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Competing interests statement

The author declares no competing financial interests.

DATABASES

The following terms in this article are linked online to: Entrez Genome Project: http://www.ncbi.nlm.nih.gov/ entrez/query.fcgi?db=genomeprj Candida albicans | Coprinopsis cinerea | Histoplasma capsulatum | Saccharomyces cerevisiae | Ustilago maydis UniProtKB: http://ca.expasy.org/sprot Pra1 | Pra2 | Yup1

FURTHER INFORMATION

Gero Steinberg's homepage: http://www.mpi-marburg.mpg.de/steinberg Munich Information Centre for Protein Sequences: http://mips.gsf.de/genre/proj/ustilago Access to this links box is available online. from the Bacteria. Moreover, I propose that the primary biochemical basis for this adaptation is membrane composition, with numerous secondary adaptations among the metabolic pathways. Based on this synthesis, I argue for the importance of chronic energy stress in archaeal evolution and raise fundamental questions regarding the ecology of life's other domains.

Archaea are adapted to energetic stress

All organisms face some form of energetic stress. For the purpose of constructing this hypothesis, energetic stress is defined for the Archaea relative to life's other domains. More specifically, two related boundary conditions are considered: maintenance energy (ME) and the biological energy quantum (BEQ). ME defines the minimum energetic flux from catabolism that is necessary to maintain cellular activity and is distinct from the energy required for growth or for survival⁶⁻⁸. The BEQ defines the minimum catabolic energy yield that is required for conservation, typically involves a chemiosmotic potential and is an important aspect of ME among anaerobes. The inability to achieve ME leads to starvation, whereas the inability to meet the BEQ leads to a decoupling of energy conservation from catabolism. More specifically, cells that are unable to achieve ME might sustain ATP synthesis, but at a rate insufficient to meet cellular demand; cells unable to achieve the BEQ might have an ample supply of substrate, but are unable to couple substrate to ATP synthesis due to unfavourable thermodynamic conditions. Both situations are lethal boundary conditions for survival. The energetic requirements of prokaryotes in nature have been reviewed recently, in terms of both ME and the BEQ6, and are summarized in FIG. 1.

Cultivated archaea can be divided into five broad physiological (halophiles, thermophiles and acidophiles) or metabolic (nitrifiers and methanogens) groups. One additional metabolic group has now been defined based on ample environmental, laboratory and metagenomic analysis: the anaerobic methane oxidizers⁹⁻¹². Numerous archaeal clades for which no physiological or biochemical function is known have also been identified in environmental samples based on the phylogenetic analysis of 16S rRNA genes. In this article, the physiology of, and energetic stresses experienced by, the six archaeal groups are reviewed and are compared with bacteria. The general capacity of archaea to dominate or outcompete bacteria under conditions of chronic energy stress leads me to propose

OPINION

Adaptations to energy stress dictate the ecology and evolution of the Archaea

David L. Valentine

Abstract | The three domains of life on Earth include the two prokaryotic groups, Archaea and Bacteria. The Archaea are distinguished from Bacteria based on phylogenetic and biochemical differences, but currently there is no unifying ecological principle to differentiate these groups. The ecology of the Archaea is reviewed here in terms of cellular bioenergetics. Adaptation to chronic energy stress is hypothesized to be the crucial factor that distinguishes the Archaea from Bacteria. The biochemical mechanisms that enable archaea to cope with chronic energy stress include low-permeability membranes and specific catabolic pathways. Based on the ecological unity and biochemical adaptations among archaea, I propose the hypothesis that chronic energy stress is the primary selective pressure governing the evolution of the Archaea.

