Sulfolobus Solfataricus

Subjects: Others
Contributor: HandWiki Liu

Saccharolobus solfataricus is a species of thermophilic archaeon. It was transferred from the genus Sulfolobus to the new genus Saccharolobus with the description of Saccharolobus caldissimus in 2018. It was first isolated and discovered in the Solfatara volcano (which it was subsequently named after) in 1980 by two Germans microbiologists Karl Setter and Wolfram Zillig, in Solfatara volcano (Pisciarelli-Campania, Italy). However, these organisms are not isolated to volcanoes but are found all over the world in places such as hot springs. The species grows best in temperatures around 80° Celsius, a pH level between 2 and 4, and enough sulfur for solfataricus to metabolize in order to gain energy. These conditions qualify it as an extremophile and it is specifically known as a thermoacidophile because of its preference to high temperatures and low pH levels and it is also in aerobic and heterotropic categories for its metabolic system. It usually has a spherical cell shape and it makes frequent lobes. Being an autotroph it receives energy from growing on sulfur or even a variety of organic compounds. Currently, it is the most widely studied organism that is within the Crenarchaeota branch. Solfataricus are researched for their methods of DNA replication, cell cycle, chromosomal integration, transcription, RNA processing, and translation. All the data points to the organism having a large percent of archaeal-specific genes, which showcases the differences between the three types of microbes: archaea, bacteria, and eukarya.

Keywords: sulfolobus ; cell shape ; saccharolobus

1. Genome

Sulfolobus solfataricus is the most studied microorganism from a molecular, genetic and biochemical point of view for its ability to thrive in extreme environments; it is easily cultivable in laboratory; moreover, it can exchange genetic material through processes of transformation, transduction and conjugation.

The major motivation for sequencing these microorganisms is because of the thermostability of proteins that normally denature at high temperature. The complete sequence the genome of *S. solfataricus* was completed in 2001.[1] On a single chromosome, there are 2,992,245 base pairs which encode for 2,977 proteins and copious RNAs. One-third of *S. solfataricus* encoded proteins have no homologs in other genomes. For the remaining encoded proteins, 40% are specific to Archaea, 12% are shared with Bacteria, and 2.3% are shared with Eukarya.;[2] 33% of these proteins is encoded exclusively in *Sulfolobus*. A high number of ORFs (open reading frame) are highly similar in *Thermoplasma*.[3]

Small nucleolar RNAs (snoRNAs), already present in eukaryotes, have also been identified in *S.Solfataricus* and *S.acidolcaldarius*. They are already known for the role they play in posttranscriptional modifications and removal of introns from ribosomal RNA in Eucarya.[4]

The genome of *Sulfolobus* is characterised by the presence of short tandem repeats, insertion and repetitive elements, it has a wide range of diversity as it has 200 different ISs insertion sequence elements.

1.1. Thermophilic Reverse Gyrase

The stabilisation of the double helix against denaturation, in the Archaea, is due to the presence of a particular specific thermophilic enzyme, reverse gyrase. It was discovered in hyperthermophilic and thermophilic Archaea and Bacteria. There are two genes in *Sulfolobus* that each encode a reverse gyrase.[5] It is defined atypical Dna topoisomerases and the basic activity consists in the production of positive supercoils in a closed circular Dna. Positive supercoiling is important to prevent the formation of open complexes. Reverse gyrases are composed of two domains : the first one is the helicase like and second one is the topoisomerase I. A possible role of reverse gyrase could be the use of positive supercoiling to assemble chromatin-like structures.[6] In 1997 scientists discovered another important feature of *Sulfolobus* : this microorganism contains a type-II topoisomerase, called TopoVI, whose A subunit is homologous to the meiotic recombination factor, Spo11 which plays a predominant role initiation of meiotic recombination in all Eucarya.[7][8]

S. solfataricus is composed of three topoisomerases of type I, TopA and two reverse gyrases, TopR1 and TopR2, and one topoisomerase of type II, TopoVI.[9]

