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# **Review Article**

# Archaeal Renaissance: New Insights into Evolution and Applications in Environmental and Industrial Biotechnology



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## **ABSTRACT**

Archaea have evolved from a once-enigmatic microbial lineage into a fundamental component of evolutionary and applied microbiology. Phylogenomic advances revealing the TACK, Asgard, and DPANN superphyla have expanded archaeal taxonomy and provided critical insights into the origin of cellular complexity in eukaryotes. The Asgard superphylum encodes multiple eukaryotic signature proteins involved in signaling, cytoskeletal organization, and membrane trafficking, reinforcing the archaeal contribution to eukaryogenesis. Concurrently, increasing attention has focused on archaeal metabolism and ecological roles. These microorganisms participate in key biogeochemical processes, including sulfur and ammonia oxidation, hydrocarbon degradation, methanogenesis, and heavy-metal transformation. Their exceptional adaptability to extreme environments underlies diverse biotechnological applications in wastewater treatment, renewable energy production, aquaculture, and cosmetics. Products such as thermostable enzymes, polyhydroxyalkanoate-based bioplastics, archaeosomes, and archaeal probiotics illustrate their growing industrial value. Moreover, recent progress in cultivation techniques, systems-level analyses, and synthetic biology has begun to overcome previous challenges in scalability, cultivation, and genetic manipulation. Collectively, these advances highlight the expanding environmental, evolutionary, and industrial significance of archaea, positioning them as essential contributors to future sustainable biotechnology and bioinnovation.

# 1. Introduction

similarities previously Morphological misclassification of the Archaea domain with Bacteria. Later on, it was recognized as an evolutionarily significant and distinct lineage in the tree of life. The rRNA sequence comparisonoriented investigations of Woese and colleagues (1970s and 1980s) redefined microbial taxonomy. They introduced a new division of life: Eukarya, Bacteria, and Archaea (Woese et al., 1990). Their crucial discovery reevaluated the five-kingdom model and emphasized the induction of a molecular classification system to identify significant genetic variations among microbial domains. The structural, genetic, and biochemical properties closely align Archaea with Eukarya, rather than Bacteria. These features mainly include the presence of histones, complex RNA polymerases, and protein synthesis initiation with methionine instead of N-formylmethionine (Baker et al., 2020).

The distinct cell membrane lipids of Archaea contain etherlinked isoprenoid chains, which further differentiate them from bacteria. This type of cell membrane assists in Archaeal adaptability to extreme environments. Despite their prokaryotic structure, their genomic and cellular traits challenge traditional phylogenetics, particularly regarding eukaryogenesis (eukaryotic cells' origin) (Guy & Ettema, 2011). Recent advances in single-cell genomics, high-throughput sequencing, and metagenomics have significantly extended the known Archaeal diversity. Traditionally, Archaeal biology was limited to only a few cultured specimens belonging to the Crenarchaeota and Euryarchaeota phyla. The environmental DNA surveys have revealed a vast Archaeal "microbial dark matter". These uncultured lineages present worldwide distribution across extreme marine and terrestrial habitats (Baker et al., 2020). Several novel archaeal phyla have been identified along with the classification of their higher taxonomic structures (TACK, Asgard superphyla, and DPANN) (Baker et al., 2020).