The Archaea remain the most enigmatic of life's three domains. Generally referred to as archaea (plural) or archaeon (singular), the representatives of this domain were first distinguished from bacteria based on differences in tRNA and rRNA, the cytoplasmic membrane and cell-wall composition, together with their restriction to unusual habitats¹. The first-characterized archaea thrived in conditions that were characterized by high salinity, high temperature and acidity, or strict anoxia — which led to the hypothesis that these organisms require extreme conditions. Subsequent investigations revealed differences in archaeal transcription and translation apparatus that further distinguished the Archaea as a separate domain of life². However, the unifying ecological perspective of the Archaea as extremophiles was largely abandoned with the discovery of archaea throughout the world's oceans^{3,4}. Surveys of phylogenetic diversity now show that archaea are abundant in a myriad of localities throughout the biosphere⁵. In this article, I consider the ecological commonalities among diverse archaea and conclude that adaptation to chronic energy stress is the crucial factor that distinguishes the Archaea



Figure 1 | **Cellular energy budgets. a** | The energy requirements for conditions of survival, maintenance and growth are shown. The ratio of energy requirements (survival: maintenance: growth) was recently estimated at 1:10³:10⁶ (REF. 8). **b** | The idealized relationship between the cellular energy supply (E), substrate flux (F_s), Gibbs free energies for catabolism ($\Delta G'_{ren}$) and ATP synthesis ($\Delta G'_{ATP}$) is shown. The figure represents a case in which energy conservation is by a chemiosmotic mechanism (chemiosmotic potential) with a net translocation of one ion per round of catabolism (biological energy quantum). ATP synthesis from ADP and Pi requires ~ 60 kJ mol⁻¹, and n represents the number of translocated protons required for ATP synthesis. Equations 1–4 assume 100% efficiency. The condition of E < ME results in inactivity or death. ME, maintenance energy.

that adaptation to chronic energy stress is the primary factor differentiating archaeal and bacterial ecology.

Extreme halophiles. Extremely halophilic archaea thrive in environments with salt concentrations above 150–200 g l⁻¹. Sodium is toxic at high intracellular levels due to electrochemical and osmotic interactions with nucleic acids and proteins, and halophiles face the chronic energetic challenge of preventing excess sodium from entering the cell. The abundance and diversity of archaea have consistently been shown to be greater than bacteria in environments that contain more than 20–25% salt^{13–15}, although many bacterial halophiles have been described. Still, archaea clearly dominate over bacteria in the most saline conditions¹³.

Hyperthermophiles. Extremely thermophilic archaea are characterized by growth optima of 80°C or more, with a current record of growth at 121°C (REF. 16). These organisms survive at temperatures that are approaching the limit for the structural integrity of cells.

Numerous energetic challenges for hyperthermophiles include increased membrane permeability^{17,18} and high rates of biochemical breakdown. A comparative analysis of the optimum growth temperatures for archaeal and bacterial species reveals a predominance of archaea at the upper extremes of temperature (FIG. 2) and is consistent with environmental observations^{19,20}. Competition with bacteria intensifies at lower temperatures, particularly in terrestrial environments where H₂ and O₂ both occur²¹.

Acidophiles. Acidophilic archaea can thrive in acidic environments (sometimes at pH values below zero) and often in acidic environments at elevated temperatures (FIG. 2). Because the inside of the cell must be maintained at near neutral pH, these organisms must withstand proton gradients of up to 5 orders of magnitude²². Evidence from environmental samples and cultivation indicates that archaea are well-adapted to thrive at low pH, and are dominant in environments that are both hot and acidic²³⁻²⁵ (FIG. 2). As with hyperthermophiles, coexistence and competition with bacteria becomes more pronounced at lower temperatures²³.

Nitrifiers. Ammonia-oxidizing archaea are now known to be abundant and important in the open ocean^{26,27} and might also be important in soils²⁸. So far one relevant genome has been sequenced²⁹ and one marine strain has been isolated and proposed as the type for a new genus and species: Candidatus Nitrosopumilus mariti*mus*³⁰. The environments that these archaeal nitrifiers inhabit are surficial sediments that are likely to have low concentrations of O₂, and the open ocean, in which ammonia concentrations are typically an order or more lower than in more replete environments; these organisms probably face chronic energy stress in the form of energy flux. Unlike the halophiles, hyperthermophiles and acidophiles, these archaea are in direct competition with bacteria across a broad range of environmental conditions. Inference can be drawn from recent studies showing that these archaea out-compete bacteria in conditions of reduced energy supply, such as in unfertilized forest soils, oligotrophic waters, and suboxic waste-water treatment plants^{26,28,30-33}. Conversely, bacteria seem to gain a competitive advantage in fertilized soils, eutrophied waters and fully aerated waste-water treatment plants. I interpret the available results to indicate that, in comparison with bacteria, nitrifying archaea thrive in conditions of low energy availability.

