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ing management criteria for qualification, and expanding their total area, building on country-level evidence and experience (recommendations 3 and 6 to MSs); (iv) develop longer-term perspectives for more effective and comprehensive protection and restoration of grasslands and peatland; (v) reevaluate the usefulness of the crop diversity measure.

Our recommendations should encourage MSs and the EU to start moving toward more sustainable agriculture, securing food provision alongside biodiversity and ecosystem services for current and future generations. ∎

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EVOLUTION

Energy at life's origin

Analysis of the bioenergetics of primitive organisms suggests that life began at hydrothermal vents

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Energy-releasing chemical reactions are at the core of the living process of all organisms. These bioenergetic reactions have myriad substrates and products, but their main by-product today is adenosine triphosphate (ATP), life's primary currency of metabolic energy. Bioenergetic reactions have been running in a sequence of uninterrupted continuity since the first prokaryotes arose on Earth more than 3.5 billion years ago, long before there was oxygen to breathe (1). Under what conditions did these bioenergetic processes first evolve?

Many ingenious ideas about energy at life's origins have nothing in common with modern life. It is conceivable that early life harnessed energy from volcanic pyrite synthesis (2), zinc sulfide–based photosynthesis (3), ultraviolet radiation, or lightning, yet none of these processes powers known microbial life forms. For biologists, the origin of energy-harnessing mechanisms used by real microbes is the issue. Recent studies point to parallels between the energy-harnessing systems of ancient microbes and the geochemistry of alkaline hydrothermal vents (see the figure), suggesting that natural ion gradients in such vents ignited life's ongoing chemical reaction.

How did the first cells harness energy? Because life arose in a world without molecular oxygen, some anaerobes are likely to be ancient, and anaerobic environments should harbor primitive bioenergetic reactions (4, 5). Ancient anaerobic niches deep in Earth's crust often contain acetogens (bacteria) and methanogens (archaea), groups that biologists have long thought to be ancient (4). However, anaerobic environments harbor very little energy to harness (6, 7). In the anaerobic environments of submarine hydrothermal vents, geochemically generated H_2 is the main source of chemical energy.

In addition to being strict anaerobes, acetogens and methanogens live from H_2, using the simplest and arguably most ancient

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forms of energy metabolism (8). Both synthesize ATP by reducing CO_2 with electrons from H_2 to make acetate and methane, respectively. They use a chemical mechanism called flavin-based electron bifurcation (6) to generate highly reactive ferredoxins—small, ancient iron-sulfur proteins (5) that are as central to their energy conservation as is ATP (6). The shared backbone of their energy metabolism is the acetyl–coenzyme A pathway, the most primitive CO_2-fixing pathway (8) and the one typical of subsurface microbes (9). Metabolism in these anaerobes is furthermore replete with reactions catalyzed by transition metals such as iron, nickel, molybdenum, or tungsten, another ancient trait (2, 5–8).

> ... the primordial ATPase could have harnessed geochemically generated gradients at an alkaline hydrothermal vent.

All known life forms, including methanogens and acetogens, use two basic mechanisms to tap environmentally available energy and harness it as ATP. The first is substrate-level phosphorylation, in which highly reactive phosphate-containing compounds phosphorylate adenosine diphosphate (ADP) to make ATP (6, 10). The energy conserved in ATP is released in a subsequent reaction that does chemical work for the cell or allows more sluggish reactions to go forward. The highly reactive phosphate compounds are generated during conversions of carbon compounds. Their synthesis is driven by environmental sources of chemical energy such as H_2 plus CO_2 that are harnessed during conversion to more thermodynamically stable compounds such as methane and acetate.

The second mechanism that cells use to harness energy involves ion gradients and is called chemiosmotic coupling. Here, an energy-releasing reaction is coupled to the pumping of ions across a membrane from inside the cell to the outside. The most common ions used for this purpose are protons,

rendering the inside of a cell alkaline relative to the outside, but organisms in low-energy environments often use sodium (Na^+) ions (6, 7). The energy stored in the ion gradient is then harnessed by an enzyme [an adenosine triphosphatase (ATPase)] to phosphorylate ADP.

Even the anaerobic energy misers, methanogens and acetogens, are chemiosmotic. They use an ATPase, but differ in the mechanism by which they generate their ion gradient (6–9, 11). Both pump Na^+ ions, but the chemical steps that energetically support pumping differ in the two anaerobes. Acetogens pump while transferring electrons from ferredoxin to nicotinamide adenine dinucleotide (NAD^+); this energetically downhill (exergonic) reaction is catalyzed by a single protein complex (9). Methanogens pump while transferring a methyl group from one cofactor to another at a methyltransferase complex (6). These pumping reactions are far simpler and more primitive than those in oxygen-consuming respiratory chains. The anaerobic pumping systems also use chemically simple substrates (methyl groups, iron-sulfur clusters), which might be bioenergetic relics from the first free-living cells (11).