Table 1. Classification of Haloarchaea with genera

Order	Family	Genus	Reference		
Halobacteriales	Haladaptataceae	Haladaptatus	Savage et al., 2007		
Halobacteriales	Haladaptataceae	Halorussus	Cui et al., 2010		
Halobacteriales	Haloarculaceae	Haloarcula	Torreblanca et al., 1986		
Halobacteriales	Haloarculaceae	Halomarina	Inoue et al., 2011		
Halobacteriales	Haloarculaceae	Halorhabdus	Wainø et al., 2000		
Halobacteriales	Haloarculaceae	Natronomonas	Kamekura et al., 1997		
Halobacteriales	Halobacteriaceae	Halobacterium	Houwink, 1956		
Halobacteriales	Halobacteriaceae	Halarchaeum	Minegishi et al., 2010		
Halobacteriales	Halococcaceae	Halococcus	Oren & Ventosa, 1996		
Halobacteriales	Halococcaceae	Halalkalicoccus	Xue et al., 2005		
Haloferacales	Haloferacaceae	Haloferax	Torreblanca et al., 1986		
Haloferacales	Haloferacaceae	Haloplanus	Elevi Bardavid et al., 2007		
Haloferacales	Haloferacaceae	Haloquadratum	Burns et al., 2007		
Haloferacales	Haloferacaceae	Halogeometricum	Montalvo-Rodríguez et al., 1998		
Haloferacales	Halorubraceae	Halorubrum	Oren & Ventosa, 1996		
Haloferacales	Halorubraceae	Halobaculum	Oren et al., 1995		
Haloferacales	Halorubraceae	Halolamina	Cui et al., 2011		
Natrialbales	Natrialbaceae	Natrialba	Kamekura & Dyall-Smith, 1995		
Natrialbales	Natrialbaceae	Natrinema	McGenity et al., 1998		
Natrialbales	Natrialbaceae	Haloterrigena	Montalvo-Rodríguez et al., 2000		
Natrialbales	Natrialbaceae	Halovivax	Castillo et al., 2006		
Natrialbales	Natrialbaceae	Halopiger	Gutiérrez et al., 2007		
Natrialbales	Natrialbaceae	Halobiforma	Hezayen et al., 2002		
Halorutilales	Halorutilaceae	Halorutilus	Durán-Viseras et al., 2023		

The TACK superphylum (Korarchaeota, Thaumarchaeota, Crenarchaeota, and Aigarchaeota) has gained particular attention because of its potential evolutionary relationship with eukaryotes. Protein-encoding gene identification in TACK Archaea via functional genomics involved various techniques such as cytoskeletal dynamics, membrane trafficking, and cytokinesis. This supports the origin of key eukaryotic features from this lineage (Guy & Ettema, 2011). Asgard archaea (Lokiarchaeota, Heimdallarchaeota, and Thorarchaeota) have complemented this perspective through molecular evidence regarding the close archaeal ancestry of eukaryotes. Several ESPs (eukaryotic signature proteins) are encoded in Asgard genomes, which include ubiquitin signaling components, cytoskeletal regulators, and endosomal sorting proteins (Seitz et al., 2019). It has triggered new investigations to identify whether eukaryotes and Archaea are sister clades or eukaryotes have emerged from Archaea through fusion and symbiotic events (Guy & Ettema, 2011). Genomic data have facilitated substantial taxonomic revision of Archaea. The introduction of recent standardized nomenclatural frameworks, utilizing the suffix "-ota" for archaeal phylum designation, has closely aligned their taxonomy with bacterial and eukaryotic nomenclature practices (Whitman et al., 2018). It indicates broader efforts toward microbial diversity-coding in this era of metagenomics.

Archaea's popularity is also rising in industrial and environmental biotechnology, in addition to its evolutionary importance. The metabolic variability facilitates their utility in sulfur cycling, methanogenesis, hydrocarbon degradation, and ammonia oxidation under extreme salinity, temperature, and pH (Orellana et al., 2019). Notably, uncultivated Helarchaeota lineages of the Asgard superphylum possess anaerobic hydrocarbon oxidation potential, which highlights their ecological importance in subsurface carbon cycling (Seitz et al., 2019).

Moreover, MGII clades of Euryarchaeota (marine groups) demonstrate photoheterotrophic and niche differentiation

lifestyles, thus indicating oceanic microbial ecosystems' underexplored dynamics (Orellana et al., 2019). Despite significant evolutionary and ecological importance, Archaea's representation in applied microbiology is lower than that of Eukarya and Bacteria. However, the current advancements in archaeal synthetic biology, cultivation, and genetic engineering have revealed their potential as efficient cell factories for pharmaceuticals, biofuels, extremozymes, and bioplastics (Pfeifer et al., 2021). This review elaborates on the multifaceted potential of Archaea in industrial and environmental applications through established and emerging biotechnological avenues.

# 2. Environmental applications

The high Archaeal tolerance and growth capacity in contaminated environments advocate their promising bioremediation applications. Other microorganisms are unable to survive under extreme conditions (salinity, temperature, and pH), which profoundly hinders the bioremediation process. The Archaean members have the potential to fill this gap and can perform under extreme conditions. They can utilize pollutants as substrates to release energy and carbon. The saline industrial wastewater discharge (oil or industries) contains poisonous compounds, which pose serious environmental and human health risks. Therefore, the pollutants in this wastewater must be degraded before their environmental discharge and reuse (Mainka et al., 2021). The survivability of Haloarchaea in in saline environments makes them promising candidates for industrial wastewater bioremediation (Table 1). This technique can eliminate various organic pollutants (petroleum, aromatic hydrocarbons, nitrites, and nitrates) from the wastewater (Amoozegar et al., 2017; Ding et al., 2010; Haque et al., 2020; Kiadehi et al., 2018; Litchfield, 2011; Rodrigo-Ban~os et al., 2015; Singh & Singh, 2017; Voica et al., 2016).

