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Draft Genome Sequence of a *Haloalkaliphilic archaeon*: *Natrialba* sp. SSL1 (ATCC 43988) Isolated from Sambhar Salt Lake, India

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A B S T R A C T

An extremely haloalkaliphilic archaeon, *Natrialba sp.* SSL1, gram-negative, rod-shaped, motile, aerobic, chemoorganotrophic belonging to the family *Halobacteriaceae* within the Phylum *Euryarchaeota* was isolated from Sambhar Salt Lake (SSL), Rajasthan, India in the 1980s. The Whole Genome Sequence (WGS) of this archaeon was deciphered for the purpose of comparative genomics with other halobacteria as well as eubacteria. The WGS raw data of the genome was assembled into 61 contigs, showing total sequence length of 4,580,837bp, comprising of 4276 genes, out of which 4126 were found to be coding genes (exons), while 96 were psuedogenes. It encodes for 4048 proteins, some of which are peptide repeats of various lengths. Comparative genomic analysis facilitated the identification of genes encoding proteins involved in glycosylation, synthesis of novel archaeal isoprenoid glycolipid identified as glucopyranosyl-1, 6-glucopyranosyl-1-glycerol diether (DGD-4), bacteriocin (halocin), adaptation to salinity stress response, etc. Based on genomic analysis, *Natrialba* sp. SSL1is metabolically versatile and can grow on various carbon and nitrogen sources. Presence of photosystem reaction centre subunit H indicates parallel photosynthetic proton generation system. Genes annotation revealed the presence of extremozymes like alpha-amylase, lipase, protease, trehalose phosphatase, etc. that can be exploited further for biotechnological purpose. This is the first haloalkaliphilic archaeal genome sequenced from India.

Introduction

The extremely halophilic archaea belonging to the family *Halobacteriaceae* (Phylum *Euryarchaeota*) are commonly found in the hypersaline environments such as salt lakes, salt ponds, marine salterns and soda lakes. Haloarchaea living in such harsh environment copes up with salinity stress by higher intracellular KCl concentration and synthesis of compatible solutes such as glycerol and glycine betaine.

Some methanogens also belong to the group haloarchaea. The haloalkaliphilic archaea survive in an environment with two

extremities, namely, high pH (>9.0) and salt concentration (>3.0M NaCl). They adapt to extreme environments by deciphering acidic protein machineries, respiratory chains, rhodopsins, and considerably different metabolism as compared to that of eubacteria (Kennedy *et al*., 2001; Sreeramulu *et al*., 1998; Berquist *et al*., 2005). All halobacteria examined possess ether linked lipids instead of ester linked lipids (present in eubacteria and eukaryotes), which are based on the lipid core 2, 3-di-O-phytanyl-sn-glycerol (C_{20}-C_{20}-diether). Extreme haloalkaliphiles also possess 2-0-sesterterpanyl-3-0-phytanyl-sn-glycerol (C_{20}-C_{25}-diether), and 2, 3-di-0-sesterterpanyl-sn-glycerol (C_{25}-C_{25}-diether) lipid cores (Kates, 1993; Falb *et al*., 2005).

The genus *Natrialba* as per Bergey's Manual of Systematic Bacteriology, vol. I, (2001) belongs to the family *Halobacteriaceae*. It has been reclassified within the novel order *Natrialbales* and family *Natrialbaceae* (Gupta *et al*., 2015). The recognized species within this genus is summarized in Table 1. It is a heterogeneous group able to survive in neutral as well as alkaline environments. A non-alkaliphilic (pH of 6.6 to 7.0) species *Natrialba asiatica* was isolated from the beach sand, Japan (10). *Nab. magadii* is an extremely halolalkaliphilic species that was isolated from Lake Magadi, Kenya that grows at pH 10.0, 20-25 (% w/v NaCl) and utilizes various range of carbohydrate and non-carbohydrate substrates. Two novel haloalkaliphilic archaea *Nab. hulunbeirensis* and *Nab. chahannaoensis* have been isolated from soda lakes in inner Mongolia Autonomous Region, China (Ventosa, 2006). There are seven genomes of species belonging to the genus *Natrialba* submitted in the NCBI database (October, 2016) namely, *Nab. magadii (2), Nab. asiatica (1), Nab. hulunbeirensis (1), Nab. chahannaoensis (1), Nab. aegyptia (1), Nab. taiwanensis (1).* However, none was reported for an isolate from India. So, we carried out the whole genome sequence (WGS) of *Natrialba* SSL1 ATCC 43988 strain isolated from Sambhar Lake, India. Comparative genomic studies with other halophilic as well as haloalkaliphilic archaea has revealed some interesting information that could be useful for future research.

