

Thermosynthetic Life

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Abstract Two categories of life are currently recognized—chemosynthetic and photosynthetic—indicating their principal free energy resource as either chemicals or electromagnetic radiation. Building on recent developments in thermodynamics, we posit a third category of life—*thermosynthetic life* (TL)—which relies on environmental heat rather than traditional free energy sources. Since thermal energy is more abundant than chemicals or light in many settings, thermosynthesis offers compelling evolutionary possibilities for new life forms. Based on variants of standard cellular machinery, a physical model is proposed for the conversion of thermal energy into biochemical work. Conditions favorable to thermosynthetic life and prospects for its discovery are assessed. Terrestrially, deep-subsurface unicellular anaerobic superthermophiles are deduced to be likely TL candidates.

Keywords Second law of thermodynamics · Entropy · Extremophiles · Thermophiles · Astrobiology · Exobiology

1 Introduction

Understanding *life* at a basic physical level is the grail of biochemistry and biophysics [1–3]. The necessary conditions for it remain elusive and its ubiquity in the universe continues to generate lively debate [4–6]. It is generally agreed, however, that life entails nonequilibrium physical and chemical processes that require the steady input of energy.

Terrestrial life is commonly characterized by the type of free energy that sustains it. Currently, two general categories are recognized—*chemosynthetic* and *photosynthetic* life—indicating that their sources of free energy are either primarily chemical

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and electromagnetic (visible, infrared, or ultraviolet light), respectively. In this paper, these will be termed *free energy life* (FEL). There are many types of free energy available in nature, including electrostatic, magnetic, gravitational, vacuum energy, and relativistic rest mass energy. For good evolutionary reasons—probably having to do with the necessities of cell size, temperature, nutrient energy density and quantum chemistry—FEL has chosen chemicals and light over these other energy sources.

Conspicuously absent from this list is an energy reservoir far more plentiful in most environments than either chemical or electromagnetic sources: thermal energy.¹ Certainly, all life forms depend to some degree on environmental heat to remain warm and biochemically viable, but thermal energy (heat) per se is not considered *free energy* because it cannot be exploited on a cellular level to run biochemical reactions irreversibly. Heat, by itself, can perform work in a cycle only in conjunction with a temperature gradient, so as to power a heat engine. On cellular size scales, only very small thermal gradients are possible, ones generally too small to be useful for life. Most cells are sufficiently small that heat conduction alone renders them nearly isothermal with their environments such that their theoretical maximum efficiencies as heat engines, given by Carnot efficiency ($e = 1 - T_{\text{cold}}/T_{\text{hot}}$), is practically zero. Thus, standard FEL endures an unfortunate situation: It is surrounded by a nearly limitless reservoir of thermal energy, but it cannot effectively exploit it for useful biological work.

In this paper we build on recent results in thermodynamics and statistical mechanics to explore the hypothesis that life might be able to exploit environmental heat to sustain itself. Life able to rectify thermal energy solely and cyclically into useful biological work will be called *thermosynthetic life* (TL).

An ostensive injunction against the possibility of TL is delivered by the second law of thermodynamics. The second law can be stated in a number of ways.² Perhaps the most salient is the Kelvin-Planck form: *No thermodynamic cycle is possible whose net result is the conversion of heat solely into work.*

The second law is one of the touchstones of science, supporting chemistry, physics, biology, and engineering. In its 150-year history, no experimental violation of it has been recognized by the scientific community and until recently few theoretical challenges to it have been tolerated in the physical literature. In the last ten years, however, over two dozen challenges, by several research groups worldwide, have appeared in the refereed scientific literature [11–62]; an international conference was convened to discuss them [63]; other mainstream scientific conferences have begun to reserve special sessions for their consideration [64–66]; the journal *Entropy* devoted an entire issue to them [67]; and quite recently a monograph reviewing their status has been published by a major scientific press [10]. Most challenges are theoretical, but many are laboratory testable; several of the latter have had their primary physical effects experimentally corroborated [46–62]. Bona fide second law violation experiments are on the horizon [61]. Taken en masse, these developments render

¹One can show that the thermal energy content of typical organisms is comparable to or greater than their daily free energy requirements and that the heat content of their immediate surroundings is orders of magnitude greater than the combined chemical and electromagnetic energy resources available to them.

²There are about a dozen common statements of the second law, not all of which are equivalent. The interested reader is directed to several compilations of them [7–10].

untenable the long-held presumption of second law inviolability and open the door to scientific inquiry into its potential violation. Thermosynthetic life is a compelling theoretical test case.

A number of second law challenges have been inspired by biological systems. Work in this area dates back 25 years to the seminal proposals of Gordon [11–16] on cell membranes operating as Maxwell demons [68, 69]. More recently, several quantum theoretic challenges by Čápek et al. have been inspired by membrane ion pumps [17–21]. Crosignani and Di Porto speculate—based on their theoretical investigations of classical, mesoscopic adiabatic pistons—that the second law should fail at the characteristic scale lengths of cells [28–32].

In this paper the hypothesis is explored that life—i.e., thermosynthetic life—can exploit second law violating processes. This discussion will be strictly theoretical since there is currently no experimental evidence that life violates the second law, either macroscopically or microscopically. Quite the contrary, life is often considered to be a strong ally of the second law since biotic chemicals typically generate far more entropy than they would otherwise create in an abiotic state.³

It is estimated that since the emergence of life on Earth roughly 3.8–4 billion years ago, on the order of a billion species have existed and that, of these, perhaps 10 million currently exist. Of this extant 1% of total species, perhaps 20% have been identified by name. Of those identified, few have been studied well enough to make general claims about their thermodynamics; however, those that have been carefully studied have shown compliance with the second law. In highly studied species—for instance, *E. coli*, *C. elegans*, mice, chimpanzees, men—only a small fraction of proteins and biochemical pathways have been thoroughly studied. (Human are estimated to contain roughly 25,000 genes and about 10^5 – 10^6 proteins of which perhaps 1–10% have been positively identified.) Despite this apparent dearth of biochemical knowledge, there is significant biochemical commonality among species such that comprehensive study of a few should give an overview of the many. Nevertheless, our current understanding of biology and biochemistry across all species is not comprehensive enough to rule conclusively that *all* biological processes, structures, and systems comply with the second law.

From an evolutionary standpoint, the case for second law subversion is compelling. The exigency of natural selection suggests that if subverting the second law confers an evolutionary reproductive advantage and if the second law can in fact be subverted, then Nature in its clever resourcefulness would with high probability achieve this end. Since there are several scenarios in which *thermosynthetic life* (TL) might compete well with or even outcompete ordinary *free-energy life* (FEL), it is reasonable to consider the case for biological second law subversion.

In the remainder of this paper, we present the case for thermosynthetic life. In Sect. 2, its likely characteristics are deduced from thermodynamic and physical considerations. In Sect. 3, a scenario is developed, based on plausible biochemical machinery, whereby the second law might be undermined on a cellular level. In Sect. 4, potential habitats for thermosynthetic life are considered and prospects for experimental searches are assessed.

³Consider, for example, an assembly of biomolecules (humans) able to create and detonate hydrogen bombs, which are copious entropy producers.

2 Thermodynamic Constraints on TL

Basic characteristics of thermosynthetic life are indicated from thermodynamic considerations. If it exists, TL is probably small and unicellular. Unicellular life is more able to exploit thermal energy than multicellular life because it has an intrinsically greater surface-to-volume ratio and, therefore, has greater access to thermal energy per cell than does multicellular life. The lower limit to the size of organisms is a subject of debate.⁴ Recent studies suggest that it may be as small as 20 nm [70]. At the temperature and size scales typical of individual cells (10^{-5} – 10^{-7} m; $T \sim 250$ – 350 K), the primary heat transfer mechanism is conduction; far less important are convection and radiation. If TL is multicellular, it must have a sufficiently large surface-to-volume ratio to accommodate its energy needs, as well as the means to transport this heat efficaciously to its interior bulk.