Methanogenic archaea effectively participate in the anaerobic processing of industrial waste, sewage sludge, and agricultural waste (Fig. 1). They can remove chlorinated

chemicals and methanol from wastewater as well as treat oil spills (Ding et al., 2010; Gill et al., 2021; Schiraldi et al., 2002; Enzmann et al., 2018). Similarly, ammonia-oxidizing archaea, known for their broad interactions in the marine environment, could eliminate nitrogen from contaminated fluids (Yin et al., 2018; Kim et al., 2021). Acidophilic Archaea, Radiophiles, and metallophiles have been reported to remove sulfur compounds, bioremediate nuclear waste, and extract heavy metals, respectively (José, 2018; , Naitam & Kaushik, 2021; Raddadi et al., 2015). Moreover, certain archaea are known to resist and disintegrate antibiotics, whereas others could degrade xenobiotics (insecticides) (Gill et al., 2021; Del Giudice et al., 2016).

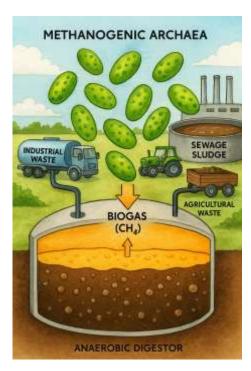


Fig. 1 Illustration of methanogenic archaea participating in anaerobic digestion of industrial, agricultural, and municipal waste, highlighting biogas (CH<sub>4</sub>) production

The high-pressure and high-temperature food processing limits the viability of beneficial microorganisms' viability and compromises their key probiotic properties. Similarly, the incompatibility of probiotics with industrial processing is the major hurdle in improving aquatic organisms' health. Traditionally, antibiotics were employed to counter disease outbreaks in aquaculture. However, probiotics' addition to animal feed has been recently suggested for antibiotics replacement to avoid resistant pathogens and associated side effects.

Other proposed alternatives include the induction of archaeobiotics due to their compatibility with industrial processing conditions and positive impacts on gut microbiota to improve animal health (Chuphal et al., 2021). The use of archaean probiotic additives in animal feed and aquaculture has been patented. Archaea added feed has been reported to profoundly increase domestic animals' immunity and growth rate while simultaneously alleviating their parasitic susceptibility. The archaea-based reduction of pollutants in aquaculture feed is known to elevate nutrient absorption and digestion, modify intestinal microbiota composition, improve growth rate, and the environmental effects of their faeces (Chuphal et al., 2021).

These findings highlight the advantages of archaea supplements in animal feed. Therefore, archaea are gaining popularity as next-generation probiotics for animal feed. They have already been adopted by popular European aquaculture feed industries, such as TwentyGreen®. However, certain factors restrict archaea's application in aquaculture, mainly including their complicated cultivation as compared to bacterial cultures. Moreover, scarce information on Archaean species in the fish intestinal microbiota and their colonization rate in the intestinal mucosa is another major hurdle. Similarly, a higher price in comparison to conventional probiotics, and potential side effects on the body in response to the archaeal increase are other limiting factors.

## 3. Industrial applications

The enzymes and proteins synthesized by extremophilic archaea maintain activities under harsh settings, which makes them potent candidates for biocatalytic functions in extreme conditions (Table 2). Extremophilic archaea are particularly beneficial to food, pharmaceuticals, leather, textiles, and paper industries. However, fungal or bacterial enzymes are more readily available commercially, whereas the share of archaea is quite low. Nonetheless, their survivability, along with bacterial and fungal enzymes, is being investigated. In this regard, various archaeal enzymes (proteases, cellulases, lipases, and amylases) have been evaluated, which are utilized in large-scale industrial applications (Jaffe et al., 2023).