Materials and Methods

Organism and growth conditions: The haloalkaliphilic archaeal isolate *Natrialba* SSL1 (ATCC 43988) was isolated from Sambhar Salt Lake situated (Longitude $75^0$05' E; Latitude $26^0$58'N) middle of the closed depression in the Aravali schist in Rajasthan, India (Figure 1). The isolate was grown at 37°C in modified Brown medium.

Isolation of genomic DNA

The biomass of the *Natrialba* strain was obtained by centrifugation at 10,000 rpm at 5-10^0C from actively growing cells (5-6 days old broth culture). The genomic DNA was isolated by using the Chromus Biotech bacterial gDNA isolation kit as per the protocol provided in the manual. The quality and quantity of gDNA obtained was determined with UV-Vis spectrophotometry at 260 and 280 nm (Tindall *et al*., 1984)**.**

Phylogenetic analysis

The 16S rDNA was amplified by PCR method of Emble (Emble, 1991), as modified by McGenity and Grant (McGenity *et al*., 1998)**.** The forward amplification primer was: 27F, TCCGGTTGATCCTGCCGGAG (positions 8-27), and the reverse amplification primer was: 1525R, AAGGAGGTGATCCAGCC (positions 1541-1525) and sequenced at Chromus Biotech Limited, Bangalore. The sequence was deposited in GenBank with accession no. D88256.1. Similar sequence homologs were

obtained by BLAST search and the phylogenetic tree was constructed by MEGA6.

Whole genome sequencing (WGS)

The WGS was carried out using the Next generation sequencing (NGS) technology using Illumina Hiseq sequencer. The gDNA sample of *Natrialba* SSL1 was subjected for genomic library preparation denoted as VUKGS01_1 Prokaryote TN1601D0815 and VUKGS01_2 Prokaryote TN1601 D0816.The raw data/reads obtained were further analysed as per the pipeline given by THERAGEN ETEX Bioinstitute, Korea.

Genome Sequencing and Raw Reads Output

The raw reads were processed by MyPro (Liao *et al*., 2015) for sequence assembly. The assembled genome consisting of 61 contigs was submitted to GenBank (NCBI), and annotated by PGAP (Prokaryotic Genome Annotation Pipeline, https://www.ncbi.nlm.nih.gov/genome/annotation_prok/).

Results and Discussion

We have isolated and characterized several haloarchaeal strains from Sambhar Lake, Rajasthan having saline and alkaline waters. The isolates have been identified based on morphological, cultural, physiological and 16S rRNA sequence homology studies. The isolate *Natrialba* SSL1 ATCC 43988 was one of the first haloarchaeal isolate reported and characterized from this soda lake that produced various hydrolases, bacteriocin, diether lipids, etc. (Upasani *et al*., 1988; 1990; 2008; 1994). Therefore, it was chosen in this study for WGS and comparative genomics. The phylogenetic tree constructed for the 16S rRNA sequence of *Natrialba* SSL1 GenBank accession no. D88256.1 using MEGA 6 showed identity with *Nab. hulunbeirensis* X21 (Figure 2). The comparative genomics data from NCBI of the *Natrialba* species genomes sequenced to date is summarized in Table 2. A total of 1.31 GB Throughput (Raw reads) was recovered out of 12941508 reads. Clean reads obtained were 11925178 (92.15%); similarly out of 1307092308 total bases, 1197576003 (91.62%) clean bases were obtained. The genome (4.58 Mb) was assembled into 61 contigs using MyPro pipeline. Assembly statistics were calculated using NGSQC toolkit (Table 2) (18). Total sequence length of 4,580,837 bases then annotated by PGAP (Prokaryotic Genome Annotation Pipeline, https://www.ncbi.nlm.nih.gov/genome/annotation_prok/). This annotated data was submitted to NCBI and assigned the accession No.: MASN00000000 BioProject: PRJNA 327293, BioSample: SAMN05328039, Organism*: Natrialba sp. SSL1* which has been validated (Table 3). This data when processed by Prokka for annotation generated 4476 genes; however BLAST analysis of these data did not match with the reference *Natrialba* genome (unpublished data). Therefore, it reveals that this annotation tool was found to be inappropriate for haloarchaeal genomes. The annotation by GenBank using PGAP pipeline generated 4272 genes, most of them matched with *Natrialba* spp. It was interesting to note that the genome sequenced contains genes for bacteriocin, bacterioopsin, amylase, phospholipase, proteases, etc.