Life forms must compete both for material and energy resources. Against FEL, TL will likely be outcompeted under everyday terrestrial conditions where rich free-energy sources are abundant, e.g., sunlight, plant and animal tissue, or raw energetic chemicals spewing from hydrothermal vents. By definition, pure TL would eschew these and so would likely be at an energetic and evolutionary disadvantage. Moreover, as later analysis will show, subversion of the second law possibly involves substantial and intricate biochemical machinery which, though it might be related to existing machinery, is probably less likely to evolve spontaneously than FEL machinery. After all, there are far more ways to comply with the second law than to break it—as evidenced by the utter failure of humans to do so up to now. In other words, for TL to evolve there must probably be strong evolutionary pressures favoring it.

Thermosynthetic life might best compete against FEL—or simply avoid competition altogether—in free-energy poor environments; if so, it is likely to be anaerobic and isolated geologically and hydrologically from chemosynthetic and photosynthetic life. This suggests TL might be best suited to life deep inside the earth. (In recent years it has become apparent that deep-rock microbes enjoy great diversity and might represent significant biomass [71].) These deep sub-surface environments can also be quite stable so as to allow TL to evolve and thrive without direct competition from FEL for long periods of time.

Thermosynthetic life might have an evolutionary edge in high-temperature environments. First, higher temperatures imply higher thermal power densities with which to drive biochemical reactions. Second, for reasons to be discussed in Sect. 3, high temperatures favors some second law violating mechanisms [52–54, 59, 60]. Again, deep subsurface environments fit the bill. Temperatures rise with increasing depth in the Earth at a rate of roughly 1.5 – 3×10^{-2} K/m. At depths of 5 km temperatures approach 400 K. If it exists in deep rock, TL is likely superthermophilic and hyperbarophilic. In deep-sea hydrothermal vent environments, the high pressures augment thermophilic tendencies by raising the boiling point of water and by compressing molecular structures that might otherwise thermally disintegrate. In the laboratory, microbes have survived exposure to pressures of 1.6 GPa (1.6×10^4 atm). Microbes have been discovered in continental rocks down to depths of 5.2 km [72].

⁴Viruses, viroids, and prions are excluded from this discussion.

The limit to the depth of life is likely set not only by temperature and pressure, but also by the pore sizes between rock grains, which are reduced at high pressures. It is expected that pressure, temperature and pore size would disallow carbon-based life below about 10 km.

To summarize, if thermosynthetic life exists, it is likely to be small, unicellular, anaerobic, hyperbarophilic superthermophiles confined to free-energy poor environments, well isolated from FEL in long-term stable locations, perhaps in the deep subsurface.

Deep rock microbes (Archaea), situated at and beyond the fringes of where FEL is known to survive, are attractive TL candidates. Archaea are among the most ancient life forms; current molecular evidence based on RNA analysis places them near the base of the tree of life.⁵ Among the most ancient archaea are hyper- and superthermophiles, suggesting—but certainly not proving—that life may have originated in high temperature environments, like deep-sea marine vents or in the earth's crust.

The high-temperature record for culturable microbes is $T = 394$ K, set by *Strain 121*, an Fe(III)-reducing archaea recovered from an active “black smoker” hydrothermal vent in the Northeast Pacific Ocean [73]. It grows between 85° and 121°C—temperatures typically used in autoclaves to sterilize laboratory equipment and samples. The upper temperature limit for microbes has been estimated as high as 475 K (200°C); more conservative estimates place the temperature limit closer to 425 K (150°C) [74–80].

Archaea and bacteria have many special adaptations for survival at high temperatures. Unlike bacteria and eukaryotes which have lipid bilayer membranes, archaea have monolayer lipid membranes (ester cross-linked lipids) that resist thermal separation. Thermophiles also employ stiff, long-chain carotenoids that span their membranes, thereby reinforcing them against thermal separation. Carotenoids are highly conjugated organics that are also known for good electrical conductivity via long-range, delocalized molecular orbitals. They can mediate direct charge transport across membranes.

Another TL scenario is that standard FEL life harvests thermal energy as a supplement to standard free energy sources, or resorts to it when its traditional free energy sources are cut off. This suggests that long-entombed and dormant microbes might also be TL candidates. For example, bacteria have been reported to remain viable for millions of years trapped in ancient salt crystals essentially absent of free energy sources and nutrients [81].

Thermosynthetic organisms would not necessarily be expected to arise *ex nihilo* from abiotic chemicals, but one can envision strong evolutionary forces by which they could evolve from standard FEL. Free energy life, wherever it first evolved—deep-ocean vents, surface, or deep rock—would naturally spread to all possible habitable regions. Where conditions were not initially favorable, in time, evolutionary forces would reshape the organism as far as possible. FEL would extend deeply into subsurface environments—as has been discovered [71, 72, 79]—down to the biochemical limits of heat and pressure, and to the lower limits of material and free energy

⁵At present, three domains are generally recognized: eukaryotes (cells with nuclei), bacteria and archaea (cells without nuclei); the latter two display superthermophilicity.

resources. At the limits of free energy resources FEL would face an evolutionary imperative to convert some (or all) of its cellular machinery over to the reclamation of thermal energy such as to push into regions uninhabitable by its competitors. As will be discussed below, variants of standard cellular machinery (membranes, carotenoids, enzymes) appear conducive to this enterprise.

3 Scenario for Second Law Violation

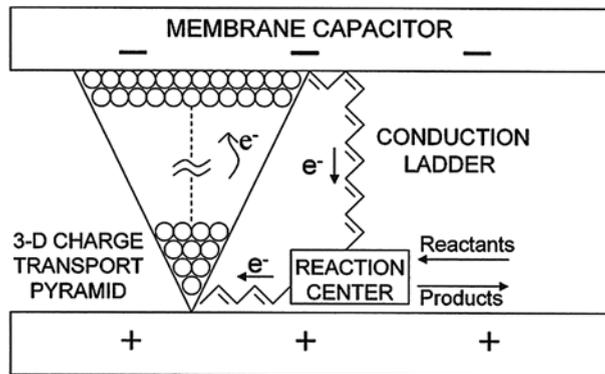
This section is the crux of the paper. Here it is argued that plausible variants of common cellular machinery might convert heat into biochemical energy and thereby subvert the second law. This draws from a class of challenges investigated at the University of San Diego (USD) [82–84]. It relies on electrostatic potential energy stored in charged molecular bilayers, like cell membranes. Cell membranes have inspired other second law challenges. For instance, the proposals by Gordon—which posit a breakdown of the principle of detailed balance and, by extension, the second law—were inspired by cell membrane transport channels [11–16]. More recently, Čápek et al. raised a series of highly theoretical quantum mechanical challenges also positing breakdown of detailed balance, inspired by cellular ion pumps [17–23]. These demonstrate that, at a quantum mechanical level, fluxes can spontaneously transport thermal energy or particles against gradients in temperature and chemical potential. Combined with Gordon’s models, they present a formidable case against the inviolability of detailed balance at equilibrium and, by extension, the second law. We now proceed with our biomembrane system, which also demonstrates failure of detailed balance.

We propose as a biochemical model for second law subversion⁶ the five-piece biochemical system depicted in Fig. 1. It consists of: (1) a membrane capacitor; (2) a 3-D pyramidal array of charge transport molecules; (3) an electrically conducting molecular ladder spanning the membrane from pyramidal base to vertex; (4) a chemical reaction center for utilization of superthermal energy; and (5) a small number of mobile charges (electrons or protons) that circulate through the system. Each of these has known biological analogs.

