

ENERGY AT LIFE'S ORIGIN



Medieval watermills and modern hydroelectric power stations are powered by the channelling of water. Funnel the flow into a confined channel and its force increases. Now it can drive work such as turning a waterwheel. Conversely, allow the flow to spread out across a wider basin, and the force diminishes. In a river, it becomes a pond or a ford. You might attempt to make a crossing, safe in the knowledge that you are unlikely to be swept away by the force of the current.

Living cells work in a similar way. A metabolic pathway is like a water channel, except that the flow is of organic carbon. In a metabolic pathway, a linear sequence of reactions is catalysed by a series of enzymes, each one acting on the product of the previous enzyme. This constrains the flow of organic carbon. A molecule enters a pathway, undergoes a succession of chemical modifications, and exits as a different molecule. The succession of reactions can be repeated reliably, with the same precursor entering and the same product leaving each time. With their various metabolic pathways, cells are like networks of water mills, in which the flow is always confined within interconnecting channels, always maximised. Such ingenious channelling means that cells need far less carbon and energy to grow than they would if flow were unconstrained. Rather than dissipating the force at each step — molecules 'escaping' to react with something else — enzymes keep biochemistry on the straight and narrow. Cells don't need a great river

surging to the sea, but drive their mills using smaller channels. From an energetic point of view, the power of enzymes is not so much that they speed up reactions, but that they channel their force, maximising the output.

So what happened at the origin of life, before there were any enzymes? Flow was necessarily less constrained. To grow – to make more organic molecules, to double, ultimately to replicate – must have cost more energy, more carbon, not less. Modern cells minimise their energy requirements, but we have already seen that they still get through colossal amounts of ATP, the standard energy 'currency'. Even the simplest cells, which grow from the reaction of hydrogen with carbon dioxide, produce about 40 times as much waste from respiration as new biomass. In other words, for every gram of new biomass produced, the energy-releasing reactions that support this production must generate at least 40 grams of waste. Life is a side reaction of a main energy-releasing reaction. That remains the case today, after 4 billion years of evolutionary refinement. If modern cells produce 40 times more waste than organic matter, just think how much the first primitive cells, without any enzymes, would have had to make! Enzymes speed up chemical reactions by millions of times the unconstrained rate. Take away those enzymes, and throughput would need to increase by a similar factor, say a millionfold, to achieve the same thing. The first cells may have needed to produce 40 tonnes of waste – literally a truck-load – to make 1 gram of cell! In terms of energy flow, that dwarfs even a river in spate; it's more like a tsunami.

The sheer scale of this energetic demand has connotations for all aspects of the origin of life, yet is rarely considered explicitly. As an experimental discipline, the origin-of-life field dates back to 1953 and the famous Miller–Urey experiment, published in the same year as Watson and Crick's double-helix paper. Both papers have hung over the field ever since, casting a shadow like the wings of two giant bats, in some respects rightly, in others regrettably. The Miller–Urey experiment, brilliant as it was, bolstered the conception of a primordial soup, which in my view has blinkered the field for two generations. Crick and Watson ushered in the hegemony of DNA and information, which is plainly of vital importance to the origin of life; but considering replication and the origins of natural selection in near

isolation has distracted attention from the importance of other factors, notably energy.

In 1953, Stanley Miller was an earnest young PhD student in the lab of Nobel laureate Harold Urey. In his iconic experiment, Miller passed electrical discharges, simulating lightning, through flasks containing water and a mixture of reduced (electron-rich) gases reminiscent of the atmosphere of Jupiter. At the time, the Jovian atmosphere was thought to reflect that of the early earth – both were presumed to be rich in hydrogen, methane and ammonia.¹ Amazingly, Miller succeeded in synthesising a number of amino acids, which are the building blocks of proteins, the workhorses of cells. Suddenly the origin of life looked easy! In the early 1950s there was far more interest in this experiment than in Watson and Crick's structure, which initially caused little stir. Miller, in contrast, featured on the cover of *Time* magazine in 1953. His work was seminal, still worth recapitulating, because it was the first to test an explicit hypothesis about the origin of life: that bolts of lightning, passing through an atmosphere of reduced gases, could produce the building blocks of cells. In the absence of existing life, these precursors were taken to accumulate in the oceans, which over time became a rich broth of organic molecules, the primordial soup.

