Origins of Life and Evolution of Biospheres (2006) 36: 177–189
DOI: 10.1007/s11084-005-9003-4

THERMAL ENERGY AND THE ORIGIN OF LIFE

ANTHONIE W. J. MULLER and DIRK SCHULZE-MAKUCH*
Department of Geology, Washington State University, Pullman, WA 99164-2812, USA
*(*author for correspondence, e-mail: dirksm@wsu.edu/mantid5@aol.com)*

(Received 15 July 2005; accepted 20 October 2005)

Abstract. Life has evolved on Earth with electromagnetic radiation (light), fermentable organic molecules, and oxidizable chemicals as sources of energy. Biological use of thermal energy has not been observed although heat, and the thermal gradients required to convert it into free energy, are ubiquitous and were even more abundant at the time of the origin of life on Earth. Nevertheless, Earth-organisms sense thermal energy, and in suitable environments may have gained the capability to use it as energy source. It has been proposed that the first organisms obtained their energy by a first protein named pF_1 that worked on a thermal variation of the binding change mechanism of today's ATP synthase enzyme. Organisms using thermosynthesis may still live where light or chemical energy sources are not available. Possible suitable examples are subsurface environments on Earth and in the outer Solar System, in particular the subsurface oceans of the icy satellites of Jupiter and Saturn.

Keywords: thermal energy, origin of life, exobiology, prebiotic chemistry, thermosynthesis, heat engine, prebiotic environments, early Earth

Introduction

Life on Earth uses light and a range of chemical substances as energy sources. Potentially a much broader range of energy sources is available, however. Organisms can sense thermal energy (Viswanath *et al.*, 2003), pressure, touch, stretch, movement of water and air, gravity, electric and magnetic fields (Schmidt-Nielsen, 1990), as well as a wide range of chemical substances. These stimuli generate responses through membrane transductions, either by altering the conductivities of ion gates that result in transmembrane potential changes, or by initiating metabolic changes through secondary messengers (Schulze-Makuch and Irwin, 2002, 2004). Due to its ubiquity, thermal energy (heat) seems especially advantageous as an energy source.

The Kelvin-Planck principle states the impossibility of the conversion into work of heat from a single source – i.e. without a heat sink – by a cyclic process (Zemansky, 1968). Free energy gain from heat requires a thermal gradient, which is available in many environments. Examples are volcanic hot springs, tidal ponds (Lathe, 2004, 2005), hydrothermal vents on the bottom of the ocean, some at moderately high temperatures (Russell and Hall, 1997; Kelley *et al.*, 2001), and many interfaces, where algae presence is often conspicuous (Round, 1981) such as at rock-air and snow-air interfaces. Thermal cycling occurs in tidal ponds and in convection cells. Obviously, just like any heat engine, biological free energy gain from a thermal gradient ("thermosynthesis") is compatible with the laws of thermodynamics. The use of thermal energy is especially attractive in dark and nutrient-poor environments, i.e. where alternative energy sources are absent (Schulze-Makuch and Irwin, 2002, 2004). The use has also been considered in theoretical models for the emergence of the chemiosmotic machinery, the basis of both photosynthesis and respiration (Muller, 1985, 1993, 1995, 1996, 2003, 2005; Muller and Schulze-Makuch, 2006). Here, we discuss the possibilities that thermal energy provides to life and its origin.

The Early Earth Environment

The early environment in which life originated on Earth is not known. Little rock evidence remains from the earliest times, but conclusions can be drawn based on comparative planetology and our understanding of geological processes. The cratering record of the Moon, Mars, Venus, Mercury and the size distribution of the asteroids imply that about 3.9 to 3.8 Ga ago the early Earth must have been subject to an intense meteorite bombardment that lasted 10 to 150 million years (Strom *et al.*, 2005). The impacts would have inhibited the accumulation of an ocean and the sustained development of life (Nisbet and Sleep, 2001). If life originated before this Late Heavy Bombardment (LHB), it could have persisted only deep inside the crust. Several researchers (Kompanichenko, 1996; Stetter, 1998) favor a hyperthermophilic origin of life, based on the rooting of the universal tree of life in the hyperthermophilic organisms, of which many are found near the hydrothermal vents on the ocean floor (Takai *et al.*, 2001). High temperatures are however detrimental to organic synthesis reactions, and the hyperthermophilic last common ancestor may have been a survivor from a meteorite impact that almost sterilized the Earth.

Heat from endogenic sources and impacts shaped Earth early in its history. Shortly after its accretion, Earth differentiated into a liquid metallic core, a mantle boundary layer of high-pressure silicate mineral phases, upper mantle, magma ocean, thin komatiitic crust, and convecting steam atmosphere. The first crust formed and cooling of the steam yielded the first oceans. Subduction of water-rich oceanic crust initiated arc volcanism and transferred water, carbonates, and sulfates to the mantle. The core dynamo initiated and the magnetosphere emerged. Finally, a thick continental crust accreted and subduction of hydrated oceanic crust yielded the mantle boundary layer and the lower mantle (Schulze-Makuch *et al.*, 2005a).