Methanogens. Methanogens are a group of strictly anaerobic archaea that are characterized by the unique ability to produce methane as a catabolic end product. These organisms thrive across a broad range of temperatures, salinities and pH. During methanogenesis, each round of catabolism results in energy conservation through a chemiosmotic potential34. In many environments the net energy conservation from catabolism is only a fraction of an ATP for each methane molecule produced^{35,36}, and low energy flux leads to chronic energy stress in terms of meeting both the BEQ and ME. Methanogens typically out-compete bacteria for common substrates when sulphate and other oxidants are depleted and CO₂ becomes the favoured electron acceptor; this results in environments in which methane is the primary metabolic product. There are no known bacterial methanogens, but methanogenic archaea do interact syntrophically and competitively with bacteria³⁶⁻³⁹.



Figure 2 | **Temperature and pH requirements for growth distinguish thermophilic bacteria and archaea.** 72 archaeal species that represent 32 genera are included (pink dots), as are 107 bacterial species that represent 61 genera (blue dots). Methanogenic archaea are excluded. Only the type strain for each species is shown, and an average temperature is given for species that have a range for the optimal growth temperature. The overlaid blue 'zone' comprises environmental conditions to which bacteria are best adapted, the overlaid pink zone comprises conditions to which archaea are best adapted, and the grey zone represents those conditions to which both archaeal and bacterial species are well adapted. Data were compiled from Bergey's Manual of Systematic Bacteriology and from the primary literature⁸⁴.

Methane oxidizers. The anaerobic methane oxidizers comprise three or more phylogenetic groups and are closely related to the methanogens. These organisms are thought to form syntrophic associations with sulphate- or nitrate-reducing bacteria and to grow by oxidizing methane^{9,12,40}. Extensive environmental, laboratory and modelling studies indicate that this mode of growth yields only small amounts of energy and often occurs at exceedingly slow rates⁴¹⁻⁴⁵. These organisms are presumed to face chronic energy stress in terms of achieving the BEQ and ME. The capacity to carry out this globally important process seems to reside exclusively with the Archaea.

Known archaeal groups are clearly adapted to energetic stress and can dominate or out-compete bacteria in ecological niches in which chronic energy stress is a feature, including environmental stresses (temperature, acidity and salinity) and low energy availability. The physiological ecology of many not-yet-isolated groups might be reasonably predicted to involve chronic energy stress as described above. In particular, the environmental distribution of 16S rRNA gene sequences can be considered in terms of the most likely energy stress, in order to hypothesize physiologies for the organisms. This rationale has been used to link archaeal 16S rRNA sequences to

archaeal lifestyles in environments that are characterized by high temperature, acidity or salinity, as well as in environments that are likely to support methanogenesis, methane oxidation or nitrification⁵. This approach can also be applied to exclude physiologies and metabolic activities of some archaea. Of particular interest in this regard are some of the sediment-dwelling (marine benthic group) archaea, which have environmental distributions that are incompatible with the six groups described above^{46–48}. Given the low availability of energy in the environments where these archaea thrive it is likely that they have distinctive metabolic functions and are adapted to low energy flux.

Biochemical adaptations

Ecological differences between the Archaea and the Bacteria must derive from genetic and biochemical adaptations. Furthermore, these must presumably be long-standing traits from an evolutionary perspective. The distinctive lipid-membrane composition among archaea is considered here as a primary adaptation to energy stress. Several secondary adaptations are also considered, including catabolic pathways and mechanisms of energy conservation. I conclude that archaea use specific membrane structures to reduce energy loss at the cellular level, thereby reducing their ME relative to bacteria. I further contend that the distribution of catabolic pathways among archaea results directly from their adaptation to chronic energy stress and that distinctive mechanisms of energy conservation allow many archaea to readily adapt to environments of differing energy availability.