1.2. Dna Binding Proteins

In the Phylum Crenarchaeota there are three proteins that bind the minor groove of Dna like histones:Alba, Cren7, and Sso7d, that are modified after the translation process. These are small and have been found in several strains of Sulfolobus but not in other genome. Chromatin protein in *Sulfolobus* represent 1-5% of the total. They can have both structural and regulatory functions. These look like human HMG-box proteins, because of their influence on genomes, for the expression and the stability, and on epigenetic processes.[10] In species lacking histones they can be acetylated and methylated like eukaryotic histones.[11][12][13][14] *Sulfolobus* strains present different peculiar DNA binding proteins, such as the Sso7d protein family. They stabilize the double helix, preventing denaturation at high temperature thus promoting annealing above the melting point.[15]

The major component of archael chromatin is represented by Sac10b family protein known as Alba (Acetylation lowers binding affinity).[16][17] These proteins are small, basic and dimeric nucleic acid-binding proteins. Furthermore, it is conserved in most sequenced archeal genomes.[18][19] The acetylation state of Alba, as an example, affects promoter access and transcription in vitro, whereas the methylation state of another *Sulfolobus* chromatin protein, Sso7D, is altered by culture temperature.[20][21]

The work of Wolfram Zillig's group, representing early evidence of the eukaryotic characteristics of the transcription in Archea, has since made *Sulfolobus* an ideal model system for transcription studies. Recent studies in Sulfolobus, in addition to other archaeal species, mainly focus on the composition, function and regulation of the transcription machinery in these organisms and on fundamental conserved aspects of this process in both Eucarya and Archaea.[22]

2. DNA Transfer

Exposure of *Saccharolobus solfataricus* to the DNA damaging agents UV-irradiation, bleomycin or mitomycin C induces cellular aggregation.[23] Other physical stressors, such as changes in pH or temperature shift, do not induce aggregation, suggesting that induction of aggregation is caused specifically by DNA damage. Ajon et al.[24] showed that UV-induced cellular aggregation mediates chromosomal marker exchange with high frequency. Recombination rates exceeded those of uninduced cultures by up to three orders of magnitude. Frols et al.[23][25] and Ajon et al.[24] hypothesized that the UV-inducible DNA transfer process and subsequent homologous recombinational repair represents an important mechanism to maintain chromosome integrity. This response may be a primitive form of sexual interaction, similar to the more well-studied bacterial transformation that is also associated with DNA transfer between cells leading to homologous recombinational repair of DNA damage.

3. Metabolism

Sulfolobus solfataricus is known to grow chemoorganotrophically, in presence of oxygen, on a variety of organic compounds such as sugars, alcohols, amino acids and aromatic compounds like phenol.[26]

It uses a modified Entner-Doudroff pathway for glucose oxidation and the resulting pyruvate molecules can be totally mineralized in TCA cycle.[26]

Molecular oxygen is the only known electron acceptor at the end of the electron tranport chain.[27] Other than organic molecules, this Archea species can also utilize hydrogen sulfide[2] and elementar sulfur as electron donors and fix CO_2, possibly by means of HP/HB cycle,[26] making it also capable of living chemoautotrophycally. Recent studies have found also the capability of growing, albeit slowly, oxidizing molecular hydrogen.[28]

3.1. Ferredoxin

Ferredoxin is suspected to act as the major metabolic electron carrier in *S. solfataricus*. This contrasts with most species within the Bacteria and Eukarya, which generally rely on NADH as the main electron carrier. *S. solfataricus* has strong eukaryotic features coupled with many uniquely archaeal-specific abilities. The results of the findings came from the varied methods of their DNA mechanisms, cell cycles, and transitional apparatus. Overall, the study was a prime example of the differences found in crenarchaea and euryarchaea.[2][29]

4. Ecology

4.1. Habitat

S. solfataricus is an extreme termophile Archea, as the rest of the species of the genus Sulfolobus, it has optimal growth conditions in strong volcanic activity areas, with high temperature and very acid pH,[30] these specific conditions are typical of volcanic area as geyser or thermal springs, in fact the most studied countries where microorganism were found are: U.S.A (Yellowstone National Park),[31] New Zealand,[32] Island and Italy, notoriously famous for volcanic phenomena like these. A study conducted by a team of Indonesian scientists has shown the presence of a Sulfolobus community also in the West Java, confirming that high fears, low ph and sulfur presence are necessary conditions for the growth of these microbes.[33]

Fumarole of Solfatara volcano - Campania, Italy. https://handwiki.org/wiki/index.php?curid=1802938