# 3.1. Cosmetic and gas industry

The ability of archaeosomes to store active substances and permeate human skin (similar to ordinary liposomes) facilitates their utility as molecular vectorization systems in skin care treatments (Rastädter et al., 2020). Furthermore, the exopolysaccharides (EPS) synthesized by the haloarchaea Haloterrigena turmenica possess higher moisture retention capacity as compared to hyaluronic acid and thus can be utilized in cosmetics (Squillaci et al., 2017). Radiophilic archaea's metabolites (carotenoids) with protective properties against photooxidation can be used in sun creams (Oren, 2010; Gabani & Singh, 2013).

Members of Archaea are the sole biogas producers among microbes. The mechanism involves organic waste's anaerobic destruction by methanogen archaea to retrieve energy. Methane yield is predominant, though minor quantities of different gases (carbon dioxide) are produced as well (Pfeifer et al., 2021; Jaffe et al., 2023). The process occurs naturally, and gases are released into the atmosphere. The identical methodology is replicated in industrial plants. In this case, archaea, water, and organic waste are introduced into bioreactors/fermenters, which yield biogas and digestate (a byproduct for green agricultural use). Biogas can be converted into thermal and electrical energy (Oren, 2010) or injected as biomethane into the natural gas network after alleviating carbon dioxide content (Straub et al., 2018). Biomethane is considered a renewable energy source with several potential applications (Gill et al., 2021).

Urban biogas plants are now serving as a reliable energy source (José, 2018). Reduced pollution and a higher calorific value favor biogas utilization as an alternative to natural gas. However, sustainable biogas supply demands high production costs in comparison to other energy sources since its storage is relatively complicated and costly. Biogas production releases a strong foul odor in the surroundings, and its removal would further raise the price. Moreover, unchecked biogas production could pose serious concerns, as its key products (methane and

Table 2. Selected extremely thermophilic archaea with biotechnological potential\*

Archaeon	T (°C)	pH	Anaerobe	Aerobe	Growth on $\alpha/\beta$ -glucans	Peptides	CO <sub>2</sub> Fixation	CO Oxidation	Carboxydotrophy	Sulfur Oxidation	Iron Oxidation	$ m H_2$ Production	Genetic System	Biotech Relevance	Reference
Pyrococcus furiosus	~100	6-7	х	Х	Х	х	х	х	×	ı	-	-	Established	Platform for 3-HP, ethanol, butanol; enzyme source	Fiala & Stetter, 1986
Thermococcus kodakarensis	~85	6-7	X	Χ	X	X	X	X	1	ı	-	-	Genetic tools	Platform; proteases & glycoside hydrolases	Fukui et al., 2005
Thermococcus onnurineus NA1	~80	~8.5	_	Х	Х	-	-	-	×	-	-	Demo nstrated	I	H <sub>2</sub> from steel mill gas effluents	Lee et al., 2008
Methanococcus jannaschii	~85	5-7	Х	-	-	-	-	-	Methane generation	-	-	-	Well- established	CH <sub>4</sub> from CO <sub>2</sub> /H <sub>2</sub>	Bult et al., 1996
Sulfolobus solfataricus	~80	2-4	ı	Х	ı	ı	#	1	ı	#	ı	Х	ı	Source of enzymes; engineered expression	She et al., 2001
Sulfolobus acidocaldarius	~75	2-3	ı	Х	1	ı	#	1	ı	#	1	ı	1	Potential metabolic engineering platform	Chen et al., 2005
Sulfolobus metallicus	~70	2-3	X	ı	ı	ı	ı	ı	1	X	ı	ı	ı	Bioleaching of ores	Huber & Stetter, 1991
Metallosphaera sedula	~73	2-3	-	-	-	-	-	-	1	Х	1	-	-	Bioleaching of ores	Auernik et al., 2008
Acidianus brierleyi	~70	~2	Х	-	-	_	_	_	I	Х	-	-	_	Iron & sulfur oxidizer	Segerer et al., 1986

carbon dioxide) could lead to the greenhouse gas effect. Despite its commercial production, biogas currently remains far away from replacing the nonrenewable traditional energy sources (Jaffe et al., 2023).

Methanogenic archaea produce biohydrogen more than they need in case of a limited hydrogen supply in the medium.

Biohydrogen production is mainly dependent on fossil fuels, whereas only a small portion is derived from renewable resources and energy. However, biohydrogen has become significant with the rising hydrogen demands in order to reduce CO2 emissions (Pfeifer et al., 2021). Despite advantages, biohydrogen production faces supply and storage limitations

(Straub et al., 2018). Therefore, formate is also being explored as another renewable energy source at the laboratory scale.