The earliest preserved rocks date from the early Archaean, nearly 4 Ga ago. Proposed bacterial fossils in 3.5 Ga old rocks (Schopf, 1993; Schopf and Packer, 1987) have been reinterpreted as non-biologic kerogen artifacts (Brasier *et al.*, 2002). The presence of life is however also indicated by isotopic evidence (Rosing, 1999) and fossils (Schulze-Makuch *et al.*, 2005b) at about the same or slightly later time. Life therefore emerged when the heat flux on Earth was large, possibly during or shortly after the LHB, which supports the notion that given the proper materials, physical conditions, and flow of energy, matter will self-organize to life (Morowitz, 1968; Goodwin, 1994; Kauffman, 1995). The atmospheric haze from massive outgassing and impact residues may have prohibited an early biological role for light as a primary energy source, whereas convection cells could have enabled thermal energy to take on this role.

Thermal Energy as an Energy Source for Life

Radioactivity produces the heat that drives the processes in the interior of planetary bodies. On Earth this heat keeps the outer core liquid, establishes a protective magnetic field, and drives plate tectonics. Radiogenic heat would be available even on “run-away” planets ejected from star systems and drifting in interstellar space. Tidal flexing also yields heat, as seen on Io, the planetary body in the Solar System with the highest volcanic activity. Every star emits radiation that is converted into heat upon absorption on the surface of a planet. All these heat sources result in thermal gradients that thermotrophic organisms could harvest.

Schulze-Makuch and Irwin (2002, 2004) have suggested a mechanism for the biological use of thermal energy based on heat storage, making use of the high heat capacity of water (about 4.2 kJ/kg × K). The Carnot ratio of a heat engine equals the ratio of the temperature difference in the engine and the absolute temperature; the maximal free energy that the engine can yield equals the product of the Carnot ratio and the entered thermal energy. Assuming the cell mass of 10^{-12} g of microbes on Earth (Madigan *et al.*, 2000), and a water vacuole comprising one tenth of this mass, the available stored thermal energy during cooling this vacuole by 1°C is 2.5×10^{6} eV (4.2×10^{-13} J). After multiplication with the Carnot ratio of 1°K/278°K, a potential free energy gain of about 9,000 eV (1.4×10^{-15} J) follows for a temperature decrease from 5 to 4 °C (Schulze-Makuch and Irwin, 2002); upon larger decreases the potential free energy gain increases proportionally. Thus, a heated vacuole would provide a huge amount of energy that could be tapped by an organism when needed. For a large cell such as the giant pantropical algae *Valonia macrophysa* (Shihira-Ishikawa and Nawata, 1992), which contains a water vacuole of about 10 g, the potential yield is close to 1 J.

Here, we distinguish four types of thermotrophs based on specific energy harvesting strategies that could live on a thermal gradient near a vent structure (black smoker or hydrothermal mound) (Figure 1). The energy transduction mechanism could involve membrane proteins that generate high-energy metabolites through temperature-dependent conformational changes.

The first type of proposed thermotroph, which contains the mentioned water vacuole, is warmed when the whole organism moves into the vicinity of a hydrothermal vent (Schulze-Makuch and Irwin, 2004). When it moves away again,

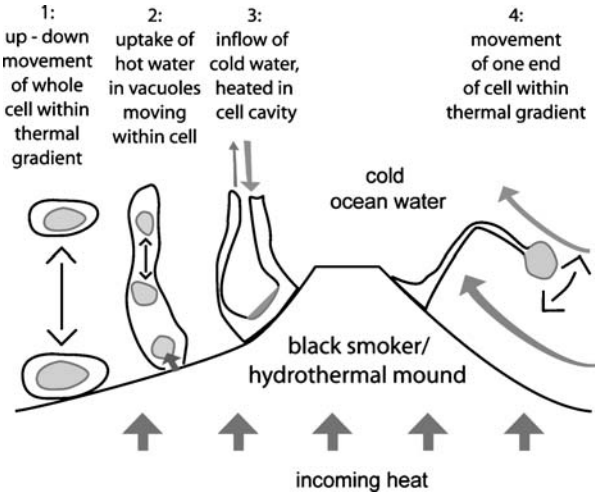

Figure 1. Four types of thermotrophs that could be present near a black smoker or hydrothermal mound structure. Areas within the organisms where the thermal gradient is tapped are marked in grey. In the first type of thermotroph the whole organism moves in and out of the vicinity of the structure, and free energy is gained when the exterior of the organism has cooled while its vacuole is still hot. The other three types remain attached, they either move the warmed up vacuoles within the cell, they allow cooling water enter the cell and let it heat up, or they let the unattached end of the cell move back and forth within the thermal gradient.

it could float in the colder ocean, using the buoyancy of the warm vacuole, and harvest the free energy present in the internal thermal gradient between the vacuole and the surrounding cell. The other three types are sessile, and remain with one end anchored to the surface of the structure.