4.2. Soil acidification

S. solfataricus is able to oxidize sulfur according to metabolic strategy, one of the products of these reactions is H+ and, consequentially, it results in a slowly acidification of surrounding area. Soil acidification increase in place where there are emissions of pollutants from industrial activity, and this process reduce the number of heterotrophic bacterial involved to decomposition, which are fundamental to recycling organic matter and ultimately to fertilizing soil.[34]

5. Biotechnologie: Untapping the Resource *Sulfolobus*

Today, in many fields of application, we are interested in using *Sulfolobus sulfataricus* as a source of thermal stability enzymes for research and diagnostics, as well as in the food, textile and cleaning industries, and the pulp and paper industry. Furthermore, this enzyme is overloaded due to its catalytic diversity, high pH and temperature stability, increased to organic solvents and resistance to proteolysis.[35][36]

At present, tetraester lipids, membrane vesicles with antimicrobial properties, trehalose components, and new β-galactooligosaccharides are coming increasingly important.[37]

5.1. β-galactosidase

The thermostable enzyme β-galactosidase isolated from the extreme thermophile archaebacterial *Sulfolobus solfataricus, strain MT-4.*

This enzyme utilized on many industrial process of lactose containing fluids by purifying and characterizing for their physicochemical properties.[38]

5.2. Proteases

The industry are interested in stable proteases as well as in many different sulfolobus proteases that have been studied.[39]

An active aminopeptidase associated with the chaperonin of Solfobulus solfataricus MT4 was described.[40]

Sommaruga et al.(2014)[41] also improved the stability and reaction yield of a well-characterized carboxypeptidase from S.solfataricus MT4 by magnetic nanoparticles immobilizing the enzyme.

5.3. Esterases/Lipases

A new thermostable extracellular lipolytic enzyme serine arylesterase which is originally discovered for their large action in the hydrolysis of organophosphates from the thermoacidophilic archaeon *Sulfolobus solfataricus P1*.[42]

5.4. Chaperonins

In reaction to temperature shock (50.4 °C) in E.Coli cells, a tiny warm stun protein (S.so-HSP20) from S.solfataricus P2 has been effectively used to improve tolerance.[43]

In view of the fact that chaperonin Ssocpn (920 kDa), which includes ATP, K+ and Mg2 + but has not produced any additional proteins in S.solfataricus to supply collapsed and dynamic proteins from denatured materials, it was stored on an ultrafiltration cell, while the renatured substrates were moving through the film.[44]

5.5. Liposomes

Because of its tetraether lipid material, the membrane of extreme thermophilic Archaea is unique in its composition. Archaea lipids are a promising source of liposomes with exceptional stability of temperature and pH and tightness against leakage of solute. Such archaeosomes are possible instruments for the delivery of medicines, vaccines, and genes.[45]

