECFABD (Fig. 5a, b). In *D. alkalophilus* AHT1T these genes are located from DealDRAFT_1685.

The *ntp* V-type ATP synthase operon

![The ntp V-type ATP synthase operon](image)

Phylogeny of *ntpD*

![Phylogeny of ntpD](image)

93 *ntpD* homologs (DealDRAFT_1677) within the genus *Clostridia* were aligned in Clustal Omega [34] and an unrooted neighbour-joining tree was generated in MEGA-6 [49]. From this tree, we picked the branch that contained the *D. alkalophilus* AHT1T *ntpD* sequence and computed a new neighbour-joining tree with gene DCR20291_1119 as an outgroup. The scale bar indicates a 0.5% sequence difference and conserved gene neighbourhoods of those genes were investigated using MGcv [50]. Large dots at the tree nodes indicate a bootstrap value of >85 (1000 replicates).
(ntpG) to DealDRAFT_1677 (ntpD). The ntpD subunit within the operon is annotated as being of the V-type. In order to confirm that the ATP synthase is indeed V-type [39], we constructed a phylogenetic tree of the transmembrane c/K subunits of Firmicutes known specifically to be V- or F-type [40] and NCBI annotation and aligned the D. alkaliphilus AHT1T ntpC sequence (DealDRAFT_1683) with these other sequences (Fig. 6a) [41]. As seen before, there was a clear separation between V-type and F-type ATP synthase, where the AHT1T sequence clustered together with the V-type ATP synthase. In addition, the sequences are tentatively clustered into separate H+ or Na+ coupled ATPase branches. The AHT1T sequence was positioned within a Na+ coupled V-type ATP synthase group, indicating that this organism’s ATP synthase is coupled specifically to Na+ translocation across the membrane. In order to explore this further, we looked at specific Na+ binding residues and ligands on the transmembrane c/K subunit [40], and created a Weblogo for the Na+ specific Firmicutes V-type ATP synthase (Fig. 6b) [42, 43]. When we aligned the ntpC sequence of D. alkaliphilus AHT1T we found that it contains all the conserved five amino acids (Ser26, Leu57, Thr60, Gln61 and Tyr64) specific for Na+ translocation [40] (Fig. 6c). Thus, the D. alkaliphilus AHT1T genome contains a Na+ coupled V-type ATP synthase.

In order to import protons to retain the intracellular pH, the genome contains the multi-subunit electrogenic sodium/proton antiporter mrp (DealDRAFT_2487–2497), that pumps protons into the cell and sodium out of the cell [44]. To retain osmotic balance, D. alkaliphilus AHT1T has numerous substrate binding regions and transporters for glycine betaine (e.g. DealDRAFT_2378, _2380 and DealDRAFT2842, _2844), leading to the conclusion that osmoprotectants are used to maintain cellular turgor pressure, instead of the salt-in strategy.

Another necessity for alkaliphilic bacteria is to prevent

![Fig. 6a](image-url) Phylogeny of the F- vs. V-type ATPase within the Firmicutes. Numbers on the tree nodes indicate bootstrap values (1000 replicates). Scale bar indicates 0.2% sequence difference.

![Fig. 6b](image-url) Weblogo of conserved region within the ntpC/K Firmicutes subunit [42, 43].

![Fig. 6c](image-url) Weblogo of aligned D. alkaliphilus AHT1T subunit ntpC (DealDRAFT_1683) where conserved Na+ binding regions (in B and C) are indicated with black arrows.
proton leakage from cells, which they can achieve through structural membrane adaptations [1]. The genome contains the genes to synthesize the squalene precursors dimethylallyl dipiphosphate and isopentenylallyl dipiphosphate through the non-mevalonate pathway [45]. The accompanying locus tags within the KEGG non-mevalonate pathway (M00096) are dxs (DealDRAFT_0731), dxxr/ispC (DealDRAFT_2409), ispD (DealDRAFT_2331), ispE (DealDRAFT_2584), ispF (DealDRAFT_2332), ispG (DealDRAFT_2411) and ispH (DealDRAFT_0659). However, we did not find genes similar to ispCDE, which function in the formation of squalene from its precursors [46]. Thus, D. alkaliphilus AHT1T does not seem to have this membrane adaptation to haloalkaline environments, although it could also be due to the incompleteness of the genome. Nevertheless, it has been shown that Bacillus licheniformis C-125, also a Firmicute, survives in the haloalkaline environment by increased levels of acidic polymers in its cellular membrane resulting in a cell wall negative charge [47]. It is possible that D. alkaliphilus AHT1T supports a similar mechanism to survive the alkaline pH values of its environment.

Conclusions
In this manuscript we globally characterize the genome of D. alkaliphilus AHT1T, which was isolated from hypersaline soda lakes sediment in north-eastern Mongolia. Investigation of the genome of this anaerobic sulfidogenic identified genes for the Wood Ljungdahl pathway (autotrophic growth, Fig. 3) and the Embden-Meyerhof pathway (heterotrophic growth Fig. 4). Thus the carbon metabolism of this microbe is fairly versatile. D. alkaliphilus AHT1T is capable of disproportionation in laboratory cultures, thus future genomic analyses with qPCR may provide insights into the disproportionation of sulfur compounds. D. alkaliphilus AHT1T is well adapted to the haloalkaline environment, we found genes for active energy generation with a sodium V-type ATP synthase (Fig. 6). In addition, transporters for the osmoprotectants glycine and betaine were found to maintain cellular homeostasis and protection from the saline external environment. Further research will extend our knowledge on the ecophysiology of haloalkaliphiles, their role in nutrient cycling in extreme environments and their adaptations to this polyextreme environment. Moreover, insight in the genome sequence and subsequent transcriptomic or proteomic analysis will be helpful to infer the potential role of D. alkaliphilus AHT1T in the biotechnological removal of sulfur compounds from wastewater and gas streams.

Abbreviations
F-type: Phosphorylation factor-type; IMG: Integrated Microbial Genomes; IMG-ER: Integrated Microbial Genomes - Expert Review; JGI: Joint Genome Institute; NCBI: National Center for Biotechnology Information; THF: tetrahydrofolate; V-type: Vacuole-type

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Authors’ contributions
EDM drafted and wrote the manuscript. DYS, GM, LO, NCK and ALL contributed to the written manuscript. LO, DYS and GM stimulated critical discussions. DS cultured AHT1T and extracted the DNA. The sequencing and annotation of the genome were performed at the JGI by ALL, MP, NL, TGR, NCK and TW. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interest.

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