The second type of thermotroph is a filamentous organism that spans the thermal gradient between the hot structure and the cold ocean. Near the structure it takes up hot water in a vacuole, and then gains free energy while the vacuole moves inside the cell to the cooler distal part (Schulze-Makuch and Irwin, 2004).

The third type takes up cold ocean water in a vacuole or cavity, and ejects it again when it has warmed up; as a result the anchored area of the organism is thermally cycled. This vacuole or cavity is not unlike the cavity of today's sponges, barnacles or mussels which is used in the filtering of water in order to obtain food, and may hint toward evolutionary trajectories. Interestingly, mussels are still commonly found near vent structures today (Van Dover and Lutz, 2004).

The fourth type of thermotroph is a filamentous organism that has its distal end moving freely in the cold ocean water, similar to the giant tubeworms present today in this environment (Van Dover and Lutz, 2004). If the heat flux through the vent structure and the flow of the ocean water that cools its exterior were constant, the resulting thermal gradient would be constant as well, and perhaps not adequate to gain sufficient energy over microscopic distances. However, the heat flux will vary on time scales as short as minutes (Tivey *et al.*, 2002), and the water flow will be turbulent. The laminar boundary layer will be thin at places, because the structure's exterior surface will not be smooth. Significant thermal fluctuations near the surface are therefore expected, especially at summits of microscopic roughness that stick out above the boundary layer (e.g., Gundersen *et al.*, 1992). These thermal fluctuations would be added to the fluctuations resulting from movement due to variation in body shape or length. The described summits constitute prime niches for this type of thermotroph, which can be compared to an organism that 'filters' temperature fluctuations from water, and may share important characteristics of a direct progenitor of water filtering organisms such as the sessile protist ciliate *Vorticella* with its long, quickly contractable stalk (Moriyama *et al.*, 1998).

Thus, organisms can be envisioned that use natural heat sources for biological energy needs. A prime candidate niche for thermotrophs is Europa's subsurface ocean (Spohn and Schubert, 2003), where volcanic vents if present would add to the tidal heat that may create large convection cells. Even on Earth, life based on thermal energy may exist deep inside the crust, near hydrothermal vents on the ocean floor, or in other environmental niches.

Thermosynthesis may have arisen later in evolution, and could be an example of the proposed second genesis of unknown life (Davies and Lineweaver, 2005). The synthesis of adenosine triphosphate (ATP) requires a proton gradient across a membrane. Since most sensory transductions are mediated by cell membranes, the emergence during evolution seems possible of membrane mechanisms that transform heat into high-energy covalent bonds, either directly or indirectly by coupling to ion pumps. These molecular heat engines would produce the same ATP as contemporary ATP synthase. The fact that such engines have gone unreported on Earth may only reflect the absence of a need for them on Earth today. On other worlds, where light energy is not available, natural selection is expected to favor the evolution of cellular mechanisms for transducing alternative forms of energy into free energy that organisms can use (Schulze-Makuch and Irwin, 2002).

The Origin of Life

The above model introduces the principle of use of thermal energy by a hypothetical organism, and describes how such an organism could function in a natural environment. It does not address the question of the origin of this organism. This origin, however, may involve the conversion of heat into free energy during thermal cycling as well.

The chemiosmotic machinery (Cruz *et al.*, 2005) drives ATP synthesis during both respiration and photosynthesis (Figure 2). Chemiosmosis takes place in chloroplasts in plants during photosynthesis and in mitochondria, the site of respiration

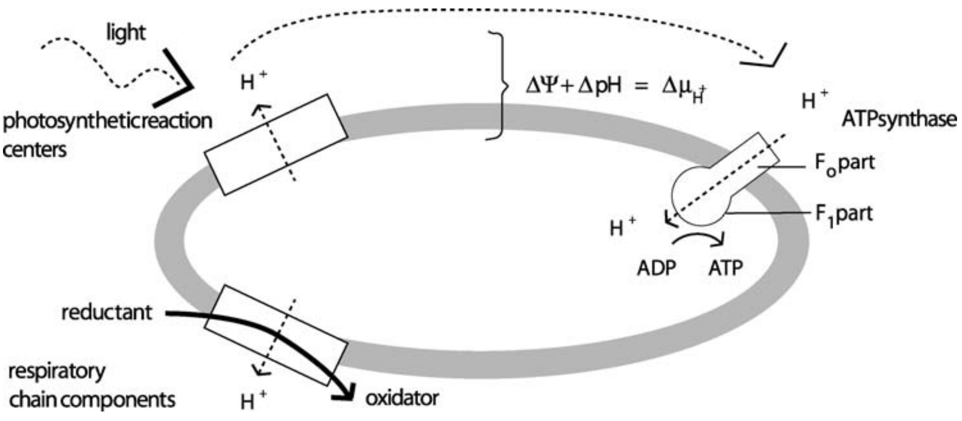

Figure 2. The chemiosmotic machinery of ATP synthesis. During both respiration and photosynthesis protons are pumped across a membrane. The resulting difference in potential across the membrane permits the synthesis of ATP by the ATP synthase enzyme while the protons fall back.