Lipid membranes. All prokaryotes face a crucial energy dilemma at the cytoplasmic membrane. Each cell must expend energy to maintain a chemiosmotic potential, which is used to drive basic cellular processes. The membrane functions as the barrier for this potential, and the inadvertent passage of ions across the membrane - futile ion cycling is a direct energy loss for the cell. Organisms require membrane fidelity to avoid futile ion cycling and minimize ME. Conversely, the membrane plays host to numerous other cellular processes that require motion or fluidity in the membrane; lateral motion is directly related to membrane permeability⁴⁹. Efflux of ions from the cell has been shown to account for approximately half the energy demand of resting mammalian cells⁵⁰, and is probably a main component of ME for active cells in nature.

One important distinction between the Archaea and the Bacteria is the chemical structure of lipids composing the cytoplasmic membrane (FIG. 3). Bacterial lipids typically consist of fatty acids esterified to a glycerol moiety, whereas archaeal lipids typically consist of isoprenoidal alcohols that are ether-linked to glycerol. Stereochemical configurations about the glycerol moiety are also different. Archaeal membranes are less permeable to ions than bacterial membranes, and tetraether-based membranes are less permeable than diether-based membranes^{51,52}. These membranes reduce the amount of futile ion cycling in vivo and provide an energetic advantage to archaea — less energy is lost during the maintenance of a chemiosmotic potential. I propose that this adaptation effectively reduces the ME for archaea compared with bacteria. The advantages of the archaeal membrane have been clearly shown in hyperthermophiles, halophiles, acidophiles and liposomes^{17,18,22,52-54}, and here I simply extend this principle to include other archaea.

Catabolic specificity. In his classic review of bacterial evolution⁵⁵, Woese writes that the Archaea "are a collection of disparate phenotypes: the methanogens, the extreme halophiles, and the extremely thermophilic sulphur-metabolizing species. Their metabolic differences are many, their known similarities few."

The known breadth of catabolic functions among archaea has expanded and now includes aerobiosis, fermentation, nitrification, methanogensis, phototrophy and numerous forms of lithotrophy⁵. I contend that the catabolic specificity of archaea is readily interpreted in terms of adaptation to chronic energy stress. Consider the competition between archaea and bacteria from a metabolic perspective. Among the known archaea there seem to be several successful modes of dominating, or competing with, bacteria. For halophiles, hyperthermophiles and thermoacidophiles dominance is achieved through environmental exclusivity — that is, these groups are adapted to cope with a level of energy stress that disables all but a select few bacterial species. This is achieved by effectively combating the environmental pressures (temperature, salinity and acidity) that tend to increase ME. Environmental exclusivity gives way to competition with bacteria as conditions become moderate (FIG. 2), and archaeal success becomes more dependent on catabolic adaptations. In the case of methanogens and methane oxidizers, dominance is achieved through metabolic exclusivity whereby these organisms have evolved to exclude or out-compete bacteria by the use of unique catabolic pathways. In the case of nitrifiers there seems to be direct competition involving similar catabolic strategies, the details of which are still emerging^{29,56}. These seemingly disparate catabolic activities are explicable in the context of energy adaptation. The thermophiles, acidophiles and halophiles rely on environmental exclusivity at extreme conditions and can maintain broad catabolic specificity as their primary energetic adaptations are for environmental factors. These organisms retain this energetic advantage in the form of reduced ME at high (but not extreme) temperatures, salinities and acidities. The level of competition between archaea and bacteria intensifies in moderate environmental conditions, and successful archaea maintain a singularity of catabolism that allows them to exclude or out-compete bacteria in specific niches with low energy availability. Methanogens, methane oxidizers and possibly nitrifiers each seemingly display such singularity, with their catabolic emphasis on a single well-defined pathway. The commonality among all these archaea is that success is dependent on their capacity to cope with chronic energy stress.