References

1. "The Sulfolobus solfataricus P2 genome project". FEBS Letters 389 (1): 88–91. June 1996. doi:10.1016/s0014-5793(97)81281-1. PMID 8682213. https://dx.doi.org/10.1016%2Fs0014-5793%2897%2981281-1
2. "The complete genome of the crenarchaeon Sulfolobus solfataricus P2". Proceedings of the National Academy of Sciences of the United States of America 98 (14): 7835–40. July 2001. doi:10.1073/pnas.141222098. PMID 11427726. Bibcode: 2001PNAS...98.7835S. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=35428
3. "Molecular biology of extremophiles: recent progress on the hyperthermophilic archaeon Sulfolobus". Antonie van Leeuwenhoek 81 (1–4): 85–97. August 2002. doi:10.1023/A:1020577510469. PMID 12448708. https://dx.doi.org/10.1023%2FA%3A1020577510469
4. "Homologs of small nucleolar RNAs in Archaea". Science 288 (5465): 517–22. April 2000. doi:10.1126/science.288.5465.517. PMID 10775111. Bibcode: 2000Sci...288..517O. https://semanticscholar.org/paper/2a65285f4fb55f59396a9a577da81f327b3e3cc7.
5. "Insight into the cellular involvement of the two reverse gyrases from the hyperthermophilic archaeon Sulfolobus solfataricus". BMC Molecular Biology 15 (1): 18. September 2014. doi:10.1186/1471-2199-15-18. PMID 25200003. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=4183072
6. "Reverse gyrase, the two domains intimately cooperate to promote positive supercoiling". The Journal of Biological Chemistry 275 (26): 19498–504. June 2000. doi:10.1074/jbc.m910091199. PMID 10748189. https://dx.doi.org/10.1074%2Fjbc.m910091199
7. "An atypical topoisomerase II from Archaea with implications for meiotic recombination". Nature 386 (6623): 414–7. March 1997. doi:10.1038/386414a0. PMID 9121560. Bibcode: 1997Natur.386..414B. https://dx.doi.org/10.1038%2F386414a0
8. "The unique DNA topology and DNA topoisomerases of hyperthermophilic archaea". FEMS Microbiology Reviews 18 (2–3): 237–48. May 1996. doi:10.1111/j.1574-6976.1996.tb00240.x. PMID 8639331. https://dx.doi.org/10.1111%2Fj.1574-6976.1996.tb00240.x
9. "The reverse gyrase TopR1 is responsible for the homeostatic control of DNA supercoiling in the hyperthermophilic archaeon Sulfolobus solfataricus". Molecular Microbiology 113 (2): 356–368. November 2019. doi:10.1111/mmi.14424. PMID 31713907. https://dx.doi.org/10.1111%2Fmmi.14424
10. "The high mobility group box: the ultimate utility player of a cell". Trends in Biochemical Sciences 37 (12): 553–62. December 2012. doi:10.1016/j.tibs.2012.09.003. PMID 23153957. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=4437563
11. "Sulfolobus solfataricus". Proceedings of the National Academy of Sciences of the United States of America 115 (48): 12271–12276. November 2018. doi:10.1073/pnas.1808221115. PMID 30425171. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=6275508
12. "The chromosomal protein sso7d of the crenarchaeon Sulfolobus solfataricus rescues aggregated proteins in an ATP hydrolysis-dependent manner". The Journal of Biological Chemistry 275 (41): 31813–8. October 2000. doi:10.1074/jbc.m002122200. PMID 10908560. https://dx.doi.org/10.1074%2Fjbc.m002122200
13. "Thermal stability and DNA binding activity of a variant form of the Sso7d protein from the archeon Sulfolobus solfataricus truncated at leucine 54". Biochemistry 42 (27): 8362–8. July 2003. doi:10.1021/bi034520t. PMID 12846585. https://dx.doi.org/10.1021%2Fbi034520t
14. "DNA-binding surface of the Sso7d protein from Sulfolobus solfataricus". Journal of Molecular Biology 247 (5): 840–6. April 1995. doi:10.1006/jmbi.1995.0184. PMID 7723036. https://dx.doi.org/10.1006%2Fjmbi.1995.0184
15. "Annealing of complementary DNA strands above the melting point of the duplex promoted by an archaeal protein". Journal of Molecular Biology 267 (4): 841–8. April 1997. doi:10.1006/jmbi.1996.0873. PMID 9135116. https://dx.doi.org/10.1006%2Fjmbi.1996.0873
16. "Identification of the gene encoding archeal-specific DNA-binding proteins of the Sac10b family". Molecular Microbiology 32 (3): 669–70. May 1999. doi:10.1046/j.1365-2958.1999.01366.x. PMID 10320587. https://dx.doi.org/10.1046%2Fj.1365-2958.1999.01366.x
17. "An abundant DNA binding protein from the hyperthermophilic archaeon Sulfolobus shibatae affects DNA supercoiling in a temperature-dependent fashion". Journal of Bacteriology 182 (14): 3929–33. July 2000. doi:10.1128/JB.182.14.3929-3933.2000. PMID 10869069. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=94576

18. "The Alba protein family: Structure and function". Biochimica et Biophysica Acta (BBA) - Proteins and Proteomics 1864 (5): 570–83. May 2016. doi:10.1016/j.bbapap.2016.02.015. PMID 26900088. https://dx.doi.org/10.1016%2Fj.bbapap.2016.02.015

19. "Structure of Alba: an archaeal chromatin protein modulated by acetylation". The EMBO Journal 21 (17): 4654–62. September 2002. doi:10.1093/emboj/cdf465. PMID 12198167. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=125410

20. "The interaction of Alba, a conserved archaeal chromatin protein, with Sir2 and its regulation by acetylation". Science 296 (5565): 148–51. April 2002. doi:10.1126/science.1070506. PMID 11935028. Bibcode: 2002Sci...296..148B. https://semanticscholar.org/paper/849e4bea494353d2b417fab2707783b0dfd2dbf6.