in many organisms including ourselves. During respiration, the free energy of the electrons that move from reductant to oxidizer is transduced into the free energy of a membrane while the protons are pumped across the membrane, which becomes charged. The ATP synthase enzyme transduces the membrane voltage to ATP while protons fall back through the membrane. The enzyme consists of two parts, the F_o part through which the energized protons move, and the F_1 part, the site of ATP synthesis. During photosynthesis, ATP synthase functions similarly; the difference between photosynthesis and respiration is that in the former the protons are pumped during light absorption whereas in the latter they are pumped during oxidation.

The chemiosmotic machinery comprises many proteins and is quite complex, even in the most simple bacterial photosynthesizers. How did this complexity emerge? A scaffolding of simpler machines is proposed that worked on thermal cycling and not on respiration or photosynthesis. According to our hypothesis, thermosynthesis produced ATP as contemporary photosynthesis and respiration do, but with much less power because the turnover time of the machinery equaled the long thermal cycle time of the convection current.

Just as a steam engine, thermosynthesis involves phase transitions: the thermotropic phase transition increases the mobility of membrane molecules. By a change in dipole potential (Clarke, 2001), this transition may change the potential of an asymmetric biomembrane (Muller, 1993). Although this change has not been directly observed in biomembranes, similar dipole potential changes during the thermotropic phase transition across lipid monolayers at the water/air interface have been observed (MacDonald and Simon, 1987; Muller, 1993). The changes can easily reach 100 mV, not much lower than the proton motive force of about 150 mV across the membrane that drives ATP synthesis today (Cruz *et al.*, 2005).

A thermosynthesis ancestry of bacterial photosynthesis is supported by the heat uptake and release that occurs during electron transfer within the bacterial photosynthetic reaction center. The reduction of the Q_A quinone causes an entropy decrease that accounts for the free energy gained from the absorbed photon. Upon electron transfer to the Q_B quinone the entropy and enthalpy increase again (Case and Parson, 1971; Callis *et al.*, 1972; Arata and Parson, 1981a,b, 1982), just as during the power stroke in a heat engine.

Thermal unfolding of proteins constitutes a second relevant phase transition, applicable to the ATP synthase enzyme. In the 'binding change mechanism' the F_1 part of ATP synthase binds ADP and phosphate in the dry enzymatic cleft and forms tightly bound ATP. This synthesis occurs without energy input and without involvement of covalent intermediates (Boyer, 1993). The ATP is released upon a relay of conformational energy from F_o (Figure 3a), which in turn obtains the energy

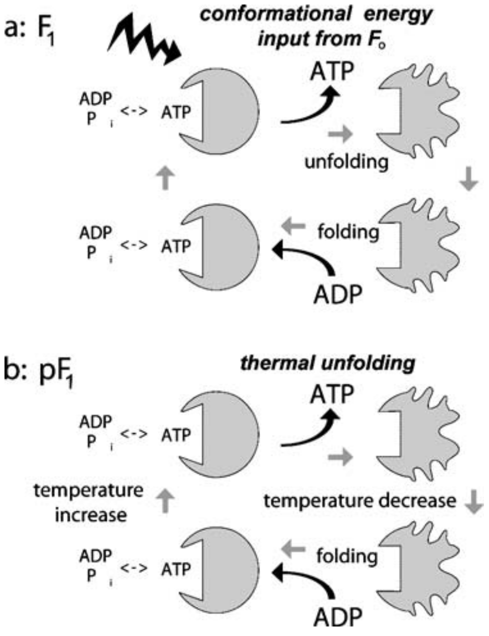

Figure 3. Binding change mechanisms, (a) in the binding change mechanism of F_1-ATP synthase as it functions today, tightly bound ATP is spontaneously formed from tightly bound ADP and phosphate. This tightly bound ATP is released upon a conformational energy transfer from the F_o part of the enzyme, (b) the thermal cycle of convection synchronized with the enzyme cycle of pF_1 in the proposed primordial "temperature-induced binding change mechanism." The proposed pF_1 enzyme could bind ADP and phosphate (bottom); when bound, these substrates were in equilibrium with strongly bound ATP (left). In pF_1 this strongly bound ATP was released by a thermal unfolding at high temperature (top). The unfolding of the protein at high temperature takes up heat, the folding at the low temperature releases it. Similar primordial condensation reactions driven by thermal-cycling are proposed for other substrates during the origin of life: the reactions include other phosphorylations and the synthesis of peptide bonds.

from proton transfer across the membrane. F_1 is itself composite and contains three α-subunits and three β-subunits, the site of ATP synthesis (Abrahams *et al.*, 1994). Binding of nucleotides such as ADP and ATP increases the thermal unfolding temperature (T) of $\sim$330°K of the enzyme by about $\sim$7.5°K (ΔT). The heat (ΔH) required for unfolding the subunits is $\sim$6.8 eV (660 kJ mol^{-1}) (Wang *et al.*, 1993; Villaverde *et al.*, 1998). Today's ATP synthase is a large, complex, efficient and well regulated enzyme (Oster and Wang, 2000) that must have undergone a long evolution from much simpler progenitors.