Each piece of this system (Fig. 1) is individually developed below. Briefly, the process for conversion of ambient heat to biochemical work is as follows. A mobile electronic charge (electron or proton) thermally diffuses up through the *charge transport pyramid* against an electrostatic potential gradient created by permanently-separated charges embedded in the faces of the planar *membrane capacitor*. The superthermally energetic charge then falls back through the entire membrane potential in a single quantum transition, down the molecular *conduction ladder*. The electrostatic energy released in this transition is utilized in the *reaction center* to drive biochemical reactions, that is, to forge high-energy products from low-energy reactants. The electron current in this reaction cycle is unidirectional due to the diodic and electronic switch behaviors of the conduction ladder and reaction center.

⁶We emphasize that this, at best, is a plausibility argument since, if second law subversion is possible, Nature will surely have evolved a cleverer scheme.

Fig. 1 Schematic of proposed biochemical machinery for thermosynthetic life. Charge cycles clockwise: diffusively up through the pyramid and ballistically down the conduction ladder through the reaction center, where high-energy chemical products are formed



This process constitutes a challenge to the second law because thermal energy (heat) is rectified to drive an irreversible chemical reaction backwards. Heat is effectively transformed solely into work in a cyclic manner, thereby compromising the Kelvin-Planck formulation of the second law. From a chemical perspective, this process represents a steady-state nonequilibrium and a violation of the principle of detailed balance by continuously creating high free-energy products from low free-energy reactants. Other second law challenges have also undermined detailed balance [11–26, 59, 60]. We now consider more carefully the individual components of the model in Fig. 1.

3.1 Membrane Capacitor

In electronics the primary device for storing electrostatic energy is the capacitor. A capacitor stores charge (Q) at an electrostatic potential (V), or equivalently, it stores potential energy in its electric field (electrostatic energy density ρ is given by $\rho = \frac{\epsilon_0}{2} E^2$, where ϵ_0 is the permittivity of free space and E is electric field strength (V/m)). A parallel plate capacitor can be as large as a flat-bottomed storm cloud above the planar earth, or as small as a cell membrane, as in the capacitive depolarization of neurons.

The capacitance of the parallel plate capacitor is $C_{pp} = Q/V = \frac{\epsilon_0 \kappa A}{d}$, where Q is the total charge on the capacitor, κ is the dielectric constant of the medium between the plates, A is the plate area, and d is the plate separation, which in the infinite plane approximation, satisfies: $\sqrt{A} \gg d$. The electrostatic potential energy (\mathcal{E}) stored in the capacitor can be expressed in several ways, including: $\mathcal{E} = \frac{1}{2} QV = \frac{1}{2} CV^2 = \frac{1}{2} \epsilon_0 \kappa E^2 Ad$.

The cell membrane is one of life's most basic structures and, in principle, it can store appreciable amounts of electrocapacitive energy. Particulars of cell membranes vary considerably across life forms so we will consider archetypical membranes consisting of ambipolar lipid layers. Simple polar lipids have a charged functional group on one end of a long organic skeleton. These can self-assemble end-to-end to form a bilayer, as shown in Fig. 2a. Polar molecules (e.g., water) outside the hydrophilic ends can stabilize the membrane, trapping the hydrophobic, non-polar organic skeleton within. In principle, opposite sides of the membrane can support permanent opposite surface charge densities. The membrane we envision here need not reside on

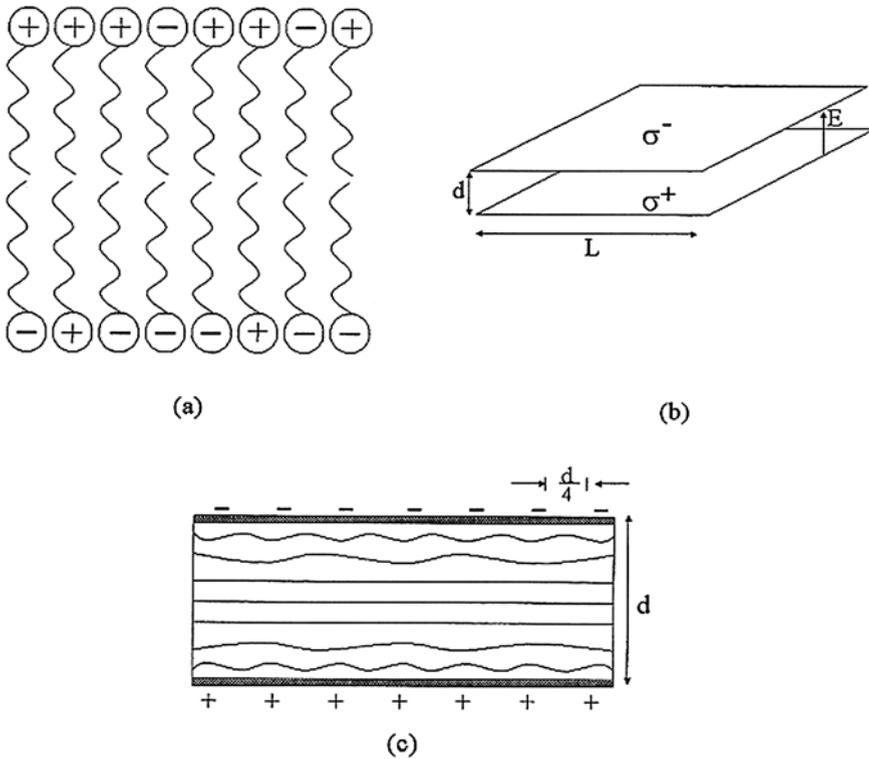


Fig. 2 Biomembrane capacitor: **a** Schematic of biomembrane lipid bilayer; **b** Lipid bilayer as parallel plate capacitor; **c** Equipotentials in biomembrane with finite point charges separated by $\frac{d}{4}$

the outer surface of a cell; in principle, it could be sequestered in the interior as a separate entity.

Consider a planar section of membrane (Fig. 2b) with fixed surface charge density σ . (These charges might be anions or cations fixed on the polar ends of the phospholipids.) In the infinite plane approximation ($\sqrt{A} \simeq l \gg d$) the membrane acts like a charged capacitor (Fig. 2b). For biomembranes, typical scale lengths are $l \sim 10^{-6}$ m and $d \sim 10^{-8}$ m. For our model membrane, let $l = 2 \times 10^{-6}$ m and $d = 10^{-7}$ m.

The maximum charge density and steady-state voltage drop supportable by a biomembrane can be estimated from the dielectric strength and compressive strength of typical organics. If the inwardly-directed electrostatic pressure due to $\pm\sigma$ exceeds the material compressive strength, the membrane will collapse; if the electric field exceeds its dielectric strength, it will arc through. (The dielectric strength and compressive strength for thin samples can significantly exceed those of thick bulk samples.) Conservatively using bulk values for typical organics, the membrane dielectric strength is taken to be $E_{\max} = 10^7$ V/m, dielectric constant $\kappa = 3$, and compressive strength 10^7 N/m². With these, one finds that the maximum charge density supportable on the membrane surface to be roughly $\sigma_{\max} = \kappa\epsilon_0 E_{\max} = 2.5 \times 10^4$ C/m² = 1.5×10^3 e⁻/μm². (Estimates from compressive strength yields

larger σ_{\max} .) This σ implies that the distance between individual charges is roughly $\frac{1}{\sqrt{\sigma}} \simeq 2.5 \times 10^{-8} \text{ m} \simeq \frac{1}{4}d$; thus, the majority of the molecules comprising the membrane need not contribute to the net surface charge. The electrostatic equipotentials are fairly parallel near the midplane of the membrane and are undulatory near the surfaces; likewise the electric field vectors are parallel in the interior and less so near the surfaces (Fig. 2c). (Note that archaean cross-linked monolayer membranes would be relatively good at retaining capacitive charge separation since membrane molecules would be less likely to invert than standard bilayer lipids in bacteria and eukaryotes. Their cross-linking also adds structural strength.)