If Watson and Crick made less of a stir in 1953, the spell of DNA has beguiled biologists ever since. For many people, life is all about the information copied in DNA. The origin of life, for them, is the origin of information, without which, all are agreed, evolution by natural selection is not possible. And the origin of information boils down to the origin of replication: how the first molecules that made copies of themselves – replicators – arose. DNA itself is too complex to be credible as the first replicator, but the simpler, more reactive precursor RNA fits the bill. RNA (ribonucleic acid) is, even today, the key intermediary between DNA and proteins, serving as both a template and a catalyst in protein synthesis. Because RNA can act as both a template (like DNA) and a catalyst (like proteins), it can in

¹ Based on the chemistry of zircon crystals and the earliest rocks, the early earth is now believed to have had a relatively neutral atmosphere, reflecting volcanic degassing, and composed mostly of carbon dioxide, nitrogen, and water vapour.

principle serve as a simpler forerunner of both proteins and DNA in a primordial 'RNA world'. But where did all the nucleotide building blocks come from, which join together into chains to form RNA? The primordial soup, of course! There is no necessary relationship between the formation of RNA and a soup, but soup is nonetheless the simplest assumption, which avoids worrying about complicated details like thermodynamics or geochemistry. Put all that to one side, and the gene-jocks can get on with the important stuff. And so, if there has been a leitmotif dominating origin-of-life research over the last 60 years, it is that a primordial soup gave rise to an RNA world, in which these simple replicators gradually evolved and became more complex, began coding for metabolism, and ultimately spawned the world of DNA, proteins and cells that we know today. By this view, life is information from the bottom up.

What is missing here is energy. Of course, energy figures in the primordial soup – all those flashes of lightning. I once calculated that to sustain a tiny primitive biosphere, equivalent in size to that before the evolution of photosynthesis, by lightning alone, would require four bolts of lightning per second, for every square kilometre of ocean. And that's assuming a modern efficiency of growth. There are just not all that many electrons in each bolt of lightning. A better alternative source of energy is UV radiation, which can fashion reactive precursors like cyanide (and derivatives like cyanamide) from a mixture of atmospheric gases including methane and nitrogen. UV radiation streams in endlessly on the earth and other planets. UV flux would have been stronger in the absence of an ozone layer, and with the more aggressive electromagnetic spectrum of the young sun. The ingenious organic chemist John Sutherland has even succeeded in synthesising activated nucleotides under so-called 'plausible primordial conditions' using UV radiation and cyanide.² But there are serious problems here too.

² That innocuous phrase 'plausible primordial conditions' actually conceals a multitude of sins. On the face of it, it means simply that the compounds and conditions used could reasonably have been found on the early earth. It is indeed plausible that there was some cyanide in the Hadean oceans; also that temperatures could range between several hundred degrees (in hydrothermal vents) and freezing on the early earth. The trouble

No life on earth uses cyanide as a source of carbon; and no known life uses UV radiation as a source of energy. Quite the contrary, both are considered dangerous killers. UV is too destructive, even for the sophisticated life forms of today, as it breaks down organic molecules rather more effectively than it promotes their formation. It is much more likely to scorch the oceans than to fill them with life. UV is a blitz. I doubt it would work as a direct source of energy, here or anywhere else.

The advocates of UV radiation don't claim that it would work as a direct source of power, but rather that it would favour the formation of small stable organic molecules like cyanide, which accumulate over time. In terms of chemistry, cyanide is indeed a good organic precursor. It is toxic to us because it blocks cell respiration; but that might be a quirk of life on earth, rather than any deeper principle. The real problem with cyanide is its concentration, which afflicts the whole idea of primordial soup. The oceans are extremely large relative to the rate of formation of cyanide, or for that matter of any other simple organic precursor, even assuming that a suitably reducing atmosphere existed here or on any other planet. At any reasonable rate of formation, the steady-state concentration of cyanide in the oceans at 25°C would have been around two-millionths of a gram per litre – not nearly enough to drive the origins of biochemistry. The only way out of this impasse is to concentrate the seawater somehow, and this has been the mainstay of prebiotic chemistry for a generation. Either freezing or evaporating to dryness could potentially increase the concentration of organics, but these are drastic methods, hardly congruent with the physically stable state that is a defining feature of all living cells. One exponent of cyanide origins turns with wild eyes to the great asteroid bombardment 4 billion years ago: it could have concentrated cyanide (as ferricyanide) by evaporat-

is that realistic concentrations of organics in a soup are far lower than tend to be used in the lab; and it is hardly feasible to have both heating and freezing in one and the same environment. So yes: all these conditions may have existed somewhere on the planet, but they could only drive prebiotic chemistry if the whole planet is taken as a single unit, engaged in a coherent set of experiments as if it were a synthetic chemist's lab. That is implausible in the extreme.

ing all the oceans! To me, that smacks of desperation to defend an unworkable idea.³ The problem here is that these environments are too variable and unstable. A succession of drastic changes in conditions are required to achieve the steps to life. In contrast, living cells are stable entities – their fabric is continually replaced, but the overall structure is unchanging.