## 3.2. Tanning and textile industry

The secretion of halocins by archaea makes them highly useful in the textile industry. Halocins are used in the leather tanning process to transform animal hides into leather. During the initial stage, animal skin is immersed in baths with high salt concentrations. These conditions favor hazardous halophilic microorganisms' growth, which can damage the skin tissues to affect the quality of the produce.

In this situation, the antibacterial activity of halocins helps in attenuating the detrimental microbial proliferation into the animal skin (Hague et al., 2020; Gill et al., 2021). Archaea enzymes are also applied to clean textile materials. For example, the cellulases from Hbt. Salinarum-based detergents are used for the cleaning of cotton garments. They disintegrate quickly after repeated washing. Cellulases induction restricts fabric modification and helps in retaining its original characteristics (José, 2018).

Serine peptidases and proteases from hyperthermophilic archaea (Pyrococcus, Desulfurococcus, and Thermococcus) are used in detergent manufacturing, which facilitates cloth washing above 80°C (Bonete et al., 1996). Contrarily, such high temperatures denature other enzymes. Similarly, psychrophilederived proteases help in manufacturing detergents for cold water cloth washing (Coker, 2019). Moreover, some haloarchaea are known to remove azo dyes from wastewater and thus can be applied in the textile industry on a large scale for decoloration (Kiadehi et al., 2018).

## 3.3. Plastic industry

Recently, plastic-degrading archaea have been discovered, which produce chemicals similar to polyhydroxyalkanoates (PHA). Bacteria and some haloarchaea species manufacture these chemicals (PHB), which serve as excessive internal energy and carbon reserve. These polymers are made up of hydroxy fatty acids developing as cytoplasmic inclusions with a polyester core and protein and phospholipid coating (Haque et al., 2020). Synthetic plastic-like elastomeric and thermoplastic features of PHA help in its biotechnology applications.

However, synthetic plastics are made from petroleum-derived non-biodegradable and non-renewable materials, which cause environmental contamination. The biodegradable PHAs (Gill et al., 2021) are ideal candidates for conventional polymer replacement in various applications. For example, they can be utilized in synthesizing artificial blood vessels and disposable wound dressings (Poli et al., 2011). Similarly, they can be used in food and packaging, agriculture, and pharmaceutical industries (Singh & Singh, 2017; Albuquerque & Malafaia, 2018).

Hfx. mediterranei is the main industrial bioplastic synthesizing haloarchaea with high PHA concentration (Poli et al., 2011). PHA content of some archaean cultures ranges from 55% to 65% of the dry cellular weight (Charlesworth & Burns, 2015; Vijayendra & Shamala, 2014), which has been patented for commercial production (Litchfield, 2011). Archaea-based biopolyesters' manufacturing has several advantages as they can synthesize different homo and heteropolymers with varying chemical and physical properties. It is achieved by simply changing substrates and carbon sources in the growth medium, which facilitates thermoplastic production with desired properties.

The required extreme saline conditions for growth reduce contamination risk, thus compensating high production cost of large salt volumes. It's simple lysis in hypotonic solutions produces PHA granules, which are subjected to low-speed centrifugation to recover the PHA pellet (Oren, 2010; Poli et al., 2011). They can also be cultivated using inexpensive carbon sources (starch and sugars) (Singh & Singh, 2017). However, PHA generation through haloarchaea remains lower than the bacterial strains (Pfeifer et al., 2021). Lower manufacturing costs of petrochemical polymers make archaean PHA production uneconomical. Therefore, despite improved process efficiency, haloarchaea bioplastics production is limited to only pilot scale and still awaits industrial scale applications.

## 3.4. Mining industry (biomining)

Hydrometallurgy and pyrometallurgy techniques are adopted to extract metals from waste materials and minerals. However, high temperatures during these processes lead to environmental contamination. Therefore, an alternative novel "biomining" approach has emerged to address contamination issues (Castro, 2016). Biomining employs microorganisms for metal mobilization and transformation. Archaea could alter metals' oxidation state for their smooth biomineralization and solubilization. Thus, their biomining potential is being increasingly investigated. Archaea used in the bioremediation of metal-contaminations can also be applied for metal extraction since they accumulate metals, which are released through lysis. Biooxidation and bioleaching are basic biomining techniques. The bioleaching method solubilizes metals through biological catalysis for the recovery.