The maximum potential drop across the model membrane surfaces will be on the order of $V_m \simeq E_{\max}d = \frac{\sigma_{\max}d}{\kappa\epsilon_o} = 1 \text{ V}$; for this model, we find $V_m = 0.8 \text{ V}$. (This agrees quantitatively with common membrane potentials, scaled to membrane thickness $d = 10^{-7} \text{ m}$.) Were an electronic charge to fall through this potential, it would have roughly the energy required to drive typical chemical reactions: $qV_m = \Delta\mathcal{E} \sim 0.5\text{--}4 \text{ eV}$. Electrons and protons would be the most convenient mobile charges for this system; they are standard currency in biochemical reactions. Low-energy chemical reactions have been exploited by life. For instance, forms of bacterial chlorophyll have spectral absorption in the near IR, corresponding to energies of roughly 1 eV. The hydrolysis of ATP (adenosine triphosphate) into ADP (adenosine diphosphate) releases roughly 0.56 eV of free energy. ATP is the primary energy releasing molecule in most cells.

In principle, multiple membranes might be stacked in electrical series and self-triggered sequentially—the high energy charge from a previous step triggering the subsequent one—so as to create a series-capacitive discharge with resultant energy in multiples of a single membrane energy,⁷ $\Delta\mathcal{E}_m$. Alternatively, each low-energy discharge might create low-energy chemical intermediates that are brought together to drive a single, more energetic chemical reaction, similarly to how ATP is utilized in cells. In this way, the energy necessary to drive even high-energy chemical reactions might obtain.

The membrane capacitor need not be planar; actually, more biologically plausible and advantageous geometries would be the cylinder or sphere. The parallel plate geometry is used for clarity and analytic tractability; the primary physical results do not differ for the other geometries. The capacitance of two concentrically-nested spheres (radii r_1, r_2 with $r_2 > r_1$) filled with dielectric is: $C_{\text{sph}} = \frac{4\pi\epsilon_o\kappa r_2 r_1}{r_1 + r_2}$. The capacitance of two axially-nested cylinders of length L ($r_2 > r_1$, with $L \gg r_{1,2}$) is $C_{\text{cyl}} \simeq 2\pi\epsilon_o L \ln(\frac{r_2}{r_1})$. For comparable length scales and construction materials, these geometries will sustain comparable electric fields and store comparable charge and electrostatic energy as the parallel plate geometry; but, additionally, the former are physically more compact and they more closely resemble cellular organelles. The spherical case is especially attractive because it has no fringing electric fields⁸ and, via Gauss' law, the electric field both inside ($r < r_1$) and outside ($r > r_2$) vanishes.

⁷Many species are known to utilize series-capacitive discharge, e.g., electric eels, rays, and catfish, achieving up to hundreds of volts in total potential.

⁸We assume smooth distribution of charge and equal total charge on inner and outer spherical surfaces.

As a result, when charged, the spherical capacitor will not attract ions, polar, or polarizable molecules from the surrounding solution, which could reduce the interior electric field.⁹ This is essentially a hollow, spherical, charge double-layer micelle: a vesicle. Micelles and vesicles are well known in biotic and abiotic settings.

In summary, the membrane capacitor represents an appreciable reservoir of ready electrostatic potential energy which, in conjunction with the charge transport pyramid below (Sect. 3.2), offers the means to rectify heat (kT) into superthermal energy; i.e., ($qV_m \gg kT$).

3.2 Charge Transport Pyramid

It is requisite for Life that at least some biochemical reactions be superthermal ($\Delta\mathcal{E} \gg kT$) because if all reactions can be thermally driven equally in the forward and reverse directions, none are irreversible and the organism will find itself at thermal equilibrium—and dead. (Also, unless bond energies are large ($\Delta\mathcal{E}_{\text{bond}} \gg kT$), molecules tend to thermally disintegrate.) A 0.8 eV potential energy drop across the membrane far exceeds the typical thermal energy associated with life (kT (300 K) $\sim \frac{1}{40}$ eV $\sim \frac{1}{30} V_m$). At first glance, it seems unlikely that thermal energy alone could drive charges up such a large electrostatic potential at room temperature, but if accomplished in probabilistically favorable steps it is physically plausible.

To see how this can be accomplished, let the model membrane be embedded with charge transporting molecules arranged in a 3-D pyramidal structure, as depicted in Fig. 3a. The actual molecular structure is unspecified—it could be simply a conductive-diffusive molecular matrix—but for the sake of visualization we consider it to be composed of rotary molecules, each with charge acceptor-donor (A-D) sites. The transport molecules spin freely, driven by thermal energy. When two A-D sites meet a charge can be transferred between them, with minimal energy of activation. This is taken to be a random process. Once charged, the electric force within the membrane will tend to constrain the rotor against charge movement up the potential gradient, as expected, but if the step sizes are small ($\Delta V \leq kT/q$) and if the transfer probability favors diffusion up the potential gradient either by favorable multiplicity of states, or as in this case, by a favorable multiplicity of transfer molecules in the direction up the gradient (Fig. 3b), then appreciable transport can occur by diffusion alone.¹⁰

Charge transport via diffusion can be placed on more quantitative footing. Let the membrane have area $l^2 \sim 4 \times 10^{-12}$ m² and let the area of an individual A-D molecule be $\delta^2 = (10^{-9}$ m)². In the membrane depicted in Fig. 2c, the base of the molecular pyramid accommodates roughly $\frac{l^2}{\delta^2} \sim 4 \times 10^6$ molecules, the vertex accommodates one; the pyramid consists of roughly 20 molecular layers. (This is consistent

⁹One complication of the non-planar geometries is that they will have electric field gradients inside ($r_1 < r < r_2$) that will act on polar or polarizable molecules via the $(\mathbf{p} \cdot \nabla)\mathbf{E}$ force. This complicates the analysis beyond that of the parallel plate case, but does not obviate the principal results.

¹⁰We emphasize that a charge's motion is a diffusive, probabilistic process. Generally, a charge will not move straight up the pyramid; rather, it will move randomly up and down many times before arriving occasionally (and transiently) at the top.

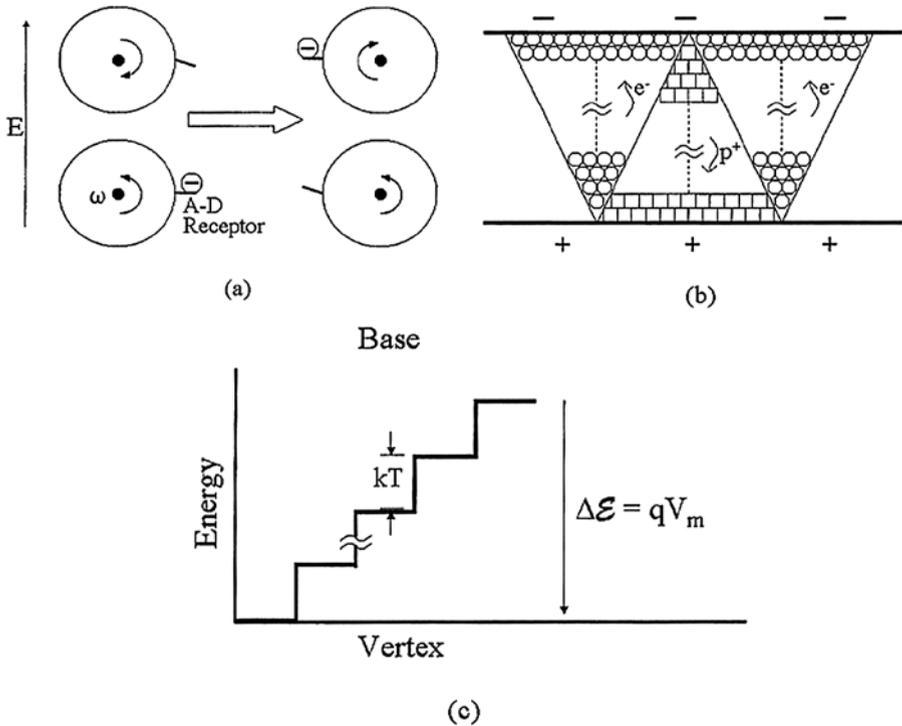


Fig. 3 Charge transport in a biomembrane: **a** Rotary molecules transferring charge; **b** Diffusive transport of electrons and protons between membrane faces by A-D molecules, up electrostatic potential gradients; **c** Energy diagram for charge thermal transport and quantum transition in biomembrane

with a doubling of the number of transport molecules per layer.) At $T = 400$ K, the electrostatic potential energy increase per level in the pyramid is roughly $q\Delta V \simeq kT$, thus permitting charges to rise comfortably upwardly against the gradient by thermal diffusion.