Out of 4272 annotated genes, 4217 are CDS genes and total 55 RNA genes. These CDS genes contain 4121 coding genes, while 96 genes were considered as pseudogenes. The 55 RNA genes included 2 rRNA, 2 complete rRNA, 49 tRNA and 2 ncRNA's. The data is compared with other six *Natrialba* genomes sequenced (Table 4). Preliminary annotation, prediction of the number of subsystems, and pairwise BLAST comparisons of protein sets

within different strains was performed using NCBI PGAP that deciphered 4048 proteins. These annotation details are provided at the web sitehttps://www.ncbi.nlm.nih.gov/protein/?term=txid1869245 [Organism:noexp]. *Natrialba* SSL 1 contained single origin of replication (orc1/cdc6) while that of other halolalkaliphilic archaea contains multiple origins of replication. Two replication origins reported in *Nab. magadii* (20)**.** The replication origin of *Halobacterium salinarium* R1 is delineated by a 31-bp inverted repeat that is flanked on one side by a Cdc6 homolog (orc7, OE4380F). On the other side the repeat is flanked by a set of three genes (OE4377R, OE4376R, OE4374R) that are also found adjacent to the replication origin in *Natronomonas pharaonis* (Paul *et al*., 2008), *Haloquadratum walsbyi* (Oren, 1994)**,** and *Haloarcula marismortui* (Ochsenreiter *et al*., 2002). These genes have no known function, but the positional conservation observed in all halophiles may indicate an involvement of the three proteins in the replication process. *Natrialba* SSL1 possesses 52 putative genes for transposes.

Haloalkaliphilic species cell wall containing acidic glycoprotein along with adaptive mechanism by accumulating inorganic cationic /organic neutral biomolecules. Halophilicarchaea maintains required water balance and osmotic pressure by pumping Na^+ out and K^+ in antiporter. *Natrialba* SSL1 possess genes for Na+/H+ antiporter, bile acid: sodium symporter, cation acetate symporter, glycine/betaine ABC transporter, peptide transporter observed at various locations. *Natrialba* SSL1 also contained genes encoding the biosynthesis of spermine as well as transporters for the uptake of amino acid, maltose, malonate and spermidine/putrescine, which may also provide protection at high-osmolarity. Thus, *Natrialba* SSL1 had multiple mechanisms for osmotic adaptation by intracellular accumulation of inorganic cations and organic solutes, charged organic compounds for osmotic adaptation. Depletion of molecular oxygen in a soda lake and similar saline environment could be a growth-limiting factor for aerobic chemoorganotrophic bacteria and archaea (Mirmohammadsadeghi *et al*., 2013). Some archaeal species accumulate intracellular gas vesicle that assist them to float on surface of salt water and help in oxidative respiration. *Nab. magadii* lacked genes related to those encoding the minor gas vesicle protein (GvpC) and the regulators (GvpD and GvpE) (Xu *et al*., 2001). Interestingly *Natrialba* SSL1 possessed various genes encoding gas vesicle proteins like GvpA, GvpFL, GvpJ and GvpN, which indicates the presence of intracellular gas vesicle for buoyancy. Various genes encoding metal transport proteins and a putative copper/Zinc resistance protein also indicate survival in homeostatic mechanism for survival in harsh saline and alkaline environments.

Table.1 Taxonomy of recognized species within the genus *Natrialba* (as of April 2017)

Family *Natrialba* Kamekura and Dyall-Smith 1995 gen. nov.	
Species	**Reference**
Natrialba magadii	(Tindall *et al.* 1984)Kamekura *et al.* 1997, comb. nov.
Natrialba asiatica	Kamekura and Dyall-Smith 1995 sp. nov.
Natrialba aegyptia	corrig. Hezayen *et al.* 2001, sp. nov.
Natrialba chahannaoensis	Xu *et al.* 2001, sp. nov.
Natrialba hulunbeirensis	
Natrialba taiwanensis	Hezayen *et al.* 2001, sp. nov.