Biooxidation involves minerals pretreatment to obstruct target metals (precious metals including gold) to facilitate their mobilization (Castro, 2016). A mesophilic microbe was initially used for this purpose. Later on, archaea were found to improve and accelerate sulfurous mineral dissolution into metal and sulfate. Acidophiles and thermophiles are commonly applied in biomining, and most of their related species belong to the Metallosphaera, Acidianus, Sulfolobus, Ferroplasma. Sfb. metallicus species possesses the highest bioleaching potential. It can solubilize the chalcopyrite (CuFeS2) films, formed during the mining process, to recover iron and copper metals (Bonete, 1996; Oren, 2010). Ferroplasma acidiphilum is capable of oxidizing ferrous ions, whereas the hyperthermophilic archaeon Pyr. furiosus can bioleach various metals, including gold (Castro, 2016; Naitam & Kaushik, 2021). Biomining efficiency of several archaeal species has been documented in various studies.

# 3.5. Other biotechnological applications

Extremozymes from hyperthermophilic and thermophilic archaea have transformed biotechnology. They are specifically effective in Molecular Biology laboratories requiring hightemperature analyses. Thermostable DNA polymerases used in PCR (Polymerase Chain Reaction) are an excellent example of thermostable enzyme applications. "Taq polymerase" was the first thermostable DNA polymerase that was used in PCR. It was derived from thermophilic bacteria (Thermus aquaticus), which facilitated rapid PCR advancement. However, it has certain drawbacks, particularly the lack of exonuclease (30-50) activity (error correction) (Zhang et al., 2015). Therefore, more reliable alternatives, such as the enzymes exhibiting

polymerization and monitoring, are preferred. DNA polymerases "Tkod", "Vent" (or "Tli"), "Pwo", and "Pfu" have been isolated from the hyperthermophilic archaea, including Thermococcus kodakarensis, Thermococcus Pyrococcus woesei, and Pyrococcus furiosus, respectively. The error rate of these enzymes is significantly lower (10 times) than that of Taq polymerase (Alqueres et al., 2007; Arora & Panosyan, 2019). Moreover, they have high processivity and extension rate, which allows longer amplification and yields more selective products (Yin et al., 2018; Counts et al., 2017). Currently, several commercial thermostable Archaean DNA polymerases are used in PCR (Gill, et al., 2021). DNA polymerases are classified into seven families (A, B, C, D, X, Y, and RT), each exhibiting unique biochemical properties (Redrejo-Rodríguez et al., 2017). "Tkod", "Vent" (or "Tli"), "Pwo", and "Pfu" DNA polymerases belong to the B family, which is known for high yield and accuracy. These features support their use in site-directed mutagenesis, high-fidelity PCR, DNA sequencing, and cloning. DNA polymerases' Y family contains the Dpo4 enzyme from Sfb. sol-fataricus, and its low fidelity favors utilization in random mutagenesis and error-prone PCR (Zhang et al., 2015).

Archaean DNA polymerases are not the only thermostable enzymes that are used in molecular biology. RNA and DNA ligases are also applied in LCR (Ligase Chain Reaction) due to their phosphodiester linkages generating capability in nucleic acids. High activity of these enzymes favors their utilization instead of Taq DNA ligase (Straub et al., 2018). Archaea restriction enzymes, containing unique recognition sites, have also been identified and commercialized. These enzymes include MaeIII, MaeII, and MaeI from the methanogenic archaeon Methanococcus aeolicus, and HsaI, HhII, and HcuI from Hbt. salinarum, Hbt. halobium, and haloarchaea Hbt. Cutirubrum, respectively (Singh & Singh, 2017; Oren, 2010).

## 4. Conclusion

The present study and previous reports highlight promising and novel archaeal applications in biotechnology. This study mainly elaborates on their survivability and adaptability to harsh conditions, which facilitates their utility in various sectors. However, novel and established protocols require further improvements. The recent development in "omics" and bioinformatics could help in exploring research techniques for inhospitable places. Moreover, next-generation sequencing (NGS) of archaea could reveal novel properties that expand their practical applications.

#### **Conflicting Interests**

The authors have declared that no conflicting interests exist.

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