The probability of an electron being found in the j th tier of the pyramid (p_j) is given by

$$p_j = 2^j \exp\left\{-\frac{j\Delta E_m}{j_{\max}kT}\right\} / \sum_{j=0}^{j_{\max}} 2^j \exp\left\{-\frac{j\Delta E_m}{j_{\max}kT}\right\}, \quad (1)$$

where 2^j is the multiplicity of states in the j th tier and $\exp\{-\frac{j\Delta E_m}{j_{\max}kT}\}$ is the standard Boltzmann factor. (Note: $\sum p_j = 1$ as required.) The geometric series in the denominator is easily summed: $S_n \equiv \sum_{j=0}^{j_{\max}} 2^j \exp\{-\frac{j\Delta E_m}{j_{\max}kT}\} = \frac{1-r^{j_{\max}+1}}{1-r} \simeq \frac{1}{1-r}$, where $r = 2e^{-\frac{\Delta E}{j_{\max}kT}} \simeq 2e^{-1}$. With energy difference $\Delta E_m = qV_m \simeq 0.8$ eV, at the temperature survivable by the superthermophile *Strain 121* (400 K), and with roughly 20 tiers in the pyramid, the electron occupation probability of the uppermost tier is $p_{j_{\max}} \simeq 2 \times 10^{-5}$. For comparison, dropping the temperature by just 25% ($T = 300$ K) reduces $p_{j_{\max}}$ by over three orders of magnitude and replacing

the upwardly-fanning pyramid by a single step reduces the occupation probability by 2×10^6 . Together, the high temperature and the pyramidal construction increase charge diffusion by more than a factor of a billion. (The probability $p_{j_{\max}}$ can be increased by further grading the quantum multiplicity of states in molecules toward the pyramid's base, for instance, by having more A-D sites per molecule at the base than at the vertex, or by simply packing more A-D molecules in the array.)

Once atop the broad pyramid base, electrons must find the conducting molecular ladder down to the reaction center. This could be mediated through a highly conjugated top-most tier—perhaps something akin to graphene—in which electrons become highly delocalized, hence able to search the base's wide lateral extent quickly and efficiently. Other biological precedents exist. For example, wavelike energy transfer facilitated by quantum coherence has been predicted theoretically for photosynthetic systems [85] and strong experimental support has been provided by recent studies of the bacteriochlorophyll complex found in green sulfur bacteria [86]. The photosynthetic complex acts as an “energy ‘wire’” between the chlorosome (a large light-harvesting molecular antenna) and the photosynthetic reaction center. Evidence indicates that, through the quantum superposition of and interference between many excited states, excitons can quickly explore vast areas of phase space, in effect performing a quantum search of all states simultaneously so as to find the center efficiently [86]. A similar mechanism can be envisioned for charges in the TL pyramid's base seeking the conduction ladder.

In all, despite a sizable potential difference ($V_m \gg \frac{kT}{q}$), charges have reasonable probability of traversing the membrane by purely thermal diffusive processes.¹¹ The molecular pyramid creates a natural mechanism for charge transport and offsets the deleterious Boltzmann exponential.

3.3 Conducting Molecular Ladder

Once a charge q has climbed the electrostatic potential via multiple small, diffusive sub- kT steps (Fig. 3c), it can fall through the entire potential (base to vertex) in a single, nearly-lossless quantum transition ($qV_m = \Delta\mathcal{E}_m$) which can drive a chemical reaction at the reaction center (e.g., formation of ATP).

Charge transfer from the pyramid's base back to its vertex can be executed across the thickness of the membrane ($d = 10^{-7}$ m) along electrically conducting molecules.¹² Aromatic and highly conjugated organics that span the entire membrane are promising candidates. Carotenoids are highly conjugated linear organics that are known to be electrically conducting and are also found in the membranes of thermophilic archaea, presumably to give structural strength against thermal disruption. Individual conducting organic molecules have demonstrated electron transport rates

¹¹This is reminiscent of how salmon surmount the sizable gravitational barriers posed by dams using a series of small steps: a fish ladder.

¹²Some bacteria are known to conduct electrons using proteins called c-cytochromes and recently, members of the group *Geobacter* have been discovered with hairlike nanostructures called pili that conduct electricity [87].