21. "Solution structure and DNA-binding properties of a thermostable protein from the archaeon Sulfolobus solfataricus". Nature Structural Biology 1 (11): 808–19. November 1994. doi:10.1038/nsb1194-808. PMID 7634092. https://dx.doi.org/10.1038%2Fnsb1194-808

22. "DNA-dependent RNA polymerase from the archaebacterium Sulfolobus acidocaldarius". European Journal of Biochemistry 96 (3): 597–604. June 1979. doi:10.1111/j.1432-1033.1979.tb13074.x. PMID 380989. https://dx.doi.org/10.1111%2Fj.1432-1033.1979.tb13074.x

23. "UV-inducible cellular aggregation of the hyperthermophilic archaeon Sulfolobus solfataricus is mediated by pili formation". Molecular Microbiology 70 (4): 938–52. November 2008. doi:10.1111/j.1365-2958.2008.06459.x. PMID 18990182. https://pure.rug.nl/ws/files/56956856/UV_inducible_cellular_aggregation_of_the_hyperthermophilic_archaeon_Sulfolobus_solfataricus_is_r

24. "UV-inducible DNA exchange in hyperthermophilic archaea mediated by type IV pili". Molecular Microbiology 82 (4): 807–17. November 2011. doi:10.1111/j.1365-2958.2011.07861.x. PMID 21999488. https://pure.rug.nl/ws/files/6771142/2011MolMicrobiolAjon.pdf.

25. "Reactions to UV damage in the model archaeon Sulfolobus solfataricus". Biochemical Society Transactions 37 (Pt 1): 36–41. February 2009. doi:10.1042/BST0370036. PMID 19143598. https://semanticscholar.org/paper/9f9e4150bf0567070d4ba5ea11ef2615325a8120.

26. "Genome-scale reconstruction and analysis of the metabolic network in the hyperthermophilic archaeon Sulfolobus solfataricus". PLOS ONE 7 (8): e43401. 2012-08-31. doi:10.1371/journal.pone.0043401. PMID 22952675. Bibcode: 2012PLoSO...743401U. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=3432047

27. "Effect of O2 concentrations on Sulfolobus solfataricus P2". FEMS Microbiology Letters 299 (2): 255–60. October 2009. doi:10.1111/j.1574-6968.2009.01759.x. PMID 19735462. https://dx.doi.org/10.1111%2Fj.1574-6968.2009.01759.x

28. "Saccharolobus caldissimus gen. nov., sp. nov., a facultatively anaerobic iron-reducing hyperthermophilic archaeon isolated from an acidic terrestrial hot spring, and reclassification of Sulfolobus solfataricus as Saccharolobus solfataricus comb. nov. and Sulfolobus shibatae as Saccharolobus shibatae comb. nov". International Journal of Systematic and Evolutionary Microbiology 68 (4): 1271–1278. April 2018. doi:10.1099/ijsem.0.002665. PMID 29485400. https://dx.doi.org/10.1099%2Fijsem.0.002665

29. "The Sulfolobus-"Caldariella" group: taxonomy on the basis of the structure of DNA-dependent RNA polymerases.". Archives of Microbiology 125 (3): 259–69. April 1980. doi:10.1007/BF00446886. https://dx.doi.org/10.1007%2FBF00446886

30. "Phenotypic characterization of the archaebacterial genus Sulfolobus: comparison of five wild-type strains". Journal of Bacteriology 171 (12): 6710–9. December 1989. doi:10.1128/jb.171.12.6710-6719.1989. PMID 2512283. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=210567

31. "Sulfolobus". https://microbewiki.kenyon.edu/index.php/Sulfolobus.