The proposed primordial progenitor consisted of a single protein that worked as heat engine during thermal cycling. Being the direct progenitor of the β-subunit of F_1, it has been named pF_1 (Muller, 1995). Similar to the binding change mechanism, pF_1 formed strongly bound ATP from ADP, but it released this ATP by thermal unfolding (Figure 3b). The maximum free energy that this heat engine can produce equals

$$\Delta H(\Delta T/T) = 0.16\ \text{eV}\,(15\ \text{kJ}\,\text{mol}^{-1}),$$

calculated from the values for the contemporary ATPsynthase given above. This 15 kJ mol^{-1} is the right magnitude for the synthesis of a phosphodiester or peptide bond. For an early pF_1 the values of ΔH and ΔT may have been more favorable, resulting in a higher free energy gain.

The simplicity of the pF_1 mechanism can be further applied. In modeling the origin of life one strives for parsimony in enzymes and enzyme mechanisms (Benner *et al.*, 1989). Whereas today's enzymes are highly substrate specific, it has been proposed that primordial enzymes were not, and that they had wide specificity at the cost of low reaction rate (Black, 1970). Today, NTPases that contain the P-loop sequence present in F_1 still account for 10–18% of the predicted gene products in the sequenced prokaryotic and eukaryotic genomes (Iyer *et al.*, 2004), and thus the universal presence of these short P-loop sequences is consistent with a simple, generally phosphorylating pF_1 as a first enzyme. It is assumed that pF_1 in addition to broadly specific phosphorylations also could condense amino acids and peptides to new peptide bonds.

This generalization to peptide bond synthesis is based on a similarity between phosphoanhydride bonds—such as in ATP—and peptide bonds. Only in water do proteins and nucleic acids have a higher free energy than their constituent monomers. Under dry conditions the free energies are equal (DeMeis, 1989; Muller, 1995). The binding change mechanism makes use of this equality to synthesize the strongly bound ATP from strongly bond ADP in the dry enzymatic cleft of ATP synthase. Peptide bond synthesis in the enzymatic cleft of pF_1 would occur by the same mechanism of local dehydration.

Regular chemical reactions result in a loss of free energy. They are exergonic. In contrast, thermosynthesis effects the endergonic synthesis of high-energy products, which considerably simplifies the modeling of primordial metabolism, as less or shorter metabolic pathways are needed. The general primordial energy generating mechanism is thus identified as the binding of a substrate in a dehydrated local environment, followed by its conversion into a product with similar free energy in that local environment, but a higher free energy in water. The higher free energy makes direct release impossible. By using a thermal cycle for the release, a simple mechanism is obtained for the conversion of thermal energy into free energy by a single protein machine that indeed performed 'dehydrating condensation reactions in aqueous solution' (Calvin, 1969). The simple metabolism, carried by a single enzyme, permits a model for the emergence of the genetic machinery that is simple as well (Muller, 2005).

Discussion

The ubiquity of thermal energy and thermal gradients in the Universe makes it plausible that somewhere organisms use it as an energy source. On Earth thermal gradients and thermal cycling are also ubiquitous, but biological use has not been observed. Possible causes are:

1. for a still to be discovered reason, biological use of thermal energy is impossible;
2. the use is possible, but did not arise on Earth because light as energy source was common, directly usable and more powerful;
3. the use does occur on Earth today but has not been observed;
4. the use has occurred on Earth in the past, but thermotrophs have lost the competition to chemotrophs and phototrophs.

Arguments in support of (4) include the binding change mechanism of today's ATP synthase, and the widespread role of thermal cycling in germination, propagation and cell division (Muller, 1985), a part of the life cycle of many organisms. These are clear possible relics of a role of thermal cycling during the origin of life. Use of thermal energy may have been the stepping stone to photosynthesis and chemosynthesis, which then outcompeted thermosynthesis or pushed it into a few niches. Such natural selection is well known for species competing for limited resources (Conway Morris, 2003). This development is also supported by the environmental history of Earth, which started with sunlight being blocked by a haze and a temperature of the Archean ocean between 55 and 85°C (Knauth, 2005), and ended in today's – for photosynthesizers and for us – more benign planet.

Organisms using thermal energy as primary energy source may also still be present in niches such as Earth's crust, of which the exploration is just starting. Hydrothermal vents and mounds on the ocean floor are prime prospect habitats for thermosynthesizers, because of their large temperature differences with the surrounding cold ocean water.