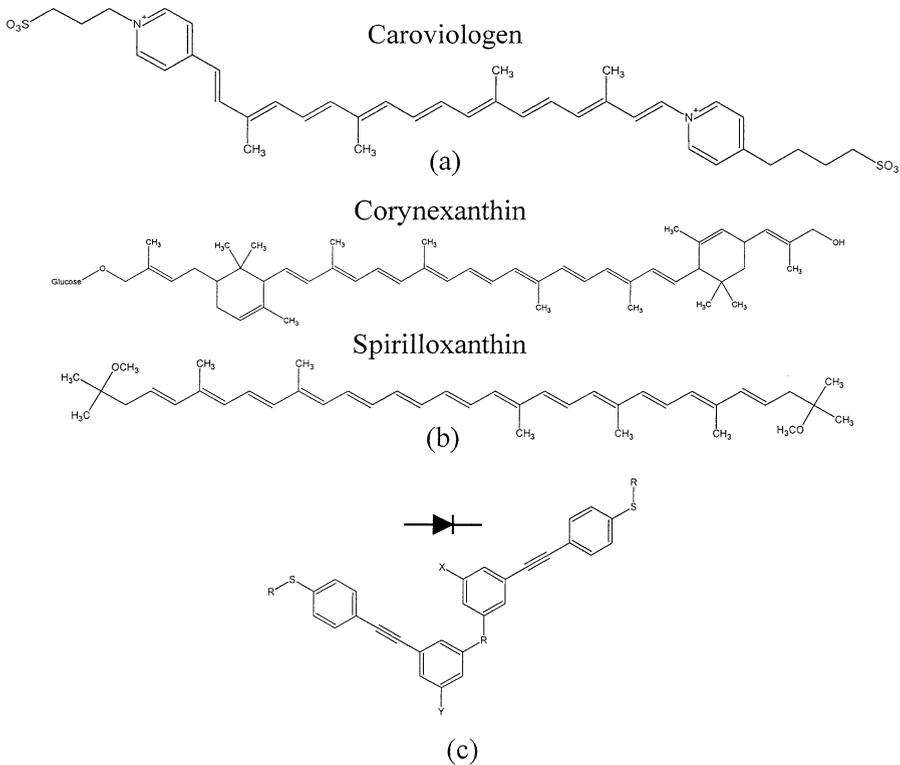


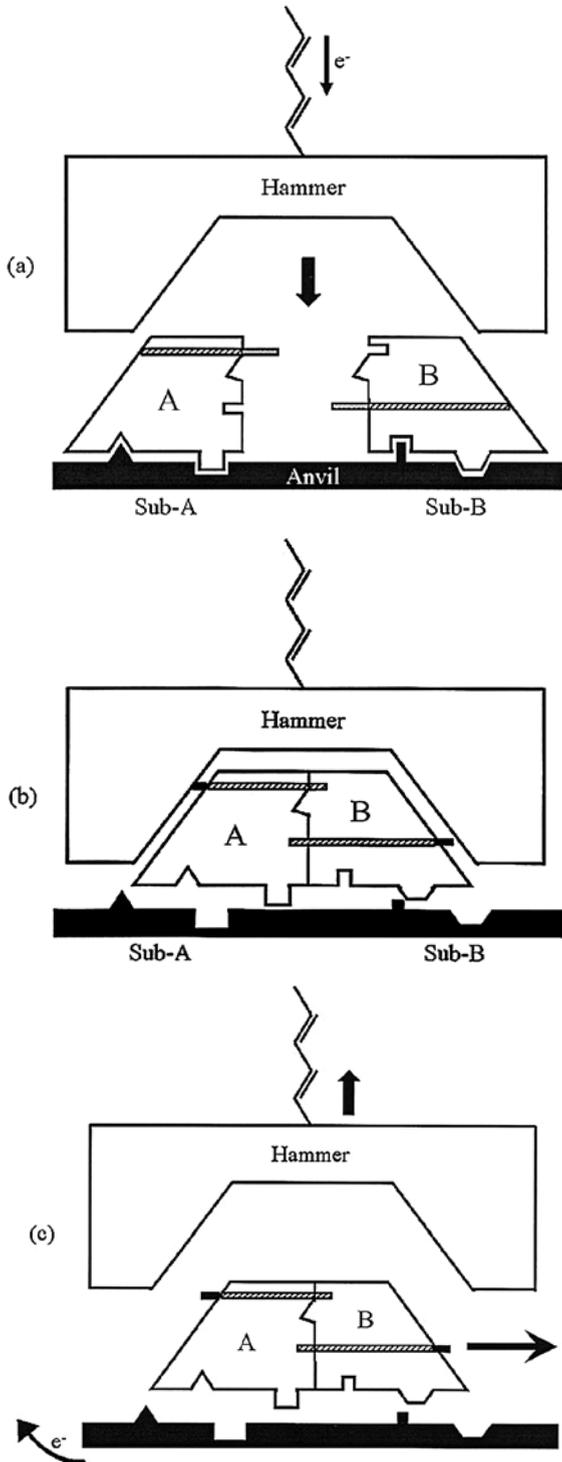
Fig. 4 Organic conductors: **a** man-made molecular wire; **b** naturally-occurring carotenoids; **c** man-made molecular diode [88]

of roughly 10^{11} /sec and support current densities far in excess of the best metallic conductors [88]. The directionality of the current might also be promoted by fashioning the conduction ladder as a molecular electronic diode: a one-way valve for electrons [88–90]. These have been engineered [88] by attaching electron-donating and electron-withdrawing chemical groups to a conducting carbon skeleton. Biological counterparts are conceivable.

A comparison of man-made and naturally occurring organic conductors is made in Fig. 4. Corynexanthin and spirilloxanthin are naturally occurring carotenoids, known both as good electrical conductors and as pigments. The synthetic, caroviologen, was designed as a molecular wire and is sufficiently long to span a lipid membrane. The similarities between the natural and synthetic conductors is striking. Figure 5c depicts a highly-conjugated aromatic thiol with electron donating and withdrawing groups (X, Y) that allow it to perform as a diode. Its potential significance to unidirectional current flow down the conduction ladder (Fig. 1) is clear. Additional mechanisms for ensuring unidirectional (diodic) current flow will be raised in Sect. 3.4.

Fig. 5 Production of high-energy products (AB) from low-energy reactants (A and B) using hammer-anvil molecular forge and energetic electron at reaction center (Fig. 1).

a Superthermal electron delivered down conduction ladder engages hammer with low-energy reactants bound on substrate anvil. Sub-A and sub-B preferentially bind A and B, aligning them for reaction. **b** Hammer forges A and B into AB. Electron energy is used to make high-energy product AB; break association between A and sub-A, B and sub-B; and drive pins through A and B so as to disengage AB from hammer. **c** Hammer retracts to original position; AB desorbs; and electron returns to apex of pyramid. Later, new A and B adsorb on anvil template. Cycle repeats



3.4 Reaction Center

Electrons falling down the conducting ladder to the reaction center in Fig. 1 can drive useful biochemical reactions since their energy is far greater than kT ; in this model, $\Delta\mathcal{E}_m = 0.8 \text{ eV} \simeq 23 \text{ kT}$, for $T = 400 \text{ K}$. Chemical nonequilibrium can be further enhanced by utilizing the preferential binding affinities of proteins, as depicted in Fig. 5. Low-energy reactants (molecules A and B in Fig. 5a), diffusing in from other parts of the cell, bind preferentially to specific locations on the reaction center substrate (sub-A and sub-B on the substrate anvil), and undergo reaction into the high-energy product molecule AB (Fig. 5c). AB then preferentially desorbs and diffuses back into the cell for use (Fig. 5c), whereupon new A and B diffuse in and bind, repeating the cycle. Like pieces of metal laid together on an anvil and artfully struck by a hammer to join them, reactants are enzymatically forged using the energy of superthermal electrons delivered down the conducting ladder, perhaps in ways akin to ATP synthase. ATP synthase is a protein complex that resides in the membranes of chloroplasts and mitochondria. It catalyses the production of ATP using proton current through the membrane [91, 92]. A proton gradient is established across the membrane by catabolic processes and the leakage current back across the membrane, down the gradient, through a channel in the ATP synthase catalyses the formation of ATP via phosphorylation of ADP. It is conceivable that thermosynthetic life could utilize similar intermolecular protein complexes as their reaction centers.

Specificity in the reaction direction can be enhanced if the binding sites in the reaction center are chemically tuned to strongly adsorb reactants and quickly desorb products (Fig. 5). In other words, reactants are tightly bound on the reaction template (Fig. 5a) until a high-energy electron falls through the membrane potential and drives the desired reaction forward ($A + B \rightarrow AB$), at which time the product becomes loosely bound (Fig. 5b) and, therefore, quickly desorbs and diffuses away (Fig. 5c). Meanwhile, new reactants A and B diffuse in and bind, blocking the return of AB, thereby suppressing the reverse reaction. This type of specificity in adsorption and desorption via allostery are hallmarks of enzymes. Enzymatic binding specificities for a particular molecule can easily vary by more than a factor of 10^9 . Gordon pioneered a number of related biochemical mechanisms pertaining to the second law [11–16].

The unidirectional (dioidic) nature of the cyclic electron current can be ensured in several ways. First, as mentioned in Sect. 3.3, the conduction ladder can be configured as a molecular wire diode (Fig. 4c). Second, the reactants, coupled with reactant-induced conformational changes in the binding enzymes (Fig. 5b, c; sub-A, sub-B), can act as an electronic switch in the reaction center; that is, electrons in the base of the pyramid can discharge through the reaction center *if and only if* the reactants are specifically bound on the anvil template (sub-A and sub-B). Third, as portrayed in Fig. 5a, the hammer-(A/B)-anvil complex itself constitutes a molecular electronic switch. Until the superthermal electron is delivered down the conduction ladder to the hammer, the open hammer-anvil gap presents an open circuit with nearly infinite electrical resistance to reverse current.¹³ The electron stimulates a conformational

¹³Quantum mechanical tunneling current between the hammer and anvil is possible, in principle; however, it will be negligible for hammer-anvil separations of more than a few atomic diameters, especially if state-to-state transition probabilities are engineered to be small.

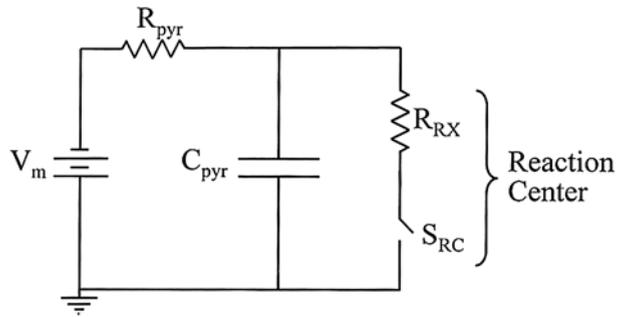
change in the hammer, thereby ‘closes the switch’ and drives the reaction forward. (Allosteric changes such as these are commonplace and critical to nearly all biochemical pathways.) The electron, now left only with thermal energy, cannot surmount the electrostatic potential back up the ladder, particularly since the AB product has desorbed and the hammer has retracted, both of which break the circuit. Thus, the electron returns to the pyramid apex, completes its thermodynamic cycle, and begins again its diffusive journey back up the pyramid.