Table.2 Assembly statistics of the *Natrialba* genome

Total sequences	61
Total bases	4580837
Min sequence length	391
Max sequence length	526792
Average sequence length	75095.69
Median sequence length	16138
N25 length	455572
N50 length	292114
N75 length	138183
N90 length	68519
N95 length	27066
As	19.31%
Ts	19.22%
Gs	30.71%
Cs	30.76%
(A + T)s	38.53%
(G + C)s	61.47%
Ns	0.00%

Table.3 Genomic data analysis of *Natrialba* SSL1, ATCC 43988

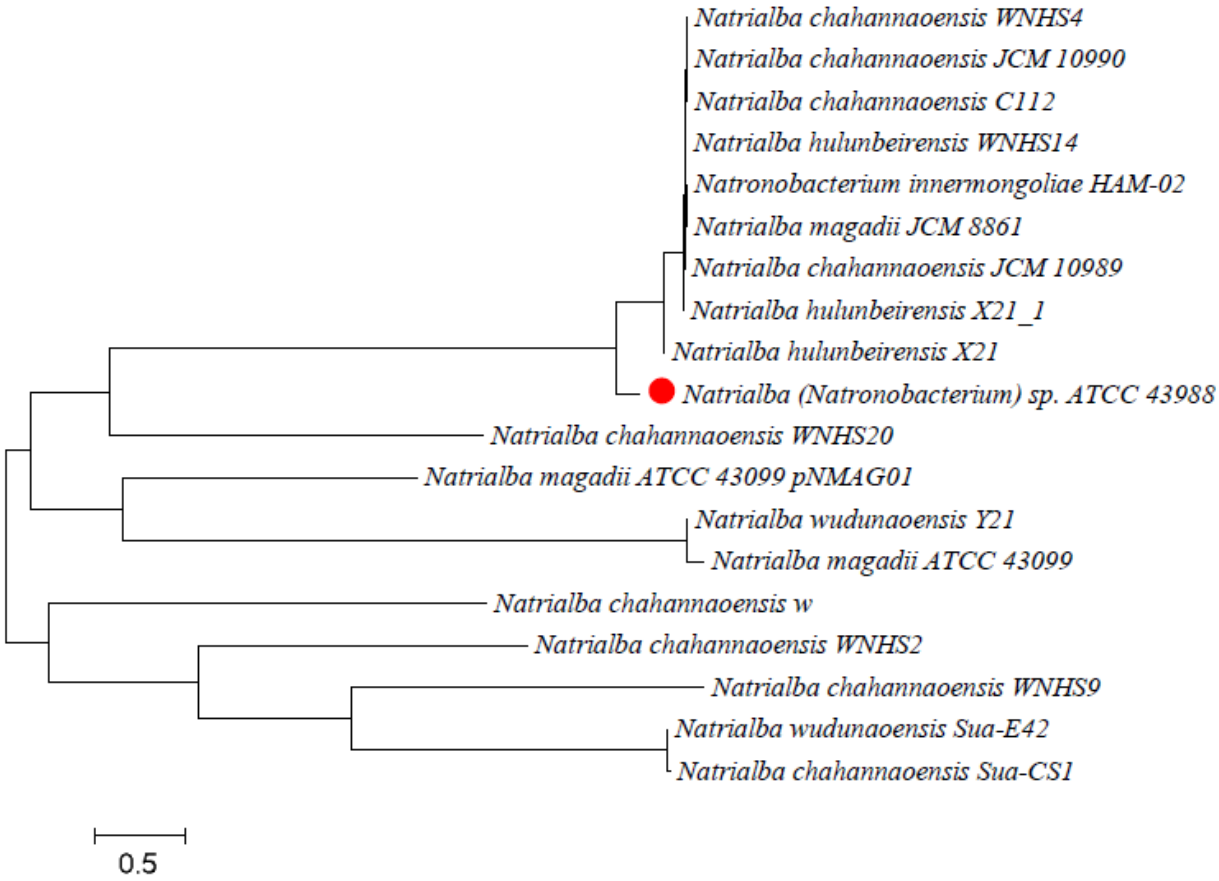
Annotation Provider	**NCBI**
Annotation Date	07-05-16 16:57
Annotation Pipeline	PGAP
Annotation Method	set; GeneMarkS+
Annotation Software revision	3.3
Features Annotated	Gene; CDS; rRNA; tRNA; ncRNA; repeat_region
Genes (total)	4,276
CDS (total)	4,222
Genes (coding)	4,126
CDS (coding)	4,126
Genes (RNA)	54
rRNAs	2, 1 (5S, 16S)
complete rRNAs	2, 1 (5S, 16S)
tRNAs	49
ncRNAs	2
Pseudo Genes (total)	96
Pseudo Genes (ambiguous residues)	0 of 96
Pseudo Genes (frameshifted)	32 of 96
Pseudo Genes (incomplete)	60 of 96
Pseudo Genes (internal stop)	15 of 96
Pseudo Genes (multiple problems)	9 of 96