Figure 3 | **Membranes of the Archaea and Bacteria.** The basic chemical structures of archaeal (left) and bacterial (right) membrane lipids are shown to illustrate the typical chemical differences. Examples of intact membrane structures used by archaea (left) and bacteria (right) are shown below, including the monolayers that are produced by some archaea and the highly unsaturated membranes produced by some bacteria. The arrow (bottom) indicates a general trend of increasing permeability to ions such as protons and sodium. Eukaryotic membranes are similar to those of bacteria.

Energy conservation. Distinctive mechanisms of energy conservation are a hallmark of many archaea. Such mechanisms include methanogenesis, anaerobic methane oxidation, proton reduction coupled directly to proton translocation, H₂-dependent sulphur reduction and phototrophy^{5,57}. H₂/CO₂-methanogenesis is among the best understood of the archaeal catabolic pathways and provides an example of how catabolism and ecology are specific to chronic energy stress (FIG. 4). Methanogens face energy stress in terms of achieving both a BEQ and ME^{6,35,58}. These archaea have a singularity of catabolism and have evolved to cope with chronic energy stress in several ways.

First, energy conservation is achieved by a chemiosmotic mechanism, often with the net translocation of only one ion per round of catabolism⁶. Second, some methanogens have been shown to vary the stoichiometry of ion translocation with the availability of energy from substrates - a clear adaptation to low and variable Gibbs free-energy yields⁵⁹. Third, some methanogens differentially express isoenzymes of the catabolic pathway according to substrate or energy availability⁶⁰. Fourth, the H₂/CO₂ pathway allows a high degree of reversibility under low energy conditions, which has been interpreted as an indication of high efficiency^{61,62}. In addition to such adaptations, the methanogens adapt their lifestyle



Figure 4 | **Adaptations of methanogens to energy stress.** This composite diagram shows the different adaptations that allow methanogens to thrive in conditions of chronic energy stress, using the example of the H_2/CO_2 catabolic pathway. Seven adaptations are included in the figure: the use of isoprenoidal, ether-linked lipids to reduce futile ion cycling (a); the regulation of isoenzyme production in the catabolic pathway as a function of H_2 (Gibbs free energy) availability^{60,85} (b); the frequently low quantity of Gibbs free energy available from catabolism (as low as ~ 10 kJ mol⁻¹ of methane produced)^{35,37–39,86} (c); the inferred capacity to thrive with the net extrusion of one ion per round of catabolism^{35,36} (d); the dynamic stoichiometry of proton extrusion during heterodisulphide (CoB-S-S-CoM) reduction as controlled by H_2 concentration⁵⁹ (e); the reversibility of the first five steps of the catabolic pathway, which allow for near-equilibrium conditions and therefore high efficiency⁶² (f); and the variations in stoichiometry of proton-coupled ATP synthesis^{61,64} that probably allow variability in the BEQ (g). BEQ, biological energy quantum; MF, methanofuran; H_4 MPT, tetrahydromethanopterin; CoM, coenzyme M; CoB, coenzyme B.

to their catabolic pathway, particularly with regard to anoxia. Their singularity of catabolism, coupled with numerous adaptations to energy stress, allows methanogens to successfully out-compete bacteria as terminal metabolizers in environments where CO₂ is the primary terminal electron acceptor^{35,37,58}. This low-energy lifestyle is very successful, as methanogens process carbon equivalent to ~1–2% of global net primary production^{62,63}.

The capacity to conserve small amounts of metabolically useful energy during catabolism is a key to survival in anaerobic, energy-stressed environments. Among many strictly anaerobic archaea and bacteria this is achieved by coupling catabolism to ion translocation (typically H⁺, sometimes Na⁺), with a minimum of one ion translocated per round of catabolism³⁶ (FIG. 1). In order to produce ATP from the established chemiosmotic gradient, the key enzyme, proton-translocating ATP synthase, is used. Recently the structures of several archaeal (A_1A_0) ATP synthases have been solved, revealing a range of predicted stoichiometries for ions translocated per ATP synthesized, with a current upper limit of 4.3 (REF. 64). The Archaea seem to maintain greater variability in $\rm H^+/ATP$ stoichiometry compared with the Bacteria^{64,65}. I interpret this variability as an evolutionary tactic to balance the energetic needs of the cell with the availability of energy in the local environment.