Living cells are inherently open, nonequilibrium chemical systems; reactants and products need not occur in equilibrium concentrations. For the association-dissociation reaction $A + B \rightleftharpoons AB$, high energy AB is presumably being depleted constantly by cellular metabolism; therefore it should be held in relatively low concentrations. (Or, its chemical energy might be quickly converted elsewhere in the cell, as in the production of fats.) Conversely, the reactants A and B should occur in relatively high concentrations since they are constantly being generated from the breakdown of AB. Thus, the nonequilibrium concentrations of A, B, and AB would tend to favor the forward reaction $A + B \rightarrow AB$ and, furthermore, they would tend to suppress the backward reaction at the reaction center.

The mechanical operation of the hammer-anvil (Fig. 5) is reminiscent of many well known biomolecular machines, like ATP-ase, RNA polymerase, and kinesin that perform cellular work such as transport, replication, transcription of DNA, and translation of RNA [93]. Kinesin, for example, ferries subcellular cargo along microtubules, powered chemically by the hydrolysis of ATP. Biomolecular machines, which range in size from 2 to 100 nm, are unlike everyday macroscopic machines in that they can harness thermal fluctuations (albeit using chemical energy). They do not subvert the second law because chemical energy (e.g., ATP) is expended irreversibly; nonetheless, they exploit “forward” fluctuations to perform work. In some sense they can be viewed as an intermediate case between everyday macroscopic machines, which do not rely at all on thermal fluctuations, and the present second law subverting hammer-anvil (Fig. 5). The biochemical hammer-anvil pushes beyond presently known biomolecular machines, however, by rectifying thermal energy into useful work, without need of auxiliary chemical reactions.

The theory of protein machines [94–97] posits that most everyday machines (e.g., motors, rotors, ratchets, or engines; latches, turbines, switches, and keys) have biomolecular analogs in the form of proteins or protein complexes; however, whereas the former are macroscopic and deterministic, the latter are mesoscopic and stochastic. One can view the mechanical coordinate of the first as the reaction coordinate of the second. Of course, both macroscopic and protein machines must have free energy sources to provide directionality to their operations; in the case of the thermosynthetic reaction center (Fig. 5) this is provided by the superthermal electrons down the conduction ladder. Thus, just as it is accepted that a macroscopic machine (e.g., one made of hammers, anvils and switches) might forge macroscopic objects in the manner depicted in Fig. 5 when powered by electricity, it is plausible that analogous molecular forging could likewise be achieved when driven by high energy electrons from the membrane capacitor.

Fig. 6 Electrical analog to biochemical circuit in Fig. 1



3.5 Biochemical Power

Figure 6 depicts an electrical analog to the biochemical circuit in Fig. 1. Comparing Fig. 6 with Fig. 1, V_m represents the static voltage across the membrane; R_{pyr} is the phenomenological electrical resistance to charge diffusion up the transport pyramid, from apex to base; and C_{pyr} is the capacitance of the pyramid/membrane capacitor. The reaction center consists of a molecular switch S_{RC} , which when closed allows electron flow through the chemical load, represented by R_{RX} , creating the high-energy AB product. The total energy dropped across the load by a single electron is qV_m . When the switch is open—for instance, while reactants are not bound to the reaction template (sub-A and sub-B), or when the hammer is retracted in Fig. 5—the capacitor C_{pyr} will charge up to voltage V_m in preparation for discharge and the ensuing chemical reaction $A + B \rightarrow AB$. (The phenomenological time constant for charging ($\tau \sim R_{pyr}C_{pyr}$) is set by the diffusion rate of electrons up the pyramid.) Presumably, the high-energy product AB will go on to drive life processes in the cell. Unlike everyday electrical circuits, which operate with continuous electron current, this system relies on discrete-electron current. Still, one can estimate time-average quantities.

The average power \mathcal{P}_m delivered by the thermosynthetic membrane should scale as $\mathcal{P}_m \sim \frac{p_{jmax} N_q \Delta \mathcal{E}_m}{\tau_{vb}}$, where N_q is the number of charges in play in the membrane and τ_{vb} is the average transit time for charges from the vertex to the base. N_q must be substantially less than σl^2 in order to not significantly distort the membrane's electric fields; for this model, let $N_q = 10 \ll l^2 \sigma$. τ_{vb} depends critically on the mechanism of charge transport; as a measure we take it to be the diffusion time of a simple molecule (H_2) through water the thickness of the membrane; that is, $\tau_{vb} \sim \tau_{diff} \sim 10^{-6}$ sec. For the model membrane, one has $\mathcal{P}_m \sim \frac{p_{jmax} N_q \Delta \mathcal{E}_m}{\tau_{diff}} \simeq 10^{-17}$ W. This is on the order of 0.01% of the resting power requirement for mammalian cells; thus, from the standpoint of these energetics, a thermosynthetic organism (with a single membrane-capacitor complex) would probably not compete well against many types of FEL. On the other hand, many FEL organisms have far lower power requirements than mammalian cells. For instance, some deep rock microbes are believed to have infinitesimal metabolisms; by some estimates they grow and reproduce on time scales approaching centuries, whereas surface-dwelling FEL bacteria can run through a generation in minutes. Based on the availability of free energy sources and nutrients and on the

amount of carbon dioxide produced from the oxidation of organic matter, it is estimated that many deep rock microbes have metabolisms that are more than a billion times slower than surface free-energy microbes, thereby possibly putting them below TL in energy utilization rates. If so, then whereas its low metabolic rates makes it unlikely to compete successfully with FEL on the surface, thermosynthetic life might compete quite well with free energy life in the deep subsurface where free energy sources are scarce.

Electrocapacitive discharges, analogous to the biochemical one described above, have been featured in a variety of second law challenges spanning plasma, chemical, and solid state physics [52–58, 81–84]. These can be gainfully compared to the present biological system. In the plasma capacitor [52–54] a switch discharges a conducting probe (capacitor) immersed in an electrically conducting plasma; in the linear electrostatic motor [55–58] a microscopic semiconducting slab acts as both a sliding switch and a working piston in the interior of an open-gap p-n junction; likewise, with the electromechanically-resonant, semiconductor cantilever oscillator [61], microcapacitor plates act as both the switch and piston; and, finally, for the electrocapacitive catalyst [62], gas ions individually discharge a self-biased nanocapacitor, driving chemical reactions. (Power densities for these can be large (e.g., $>10^8$ W/m³.) Of these, the latter bears the closest resemblance to the membrane capacitor system, but it is far less complex since it operates merely in the gas phase. Thus, the present biological membrane capacitor is a natural extension of other well-developed capacitor-based second law challenges.

4 Discussion and Experimental Prospects

Thermosynthetic life would seem to enjoy several evolutionary advantages over free energy life. Most obvious is freedom from reliance on free energy sources since TL simply harvests thermal energy from its environment. It is unclear whether this would allow it to economize on its metabolic machinery, but insofar as it does not require large bursts of energy, one can imagine that TL might not be so dependent on energy storage mechanisms (e.g., fats) as FEL, nor on the vicissitudes of free energy availability; after all in terrestrial settings, thermal energy is plentiful. Once fully grown, TL could, in principle, operate as a closed thermodynamic cycle, neither taking in nutrients nor expelling wastes as FEL must. Its material needs would be simply those required for reproduction. This economy would confer evolutionary advantage both in reducing the necessary conditions for survival but also in reducing local biopollution, which can be harmful or even fatal in closed environments. Third, supposing TL competed with FEL at the spatial margins of energy resources, TL could more easily strike off, explore, and inhabit niches unavailable to FEL. For instance, were superthermophiles to push more deeply into the subsurface, according to the discussion above, the temperature rise would further favor TL's heat-driven biochemistry.