Thermal energy is an especially suitable option for life on planetary bodies where other energy sources are limited. One suitable niche may be convection currents within planetesimals in the early Solar System (Young *et al.*, 2003). Other prime niches are today's ice-covered oceans of the moons of the outer Solar System such as Europa, Ganymede, and Titan (Spohn and Schubert, 2003). Large convection cells and internal cycling can be expected in these oceans due to endogenic activity and tidal stresses from the gravitational interaction with the central planet. Planetary bodies such as Venus, Mars, Io, and Triton should however also be considered. Any planetary body with endogenic heat, convecting fluids on its surface or in its subsurface is a potential abode of life based on thermal energy, even "run-away" planets or a planet such as Neptune with its interior liquid water ocean (Hubbard, 1984).

The absence of an accepted model for the origin of life makes it hard to point to places in the Universe where life may have arisen. Planets are generally considered habitable based on the possibility of photosynthesis, which needs sunlight. Alternative biological energy sources can however be imagined (Schulze-Makuch and Irwin, 2004). The removal of the requirement of sunlight for the origin and evolution of life significantly increases the number of potential environments where life could have arisen and where it still may be present, both in the Solar System and beyond (Muller, 2003).

Thermosynthesis may be detectable by either a top down method, applying thermal cycling to present day organisms, or by a bottom up method, applying it to model systems for the origin of life, such as clay with adsorbed biomolecules, lipid vesicles, and extraterrestrial material. Living on thermal cycling may be proven in the absence of nutrients and in the dark. The synthesis of high energy compounds during thermal cycling might be demonstrated using radioactive tracers such as ^{32}P or ^{14}C, or similar sensitive detection methods.

Conclusion

Given the ubiquity of thermal gradients and thermal cycling today and in the early Solar System, it would not be surprising if organisms have evolved that use it. Obstacles for a biological use of thermal energy as principal energy source, such as the low free energy gain in a cyclic thermal process seem surmountable. The use of thermal energy as a primary energy source and as a predecessor of photosynthesis could resolve many of today's open questions in regard to the origin of life.

References

Abrahams, J.P., Leslie, A.G.W., Lutter, R. and Walker, J.E.: 1994, Structure at 2.8 Å Resolution of F_1-ATPase from Bovine Heart Mitochondria, *Nature* **370**, 621–628.

Arata, H. and Parson, W.W.: 1981a, Enthalpy and Volume Changes Accompanying Electron Transfer from P870 to Quinones in *Rhodopseudomonas sphaeroides* Reaction Centers, *Biochim. Biophys. Acta* **636**, 70–81.

Arata, H. and Parson, W.W.: 1981b, Delayed Fluorescence from *Rhodopseudomonas sphaeroides* Reaction Centers. Enthalpy and Free Energy Changes Accompanying Electron Transfer from P870 to Quinones, *Biochim. Biophys. Acta* **638**, 201–209.

Arata, H. and Parson, W.W.: 1982, Enthalpy and Volume Changes Accompanying Electron Transfer from P_{870} to the Primary and Secondary Quinones in Photosynthetic Reaction Centers, in: Trumpower, B.L. (Ed.), *Function of Quinones in Energy Conserving Systems*. Academic Press, New York, pp. 199–212.

Benner, S.A., Ellington, A.D. and Tauer, A.: 1989, Modern Metabolism as a Palimpsest of the RNA World, *Proc. Natl Acad. Sci. USA* **86**, 7054–7058.

Black, S.: 1970, Pre-Cell Evolution and the Origin of Enzymes, *Nature* **226**, 754–755.

Boyer, P.D.: 1993, The Binding Change Mechanism for ATP-Synthase – Some Probabilities and Possibilities, *Biochim. Biophys. Acta* **1140**, 215–250.

Brasier, M.D., Green, O.R., Jepherat, A.P., Kleppe, A.K., Kranendonk, M.J., Lindsay, J.F., Steele, A. and Grassineau, N.V.: 2002, Questioning the Evidence for Earth's Oldest Fossils, *Nature* **416**, 76–81.

Callis, J.B., Parson, W.W. and Gouterman, M.: 1972, Fast Changes of Enthalpy and Volume on Flash Excitation of *Chromatium* Chromatophores, *Biochim. Biophys. Acta* **1015**, 180–188.

Calvin, M.: 1969, *Chemical Evolution*, Oxford U.P., Oxford, p. 159.

Case, G.D. and Parson, W.W.: 1971, Thermodynamics of the Primary and Secondary Photochemical Reactions in *Chromatium*, *Biochim. Biophys. Acta* **292**, 677–684.

Clarke, R.J.: 2001, The Dipole Potential of Phospholipid Membranes and Methods for its Detection. *Adv. Coll. Interface Sci.* **89–90**, 263–281.

Conway Morris, S.: 2003, *Life's Solution: Inevitable Humans in a Lonely Universe*, Cambridge University Press, Cambridge, U.K.