Archaeal evolution

Archaea and bacteria coexist throughout much of the biosphere, and are known to readily exchange genetic information². In order to understand the evolution of these two domains it is imperative to understand why they remain segregated in the face of similar ecological pressures. From the perspective of energetic adaptation, the continued distinction of these groups is evident - core archaeal identity is maintained by the ecological pressure of chronic energetic stress and through the related adaptations of each archaeon. Energy stress might therefore be considered as a dominant selective pressure for evolutionary change among the Archaea — more so than for the Bacteria.

Support for this evolutionary perspective comes from the general observation that phylogeny and physiology are more closely related among the Archaea than among the Bacteria. Each of the six physiological groups used to characterize known archaea displays a high degree of internal phylogenetic coherence when compared with bacteria. As an extreme example, consider the archaeal class of halobacteria, which consists of 22 genera of extreme halophiles. By contrast, consider the bacterial class γ -proteobacteria, which comprises over 160 genera with no apparent physiological unity66, or that bacterial halophiles are spread among ten or more phylogenetic classes. Such observations are consistent with a physiological force such as energy stress functioning as a selective pressure on archaeal evolution. That is, because the dominant selective force in archaeal evolution relates directly to a fundamental physiological trait, it seems reasonable that phylogeny and physiology remain tightly coupled.

Implications for Bacteria and Eukarya

The case for energy adaptation among the Archaea is well grounded in the physiology of known archaea, and is generally supported by numerous environmental observations. However, the unification of archaeal ecology raises a number of fundamental questions regarding the ecology of the Bacteria and Eukarya.

If archaea out-compete bacteria in conditions of chronic energy stress, what properties allow bacteria to out-compete archaea under other conditions? Presumably the ability of bacteria to out-compete archaea in so many

environments is integrally tied to the innate advantages of being an archaeon - otherwise such traits would be shared during evolution. The apparent exclusivity of archaeal membrane structures and of catabolic pathways for methanogenesis and anaerobic methane oxidation are examples of such traits. Bacteria maintain a broad array of genetic, metabolic and physiological capacities that allow for a high degree of adaptability, and metabolic diversification into numerous environmental niches and habitats. These capacities allow bacteria to dominate archaea in many environments, especially those in which energy stress is not chronic. Based on these generalizations I contend that archaea have evolved to thrive with energy stress, whereas bacteria can adapt to maximize the availability of energy and other resources. Numerous

physiological characteristics found primarily or exclusively in the Bacteria support this concept of enhanced bacterial adaptability, including pathogenesis, extensive synthesis of natural products, formation of complex morphological structures, photosynthesis and spore formation, among others. I further contend that these distinctions have led to two divergent evolutionary paths: the archaeal path in which evolutionary change is tempered by the inherent advantages in thriving with chronic energy stress, and the bacterial path in which function is more variable and cells tend to undergo more radical evolutionary change. Put another way, the many adaptations of an archaeon to combat energy stress limit its capacity to compete directly with bacteria in dynamic environments in which energy stress is not chronic.

If archaeal membranes provide a more effective barrier against ions, why do eukaryotes have membranes that are most similar to bacterial membranes? One explanation is that low-permeability membranes have lower rates of lateral diffusion^{67,68}, a factor which is thought to be important for photosynthesis, respiration and signal transduction⁶⁹. The use of more laterally mobile membranes might be an adaptation to enhanced rates of energy production at the expense of energy conservation, with highly unsaturated membranes being an extreme case69. Chemical modification of the membrane, such as the inclusion of sterols, might be a dynamic approach to controlling membrane permeability while maintaining advantages afforded by the bacterial membranes70.