Of these three potential evolutionary advantages, perhaps the most counter-intuitive is that TL might operate in a materially-closed thermodynamic cycle, flouting the usual demand that life continuously take in nutrients and discard waste products. Put another way, life—and, for that matter, the entire biosphere—normally operates by virtue of *entropy gradients*, wherein high-grade, low-entropy free energy

is converted into lower-grade, higher-entropy thermal energy. During the conversion processes, life is sustained—and the second law upheld. This entropy gradient can be traced from the nuclear reactions at the core of the Sun (or even back to the Big Bang) down to energy's final exhaustion as heat in the 3 K cosmic microwave black-body radiation [10, 98].

The necessity of an entropy gradient for FEL has been appreciated for more than a century. This necessity, however, is predicated on the presumed inviolability of the second law. High-energy reactants are taken into a cell, metabolized, and later expelled as lower-energy products. In compliance with the second law, the net entropy of the products (atoms, molecules, ions, photons, phonons, etc.) must exceed the entropy of the reactants, thus establishing the entropy gradient. If the second law can be subverted, however, the traditional entropy gradient is unnecessary. Instead, biologically useful energy can be harvested directly from the background thermal reservoir, metabolized to drive life processes, and then expelled back into the reservoir as heat, perhaps to be reused again later by the cell. From a materials standpoint, a mature thermosynthetic cell can be a closed thermodynamic system. Intake of matter from the surroundings is required solely for cellular construction and reproduction, rather than for metabolism. Even from an energy standpoint, there should be no net energy input or output (work plus heat) from the mature TL cell unless it needs an energy spurt, in which case it would simply draw more heavily from the thermal field temporarily. To a casual observer, unaware of its ongoing internal cellular processes, a thermosynthetic cell would outwardly appear either dead or dormant.

An experimental search for terrestrial thermosynthetic life will prove problematic at present. First, in most terrestrial environments FEL should dominate over TL, rendering TL a trace population, at best. In more extreme environments where FEL is crippled, perhaps in hot, deep, subsurface realms, a search might prove fruitful. It has been estimated that the depth-integrated biomass of subsurface microbes might be equivalent to a meter or more thick of surface biomass over the entire planetary surface [71, 79]. The vast majority of these organisms have not been cataloged or studied. Second, the majority of *all* microbes—either surface or subsurface dwelling—are either difficult or impossible to culture in the laboratory; it is estimated that perhaps less than 10% of microbes from *any* random natural sample can be cultured with present techniques. Since full-fledged TL might ingest little or no chemical fuel (aside from that required for reproduction) and expel little or no chemical waste, many standard tests for life will fail.

The above profile for TL—small, unicellular, anaerobic, hyperbarophilic superthermophiles, geologically and hydrologically isolated from FEL in long-term, stable, free-energy poor environments—suggests how and where TL might be discovered. For pure TL, a search should be conducted in deep, geologically stable rock that is nearly biochemically barren both of material and energy resources. That is, look where there is little hope of finding anything alive. Rock samples with organisms, but lacking appropriate levels of biological wastes would be signposts for TL.

Recovery of deep subsurface microbes has been carried out to depths of 5.2 km in igneous rock aquifers. Boreholes (without microbe recovery) have been conducted to depths of 9.1 km, so searches for proposed thermosynthetic life appear feasible. Culturing would probably be problematic. One might suppose that TL can be discriminated from FEL by simply isolating a mixed culture from all free energy sources

for a sufficiently long time to starve FEL, thereby isolating pure TL. Unfortunately, *sufficiently* long can mean *very* long. Microbes can place themselves in low-energy, sporulating, static modes for years, decades, and perhaps centuries or millenia awaiting favorable conditions. With microbes, sometimes there seems to be no clear distinction between *fully alive* and *truly dead*.

Since, in principle, TL need not be barophilic or thermophilic—although high temperatures can favor some thermosynthetic processes (Sect. 3.1)—TL might be found under everyday terrestrial conditions among FEL. Although it need not compete with FEL for energy resources, it must compete for material resources. If TL can protect what material resources it has and slowly accrue those necessary for reproduction, then it might compete successfully against FEL.¹⁴ As previously noted, thermosynthetic organisms might grow slowly and mature TL cells might appear dead or dormant to casual observation.

Ancient samples might also provide candidates for TL searches. Recently, viable cultures have been made of a halotolerant bacterium believed to have been entombed in salt crystals for 2.5×10^8 years [81]. It is unclear how such organisms remain viable for millenia against the ravages of natural radioactivity and thermal degradation. There are a number of biochemical and genetic repair processes that contribute but, presumably, all require free energy. A reliable energy source like thermosynthesis would be convenient for ongoing repair. Likewise, thermosynthesis would be handy for million-year long panspermian transport between planets in meteors and asteroids.

As a further possibility, thermosynthetic life might be physically subsumed into the cells of standard free energy life, perhaps in a role similar to that of mitochondria, which are believed to have once been free-living cells before being captured and incorporated as the energy-producing machinery of eukaryotes. Or, thermosynthesis might have evolved on a parallel track with free energy capabilities within a single species. Such hybrid FEL-TL might display the advantages of both types of life. A hybrid's latent thermosynthesis might be tapped when free energy becomes scarce or it might simply be a 'bonus' energy source—a sort of thermodynamic afterburner.

In summary, thermosynthetic life could plausibly be found in several terrestrial environments and in several guises, including:

- (i) Superthermophilic bacteria in deep, subsurface free-energy deserts;
- (ii) Low-metabolism bacteria in traditional free energy environments;
- (iii) Ancient, dormant cells in free energy voids (e.g., salt crystals); or
- (iv) Hybrid FEL-TL cells.

DNA/RNA analysis might eventually help identify TL. Currently, it can be used to identify species, but it cannot yet be used to predict the function, structure, or viability of an organism. Presumably, genomics and proteomics will eventually advance to the point where cellular structure and biochemical function can be predicted from DNA/RNA analysis alone, at which time thermosynthetic life forms can be identified

¹⁴This is perhaps easier said than done; as in the human sphere, those who control the energy resources are likely to control the material resources too.

solely from their genetic maps. This type of search, however, is still many years or decades away.

The implications of TL are several. First, thermosynthesis extends the repertoire of biological energy sources beyond chemo- and photosynthesis. Second, by relaxing the longstanding requirement for free energy, thermosynthesis expands the potential niches for life well beyond those previously thought habitable. Presumably, life still requires matter for its corporality, but its requirement for energy can be relaxed since heat is often plentiful even where free energy sources are absent. Searches in free-energy deserts even more barren than the deep terrestrial subsurface could, in principle, be fruitful. Third, the novel chemical and thermodynamic aspects of TL offer new opportunities and challenges for mundane and ultramundane life searches. For instance, terrestrial microbes that appear dead or dormant—perhaps a fraction of the 90% of unculturable ones under standard conditions—might be thriving under thermosynthesis. Or, one can imagine that life might evolve new structures to facilitate second law subversion, for instance, ‘reverse radiators’ to capture environmental heat. Fourth, the possibility of thermosynthesis should encourage biophysicists, biochemists and biologists to re-examine known systems. For example, perhaps some of the biomolecular machines currently acknowledged to exploit thermal fluctuations, like kinesin, might actually rely on thermosynthesis under some circumstances. In summary, insofar as second law violation revises the foundations of thermodynamics one should expect it to revise traditional biology, biochemistry, biophysics and astrobiology.

In conclusion, given the exigencies of natural selection and the plausibility of second law violation by biologically-inspired systems, we predict that thermosynthetic life will be discovered terrestrially and extraterrestrially, perhaps in one of the forms listed above. Thermosynthetic life would not only add to Life’s diversity and bespeak its cleverness, it would also shed significant new light on the second law of thermodynamics.

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