Cruz, J.A., Kanazawa, A., Treff, N. and Kramer, D.M.: 2005, Storage of Light-Driven Transthylakoid Proton Motive Force as an Electric Field ($\Delta\Psi$) Under Steady-State Conditions in Intact Cells of *Chlamydomonas reinhardtii*, *Photosynth. Res.* **85**, 221–233.

Davies, P.C.W. and Lineweaver, C.H.: 2005, Finding a Second Sample of Life on Earth, *Astrobiology* **5**, 154–163.

DeMeis, L.: 1989, Role of Water in Energy of Hydrolysis of Phosphate Compounds – Energy Transduction in Biological Membranes, *Biochim. Biophys. Acta* **973**, 333–349.

Goodwin, B.: 1994, *How the Leopard Changed its Spots: The Evolution of Complexity.* Charles Scribner's Sons, New York.

Gundersen, J.K., Jørgensen, B.B., Larsen, E. and Jannasch, H.W.: 1992, Mats of Giant Sulphur Bacteria on Deep-Sea Sediments due to Fluctuating Hydrothermal Flow, *Nature* **360**, 454–456.

Hubbard, W.: 1984. *Planetary Interiors*. Van Nostrand Reinhold, New York.

Iyer, L.M., Leipe, D.D., Koonin, E.V. and Aravind, L.: 2004, Evolutionary History and Higher Order Classification of AAA+ ATPases, *J. Struct. Biol.* **146**, 11–31.

Kauffman, S.A.: 1995, *At Home in the Universe: The Search for Laws of Self-Organization and Complexity*, Oxford University Press, Oxford.

Kelley, D.S., Karson, J.A., Blackman, D.K., Früh-Green, G.L., Butterfield, D.A., Lilley, M.D., Olson, E.J., Schrenk, M.O., Roe, K.K., Lebon, G.T., Rivizzigno, P., and the AT3-60 Shipboard Party: 2001, An off-axis hydrothermal vent near the Mid-Atlantic Ridge at 30°N, *Nature* **412**, 145–148.

Knauth, L.P.: 2005, Temperature and Salinity History of the Precambrian Ocean: Implications for the Course of Microbial Evolution, *Palaeogeography, Palaeoclimatology, Palaeoecology* **219**, 53–69.

Kompanichenko, V.N.: 1996, Transition of Precellular Organic Microsystems to a Biotic State: Environment and Mechanism, *Nanobiology* **4**, 39–45.

Lathe, R.: 2004, Fast Tidal Cycling and the Origin of Life, *Icarus* **168**, 18–22.

Lathe, R.: 2005, Tidal Chain Reaction and the Origin of Replicating Biopolymers, *International Journal of Astrobiology* **4**, 19–31.

MacDonald, R.C. and Simon, S.A.: 1987, Lipid Monolayer States and Their Relationships to Bilayers, *Proc. Natl. Acad. Sci.* **84**, 4089–4093.

Madigan, M.T., Martinko, J.M. and Parker, J.: 2000, *Brock Biology of Microorganisms*, 9th edition, Prentice Hall.

Moriyama, Y., Hiyama, S. and Asai, H.: 1998, High-Speed Video Cinematographic Demonstration of Stalk and Zooid Contraction of *Vorticella Convallari*. *Biophys. J.* **74**, 487–491.

Morowitz, H.J.: 1968, *Energy Flow in Biology*. Academic Press, New York

Muller, A.W. J.: 1985, Thermosynthesis by Biomembranes: Energy Gain From Cyclic Temperature Changes, *J. Theor. Biol.* **115**, 429–453.

Muller, A.W.J.: 1993, A Mechanism for Thermosynthesis Based on a Thermotropic Phase Transition in an Asymmetric Biomembrane, *Physiol. Chem. Phys. Med. NMR* **25**, 95–111.

Muller, A.W.J.: 1995, Were the First Organisms Heat Engines? A New Model for Biogenesis and the Early Evolution of Biological Energy Conversion, *Prog. Biophys. Mol. Biol.* **63**, 193–231.

Muller, A.W.J.: 1996, Hypothesis: The Thermosynthesis Model for the Origin of Life and the Emergence of Regulation by Ca^{2+}, *Essays Biochem.* **31**, 103–119.

Muller, A.W.J.: 2003, Finding Extraterrestrial Organisms Living on Thermosynthesis, *Astrobiology* **3,** 555–562.

Muller, A.W.J.: 2005, Thermosynthesis as Energy Source for the RNA World: A Model for the Bioenergetics of the Origin of Life, *BioSystems* **82**, 93–102.

Muller, A.W.J. and Schulze-Makuch, D.: 2006, Sorption Heat Engines: Simple Inanimate Negative Entropy Generators, *Physica A*, in press (www.arxiv.org/physics/0507173).

Nisbet, E.G. and Sleep, N.H.: 2001, The Habitat and Nature of Early Life, *Nature* **409**, 1083–1091.