Box 1 | Predictions and generalizations

The concepts developed in this work allow for generalizations regarding the evolutionary history, diversity, physiology and ecology of the Archaea, and lead to several predictions:

- Evolutionary divergence of the Archaea and Bacteria arose with the selective pressure of energy stress. The archaeal branch is probably an adaptation to extreme temperature and acidity. The capacity of the Archaea to thrive with chronic energy stress has defined the subsequent radiation of this group to occupy other niches.
- The Archaea tend to evolve smaller genomes than the Bacteria. Energy stress is one important factor that controls genome size. Archaea evolving larger genomes include some methanogens and halophiles. These archaeal species also seem to have evolved some bacterial-like qualities such as broad substrate specificity and moderately fluid membrane bilayers.
- According to one marine sedimentary record, a major radiation of taxa producing tetraether-based membranes occurred during a midcretaceous anoxic event⁷⁹. Such a radiation might have been related to energy availability, such as competition for ammonia and O₂ across a broad oceanic redox boundary.
- The overall diversity of the Archaea is lower than that of the Bacteria because their tendency to adapt to conditions of chronic energy stress has hindered their capacity to speciate in replete environments. This limitation is generally supported by the observation that there are currently only 89 validly described archaeal genera compared with over 1,400 bacterial genera⁵⁶.
- Archaea control the structure and dynamics of their membranes by using tetraethers, diethers, macrocyclic diethers and/or diether zipper structures, and various polar head groups. A secondary level of control is achieved through the alteration of the core lipid structures to incorporate unsaturation, hydroxyl groups and cyclic structures. Archaeal membranes are blended to optimize metabolic function for a given environment while minimizing energy loss, but probably have less dynamic capacity than bacterial membranes.
- Nitrifying marine archaea produce tetraether–based membranes in order to minimize futile ion cycling. This resulting reduction in maintenance energy (ME) is crucial to their lifestyle, which involves chronic energy stress that is due to low ammonia and/or O₂ concentrations.
- The lack of lateral mobility in archaeal tetraether-based membranes might limit the rate of electron transport thereby providing a

competitive advantage to bacteria in some environments. This might explain the capacity of many *Aquificales* to dominate archaea in oxic hot springs, and might also explain the emerging association of putative nitrifying archaea with low O_2 conditions^{21,31}.

- Actively growing archaea have similar energy requirements to bacteria, as the energetic advantages of being archaea are realized primarily in the form of reduced ME.
- Archaea favour active maintenance over survival modes, such as cyst formation and sporulation because they are adapted to thrive with chronic energy stress. Such survival modes are more common in the Bacteria and might not exist among the Archaea.
- Pathogenic archaea are rare or nonexistent^{80,81} because the inherent tendency of archaea to thrive with chronic energy stress is incompatible with the dynamic nature of pathogenesis. Bacteria are inherently better suited to pathogenesis as it is consistent with their capacity to seek new resources and adapt to changing environments. The mode of action for any obligate pathogenic archaeon would probably relate to overcoming chronic energy stress in the host.
- Mesophilic archaea such as methanogens can out-compete bacteria when conditions are stable, whereas bacteria thrive better in conditions of rapid environmental change. The seasonal interplay between methanogens and acetogenic bacteria in marine sediments is one example of this⁸².
- Archaeal symbionts, such as those inhabiting a marine sponge⁸³, might be favoured in conditions in which energy supply from the host is restricted for long periods of time and low ME is advantageous for survival of the symbiont.
- Adaptations to chronic energy stress might extend beyond those presented here, particularly for cellular functions that are prevalent during the maintenance phase. Possibilities include reduced turnover rates of proteins and nucleic acids, and more efficient recycling of key macromolecules.
- With their unique repertoire of informational processing components, archaea might have evolved transcriptional and translational regulatory mechanisms that reduce energy expenditure.
- Uncultivated archaea thriving at moderate temperature, salinity and circumneutral pH are adapted for low ME. As a result, many have adaptations specific to low energy availability, and laboratory cultivation will be challenging for most strains.

Glossary

Archaea

One of the three primary domains of life inclusive of all organisms in the domain.

Archaeon

(archaea). An organism (organisms) belonging to the domain Archaea

bacteria

A population or group of organisms belonging to the domain Bacteria

Bacteria

One of the three primary domains of life, inclusive of all organisms within the domain.

Biological energy quantum

(BEQ). Finite minimum level of energy that an organism can conserve from catabolism.

Chemiosmotic

The use of an ion gradient across a membrane to generate ATP.