32. "Microbial life in Champagne Pool, a geothermal spring in Waiotapu, New Zealand". Extremophiles 11 (4): 605–14. July 2007. doi:10.1007/s00792-007-0073-2. PMID 17426919. https://dx.doi.org/10.1007%2Fs00792-007-0073-2

33. "Microbial diversity of acidic hot spring (kawah hujan B) in geothermal field of kamojang area, west java-indonesia". The Open Microbiology Journal 3: 58–66. 2009. doi:10.2174/1874285800903010058. PMID 19440252. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=2681175

34. "Effect of soil acidification on the soil microflora". Water, Air, and Soil Pollution 11 (4): 437. 1979. doi:10.1007/BF00283435. Bibcode: 1979WASP...11..437B. https://dx.doi.org/10.1007%2FBF00283435

35. Stepankova, Veronika (October 14, 2013). "Strategies for Stabilization of Enzymes in Organic Solvents". ACS Catalysis 3 (12): 2823–2836. doi:10.1021/cs400684x. https://dx.doi.org/10.1021%2Fcs400684x

36. DANIEL, R. M. (1982). "A correlation between protein thermostability and resistance to proteolysis". Biochemical Journal 207 (3): 641–644. doi:10.1042/bj2070641. PMID 6819862. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=1153914

37. Quehenberger, Julian (2017). "Sulfolobus – A Potential Key Organism in Future Biotechnology". Frontiers in Microbiology 8: 2474. doi:10.3389/fmicb.2017.02474. PMID 29312184. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=5733018

38. M. PISANI, Francesca (1990). "Thermostable P-galactosidase from the archaebacterium Sulfolobus solfataricus". European Journal of Biochemistry 187 (2): 321–328. doi:10.1111/j.1432-1033.1990.tb15308.x. PMID 2105216.

https://dx.doi.org/10.1111%2Fj.1432-1033.1990.tb15308.x

39. Hanner, Markus (1990). Isolation and characterization of an intracellular aminopeptidase from the extreme thermophilic archaebacterium Sulfolobus solfataricus. 1033. Elsevier B.V.. 148–153. doi:10.1016/0304-4165(90)90005-H. ISBN 0117536121. https://dx.doi.org/10.1016%2F0304-4165%2890%2990005-H
40. Condo, Ivano; Ruggero, Davide (1998). "A novel aminopeptidase associated with the 60 kDa chaperonin in the thermophilic archaeon Sulfolobus solfataricus. Mol. Microbiol.". Molecular Microbiology 29 (3): 775–785. doi:10.1046/j.1365-2958.1998.00971.x. PMID 9723917. https://dx.doi.org/10.1046%2Fj.1365-2958.1998.00971.x
41. Sommaruga, Silvia (2014). "mmobilization of carboxypeptidase from Sulfolobus solfataricus on magnetic nanoparticles improves enzyme stability and functionality in organic media. BMC Biotechnol.". BMC Biotechnology 14 (1): 82. doi:10.1186/1472-6750-14-82. PMID 25193105. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=4177664
42. Park, Young-Jun (2016). "Purification and characterization of a new inducible thermostable extracellular lipolytic enzyme from the thermoacidophilic archaeon Sulfolobus solfataricus P1". Journal of Molecular Catalysis B: Enzymatic 124: 11–19. doi:10.1016/j.molcatb.2015.11.023. https://dx.doi.org/10.1016%2Fj.molcatb.2015.11.023
43. Li, Dong-Chol (August 2011). "Thermotolerance and molecular chaperone function of the small heat shock protein HSP20 from hyperthermophilic archaeon, Sulfolobus solfataricus P2. Cell Stress Chaperones". Cell Stress & Chaperones 17 (1): 103–108. doi:10.1007/s12192-011-0289-z. PMID 21853411. http://www.pubmedcentral.nih.gov/articlerender.fcgi?tool=pmcentrez&artid=3227843
44. Cerchia, Laura (7 August 1999). "An archaeal chaperonin-based reactor for renaturation of denatured proteins. Extremophile". Extremophiles : Life Under Extreme Conditions 4 (1): 1–7. doi:10.1007/s007920050001. PMID 10741831. https://dx.doi.org/10.1007%2Fs007920050001
45. B. Patel, Girishchandra (1999). "Archaeobacterial Ether Lipid Liposomes (Archaeosomes) as Novel Vaccine and Drug Delivery Systems". Critical Reviews in Biotechnology 19 (4): 317–357. doi:10.1080/0738-859991229170. PMID 10723627. https://dx.doi.org/10.1080%2F0738-859991229170