Oster, G. and Wang, H.: 2000, Why is the Mechanical Efficiency of F_1-ATPase so High? *J. Bioenerg. Biomemb.* **32**, 459–469.

Rosing, M.T.: 1999, ^{13}C-Depleted Carbon Microparticles in >3700-Ma Sea-Floor Sedimentary Rocks from West Greenland, *Science* **283**, 674–676.

Round, F.E.: 1981, *The Ecology of Algae*, Cambridge U.P., Cambridge

Russell, M.J. and Hall, A.J.: 1997, The Emergence of Life From Iron Monosulphide Bubbles at a Submarine Hydrothermal Redox and pH Front, *J. Geol. Soc. London* **154**, 377–402.

Schmidt-Nielsen, K.: 1990, *Animal Physiology: Adaptation and Environment*, 4th ed., Cambridge U.P., Cambridge, p. 521.

Schopf, J.W.: 1993, Microfossils of the Early Archean Apex Chert; New Evidence of the Antiquity of Life, *Science*, **260**, 640–645.

Schopf, J.W. and Packer, B.M.: 1987, Early Archean (3.3 billion to 3.5 Billion-Year-Old) Microfossils from Warrawoona Group, Australia, *Science* **237**, 70–73.

Schulze-Makuch, D. and Irwin, L.N.: 2002, Energy Cycling and Hypothetical Organisms in Europa's Ocean, *Astrobiology* **2**, 105–121.

Schulze-Makuch, D. and Irwin, L.N.: 2004, *Life in the Universe: Expectations and Constraints*, Springer, Berlin, New York.

Schulze-Makuch, D., Dohm, J.M., Fairén, A.G., Baker, V.R., Fink, W. and Strom, R.G.: 2005a, Venus, Mars, and the Ices on Mercury and the Moon: Astrobiological Implications and Proposed Mission Designs, *Astrobiology* **5**, 778–795.

Schulze-Makuch, D., Irwin, L.N., Lipps, J.H., LeMone, D., Dohm, J.M. and Fairén, A.G.: 2005b, Scenarios for the Evolution of Life on Mars. Special Edition on Early Mars of *Journal of Geophysical Research – Planets* 110, E12S23, doi:10.1029/2005JE002430

Shihira-Ishikawa, I. and Nawata, T.: 1992, The Structure and Physiological Properties of the Cytoplasm in Intact Valonia Cell. *Jpn. J. Phycol. (Sorui)* **40**, 151–159.

Spohn, T. and Schubert, G.: 2003, Oceans in the Icy Galilean Satellites of Jupiter? *Icarus* **161**, 456–467.

Stetter, K.O.: 1998, Hyperthermophiles and their Possible Role as Ancestors of Modern Life, in: Brack A. (Ed.), *The Molecular Origins of Life*, Cambridge U.P., pp. 315–335.

Strom, R.G., Malhotra, R., Ito, T., Yoshida, F. and Kring, D.A.: 2005, The Origin of Planetary Impactors in the Inner Solar System, *Science* **309**, 1847–1850.

Takai, K., Komatsu, T., Inagaki, F. and Horikoshi, K.: 2001, Distribution of Archaea in a Black Smoker Chimney Structure, *Appl. Environm. Microbiol.* **67**, 3618–3629.

Tivey, M.K., Bradley, A.M., Joyce, T.M. and Kado, D.: 2002, Insights Into Tide-Related Variability at Seafloor Hydrothermal Vents from Time-Series Temperature Measurements, *Earth Planet. Sci. Lett.* **202**, 693–707.

Van Dover, C.L. and Lutz, R.A.: 2004, Experimental Ecology at Deep-Sea Hydrothermal Vents: A Perspective, *J. Exp. Mar. Biol. Ecol.* **300**, 273–307.

Villaverde, J., Cladera, J., Hartog, A., Berden, J., Padros, E. and Dunach, M.: 1998, Nucleotide and Mg^{2+} dependency of the thermal denaturation of mitochondrial F_1-ATPase, *Biophys. J.* **75**, 1980–1988.

Viswanath, V., Story, G.M., Peier, A.M., Petrus, M.J., Lee, V.M., Hwang, S.W., Patapoutian, A., and Jegla, T.: 2003, Opposite Thermosensor in Fruitfly and Mouse, *Nature* **423**, 822–823.

Wang, Z.-Y., Freire, E. and McCarthy, R.E.: 1993, Influence of Nucleotide Binding Site Occupancy on the Thermal Stability of the F_1 Portion of the Chloroplast ATPsynthase, *J. Biol. Chem.* **268**, 20785–20790.

Young, E.D., Zhang, K.K. and Schubert, G.: 2003, Conditions for Pore Water Convection within Carbonaceous Chondrite Parent Bodies – Implications for Planetesimal Size and Heat Production. *Earth Planet. Sci. Lett.* **213**, 249–259.

Zemansky, M.W.: 1968, *Heat and Thermodynamics*, McGraw Hill, New York.