Many bacteria are known to thrive under extreme environmental conditions^{23,71,72}, and conditions of low energy flux73-75, and numerous adaptations have evolved. So why do bacteria occupy such niches if archaea are inherently better suited to do so? For growth in conditions of high salinity and temperature, some bacteria have evolved archaeal-like qualities. For example, known hyperthermophilic bacteria of the order Aquificales use (non-isoprenoidal) ether lipids in their membranes that facilitate growth at temperatures exceeding 80°C, while still supporting a respiratory catabolism typically involving formate/H₂ and O₂. The extremely halophilic bacterium Salinibacter ruber uses an unusual sulphonolipid, hyperconcentrates potassium for osmotic balance and produces pigments — similar to halophilic archaea^{71,76}. This tendency of bacteria to undergo such radical evolutionary changes might explain their capacity to compete with archaea in select environmental conditions (Fig 2). In many other cases, bacterial adaptations to chronic energy stress are less obvious, and the adaptation of bacteria to low energy flux is notable for the processes of sulphate reduction³⁵ and syntrophic fermentation³⁶. The subsurface biosphere and other endolithic communities are also characterized by low energy availability and seem to be dominated by bacteria in some locations^{77,78}. The low levels of available energy for such organisms should seemingly favour archaea over bacteria, but this does not seem to always be the case. The prevalence of organotrophy among bacteria stands in contrast to the prevalence of autotrophy among archaea, and might result in an advantage for bacteria

Clade

A hypothesis of evolutionary relatedness in which a group of organisms share a single common ancestor. In the context of microbial ecology this term is often used to indicate a group of organisms that have been shown to be monophyletic by comparative analysis of 16S rRNA or other conserved gene sequences.

Chronic energy stress

Condition in which cells are consistently faced with an insufficient supply of cellular energy. The stresses considered here to comprise chronic energy stress include the high rates of futile ion cycling driven by extreme temperature, acidity or salinity, as well as low rates of cellular energy generation due to limited substrate availability and/or unfavourable thermodynamic conditions

Environmental exclusivity

The concept that some archaea are adapted to thrive in conditions that are inhospitable to bacteria.

in environments where energy must be derived from a diverse array of organic molecules. However, such a generalization is not inclusive, and too little is known about the physiology of anaerobic archaea to draw more meaningful conclusions.

Conclusions

Diverse evidence indicates that archaea are better adapted to chronic energy stress than bacteria. The capacity to thrive in spite of energy stress seems central to the archaeal lifestyle. Bacteria seem to focus less on adapting to energy stress, and more on exploiting new or variable resources. The adaptations of archaea to energy stress provide a competitive advantage under a range of environmental conditions. Most obvious are the ability to grow in conditions of extreme salinity, temperature and pH, in which bacteria and eukaryotes cannot grow. More subtle is the advantage conferred on archaea when faced with energy limitation, including limited substrate supply, such as for nitrification, and minimal free-energy yields from catabolism, such as for methanogenesis and anaerobic methane oxidation. Archaeal adaptation to chronic energy stress points to the central importance of energy stress as a selective pressure in prokaryotic evolution, as is highlighted further in the BOX 1. That an entire domain of life might rely so heavily on this principle is a major departure from traditional ecological thinking. I propose that not only does chronic energy stress unify archaeal ecology, but it is also a powerful and divergent selective pressure for prokaryotic evolution.

Extremely halophilic

An organism that grows best in media that contains 2.5-5.2 M salt

Maintenance energy

(ME). Minimum intake flux of energy (power) that is required to maintain molecular and cellular integrity as well as activity

Metabolic exclusivity

The concept that dominance can be achieved by way of catabolic specialization.

Singularity of catabolism

Exclusive reliance on a single, highly specialized form of catabolism, such as methanogenesis.

Syntrophically

A syntrophic reaction is one in which two (or more) organisms interact metabolically to consume a substrate that neither can consume independently

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Competing interests statement

The author declares no competing financial interests.

DATABASES

The following terms in this article are linked online to: Entrez Genome Project: http://www.ncbi.nlm.nih.gov/ entrez/query.fcgi?db=genomeprj Salinibacter ruber

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