Table.4 Comparison of basic data for the *Natrialba* genomes sequenced to date (Source: NCBI)

	Nab. SSL1	*Nab. asiatica*	*Nab. aegyptia*	*Nab. chahannaeonsis*	*Nab. magadii**	*Nab. taiwanensis*	*Nab. hulunbeirensis*
BioProject	PRJNA327293	PRJNA174930	PRJNA174929	PRJNA174931	NA	PRJNA174933	PRJNA174932
Length (Mb)	4.58	4.40	4.61	4.30	3.75	4.64	4.16
GC%	61.5	62.4	62.0	60.4	61.4	61.5	61.7
Contigs	61	49	66	106	NA	70	48
% coding	96.4	95.55	95.33	93.75	89.95	94.79	94.06
Encoded proteins	4121	3995	4186	3765	3142	4136	3662
Genes	4272	4181	4391	4016	3493	4363	3839
Encoded stable RNAs	55	54	58	54	55	50	54
*its 3 plasmids have been sequenced (0.378, 0.254 and 0.058 Mb, respectively); NA=Not available/applicable							

Fig.1 Recent satellite image of Sambhar lake, Rajasthan, India showing dark green and red coloration indicating the mass bloom of haloalkaliphilic algae and archaea. (Source: Google maps). It also shows the shrinking of lake area

Fig.2 Phylogenetic tree of *Natrialba* SSL1 (ATCC 43988) showing relationship with other species constructed using MEGA6



Presence of DNA damage and repair proteins RadA and RadB indicate survival strategy against UV exposure.

Halophilic and haloalkaliphilic archaea thrive on different nutritional demand (Gupta *et al*., 2015). The analysis of the genome sequence of *Natrialba* SSL1 provides information for their ability to assimilate C4, C5 and C6 carbon compounds. Interestingly, the species also survives by assimilating non-carbohydrate sources like proteins and fats. Furthermore, genes encoding putative enzymes for archaeal modified pathways of gluconeogenesis and glycolysis as well as those of ribose metabolism and the tricarboxylic acid cycle were present in *Natrialba* SSL1. Genes that deciphered to putative enzymes for glycerol utilization, branched chain and aromatic amino acid catabolism, proteasome synthesis, ABC transporters, co-factor molybdopterin biosynthesis protein, cationic antiporter, symporter and transporter proteins were also present.

Extremozymes from archaea have biotechnological and industrial importance. In *Natrialba* SSL1 genes encoding for serine protease, cystein protease, metallo-protease, lipase, phospholipase, alpha-amylase and cytoplasmic alpha-amylase have been found to be present. The production of halocin by *Natrialba* SSL1 has been reported (Upasani, 1988), this is also substantiated by the evidence for the genes for the same in the genome.

There are several reports on the presence of phages in haloarchaea (Siddaramappa *et al*., 2012; Schnabel *et al*., 1982; Torsvik *et al*., 1974). The genes encoding phage tail and base plate proteins indicate the lysogenic nature of *Natrialba* SSL1. The phage encoded proteins have also been reported in *Hbt. salinarum* R1, *Halobacterium* NRC-1, *Hqr. walsbyi* DSM 16790, *Haloterrigena turkmenica* DSM 5511, *Nmn. moolapensis*, *Nmn. pharaonis* DSM 2160 and *Nab. magadii*. *Natrialba* SSL 1 genome also contains genes for rhodopsins and lycopene biosynthesis. These genes are involved in unique phototphosphorylation and imparting colour to this haloarchaeon.

In conclusion, genome sequencing of the first haloalkaliphilic archaeon from Sambhar lake, India *Natrialba* SSL1 (ATCC 43988) revealed that it is genetically distinct with that of *Nab. magadii* species, as it possesses genes for intracellular gas vesicle and trehalose synthesis. Presence of genes encoding for phage base plate and tail proteins suggests further studiesto isolate and characterize the bacteriophage. The whole genome sequence data has been deposited with GenBank accession No.: MASN00000000 BioProject: PRJNA327293. Further, comparative genomic and proteomic studies will help in understanding the evolution of this extremophile and its biotechnological applications.

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