The chemistry that links acetogens and methanogens to each other also links them to alkaline hydrothermal vents. These vents harbor geological manifestations of both kinds of energy that are used by life: chemically reactive compounds (12) and natural proton gradients (13). And in contrast to "black smokers," which have life spans on the order of dozens of years, alkaline hydrothermal vents like Lost City (see the figure) (14) can remain active for up to 100,000 years (15), providing a constant source of gradients and chemical energy over geological time scales. This makes them unique among possible sites for life's origin. In addition, hydrothermal vents derive from reactions in Earth's crust and thus contain large amounts of catalytic transition metals (12, 13). Vast networks of inorganic microcompartments in the vents provide mineral surfaces on which organic compounds can readily adsorb, providing a natural environment for concentrating these compounds on the early Earth. This process may have rendered the steep hurdles en route to chemical complexity more readily surmountable.

There are further similarities between geochemical reactions in hydrothermal vents and biological energy conversions. This is especially true for vents whose fluid contents are controlled by serpentinization, a sequence of geochemical reactions in which seawater circulating through hydrothermal systems reacts with Fe^{2+} in submarine crust, generating orders of magnitude more H_2 than acetogens or methanogens require (6)
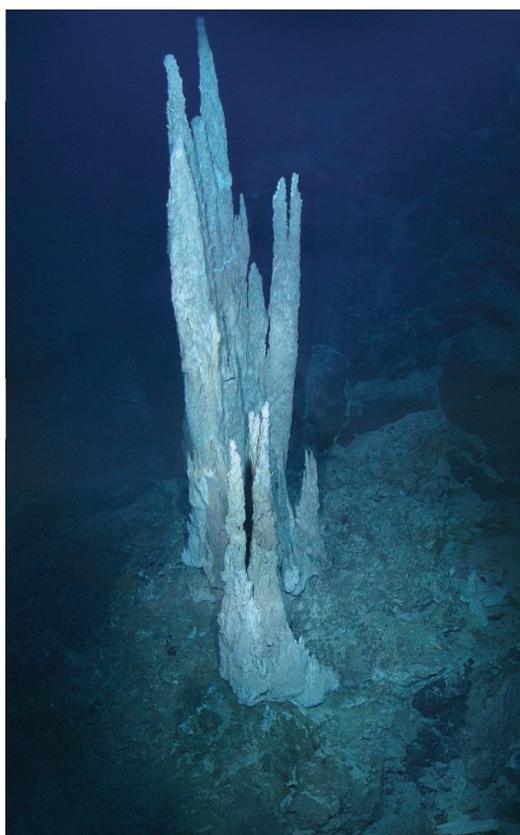
Clues to where life evolved. Similarities between bioenergetic processes and those at hydrothermal vents such as Lost City suggest that life may have evolved at such vents on the early Earth. This photo was taken at Lost City in 2005 using the remotely operated vehicle *Hercules*.

while also generating Fe^{3+} in the crust. At the same time, CO_2 is reduced to methane and formate, which are found at 1 and 0.1 mM concentrations, respectively, in the effluent of Lost City (15), one of the few alkaline vents that has been studied. Serpentinization and the accompanying CO_2 reduction are energy-releasing geochemical reactions (14). And chemiosmosis? The process of serpentinization not only generates a strongly reducing environment; it also makes the effluent alkaline. The Lost City effluent has a pH of about 10 (14, 15), far more alkaline than ocean water, either now or 4 billion years ago, making these vents naturally chemiosmotic (13). The natural proton gradients at Lost City have the same magnitude and orientation as those in modern autotrophic cells.

The synthesis of high-energy bonds that underpin substrate-level phosphorylation can be catalyzed by metal ions alone (2); it does not require either proteins or membranes, whereas chemiosmotic synthesis of ATP requires both. This indicates that substrate-level phosphorylation came before chemiosmosis (10) in early bioenergetic evolution and powered the evolution of genes and proteins. The ATPase is as universal

among cells as the ribosome and the genetic code and was clearly one of the earliest biological innovations. Indeed, the primordial ATPase could have harnessed geochemically generated gradients at an alkaline hydrothermal vent. This would explain why ATPase is universally conserved but ion-pumping mechanisms are not. What were the first ion-pumping mechanisms? The first step could have entailed a simple H^+/Na^+ antiporter that converted the proton gradient to a Na^+ gradient, as found in acetogens and methanogens. The invention of their simple pumping complexes, which use iron-sulfur clusters and methyl groups as substrates, would have enabled the emergence of the first free-living bacteria and archaea (11).

Research on the origin of life has long focused on chemical synthesis and the RNA world, neither of which pointed to specific early-Earth environments or specific groups of organisms as ancient. Hydrothermal vents like Lost City reveal exciting similarities between the energy-releasing geochemical reactions that occur there and the physiology of acetogens and methanogens. This striking convergence of geochemistry and microbiology unearths new opportunities for discovery. The chemistry of hydrothermal vents is vastly underexplored, and H_2-dependent anaerobic autotrophs are only beginning to relinquish their bioenergetic secrets. Energy-releasing processes that link the two might shed new light on biology's biggest question. ∎

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