Heraclitus taught that 'no man ever steps in the same river twice'; but he didn't mean that the river had evaporated or frozen (or been exploded into space) in the meantime. As water flows between unchanging banks, at least on our human timescale, so life is continuously renewing itself without changing its form. Living cells remain cells, even when all their constituent parts are replaced in an unceasing turnover. Could it be any other way? I doubt it. In the absence of information specifying structure – as must logically have been the case at the origin of life, before the advent of replicators – structure is not absent, but it does require a continuous flux of energy. Energy flux promotes self-organisation of matter. We are all familiar with what the great Russian-born Belgian physicist Ilya Prigogine called 'dissipative structures': just think of convection currents in a boiling kettle, or for that matter water swirling down a plughole. No information is required – just heat in the case of the kettle and angular momentum for the plug hole. Dissipative structures are produced by the flux of energy and matter. Hurricanes, typhoons and whirlpools are all striking natural examples of dissipative structures. We find them on a vast scale in the oceans and atmosphere too, driven by the differences in energy flux from the sun at the equator

³ I have discussed soup as if it was 'made on earth' by lightning or UV radiation. An alternative source of organics is delivery from space by chemical panspermia. There is no doubt that organic molecules are abundant in space and on asteroids; and there certainly was a steady delivery of organics to earth on meteorites. But once here, these organics must have dissolved in the oceans, at best stocking a primordial soup. That means that chemical panspermia is no answer to the origin of life: it suffers from the same intractable problems as soup. The delivery of whole cells, as advocated by Fred Hoyle, Francis Crick, and others, is likewise no solution: it simply pushes the problem somewhere else. We may never be able to say exactly how life originated on earth, but we can explore the principles that must govern the emergence of living cells here or anywhere else. Panspermia fails utterly to address those principles, and so is irrelevant.

relative to the poles. Reliable ocean currents, such as the Gulf Stream, and winds, such as the Roaring Forties or the North Atlantic jet stream, are not specified by information, but are as stable and continuous as the energy flux that sustains them. The Great Red Spot of Jupiter is a huge storm, an anticyclone several times the size of the earth, which has persisted for at least a few hundred years. Just as the convection cells in a kettle persist for as long as the electric current keeps the water boiling and steam evaporating, all these dissipative structures require a continuous flux of energy. In more general terms, they are the visible products of sustained far-from-equilibrium conditions, in which energy flux maintains a structure indefinitely, until at last (after billions of years in the case of stars) equilibrium is attained and the structure finally collapses. The main point is that sustained and predictable physical structures can be produced by energy flux. This has nothing to do with information, but we'll see that it can create environments where the origin of biological information – replication and selection – is favoured.

All living organisms are sustained by far-from-equilibrium conditions in their environment: we, too, are dissipative structures. The continuous reaction of respiration provides the free energy that cells need to fix carbon, to grow, to form reactive intermediates, to join these building blocks together into long-chain polymers such as carbohydrates, RNA, DNA and proteins, and to maintain their low-entropy state by increasing the entropy of the surroundings. In the absence of genes or information, certain cell structures, such as membranes and polypeptides, should form spontaneously, so long as there is a continuous supply of reactive precursors – activated amino acids, nucleotides, fatty acids; so long as there is a continuous flux of energy providing the requisite building blocks. Cell structures are forced into existence by the flux of energy and matter. The parts can be replaced but the structure is stable and will persist for as long as the flux persists. This continuous flux of energy and matter is precisely what is missing from the primordial soup. There is nothing in soup that can drive the formation of the dissipative structures that we call cells, nothing to make these cells grow and divide, and come alive, all in the absence of enzymes that channel and drive metabolism. That sounds like a tall order. Is there really an environment

that can drive the formation of the first primitive cells? There most certainly must have been. But before we explore that environment, let's consider exactly what is needed.

How to make a cell

What does it take to make a cell? Six basic properties are shared by all living cells on earth. Without wishing to sound like a textbook, let's just enumerate them. All need:

- (i) a continuous supply of reactive carbon for synthesising new organics;
- (ii) a supply of free energy to drive metabolic biochemistry – the formation of new proteins, DNA, and so on;
- (iii) catalysts to speed up and channel these metabolic reactions;
- (iv) excretion of waste, to pay the debt to the second law of thermodynamics and drive chemical reactions in the correct direction;
- (v) compartmentalisation – a cell-like structure that separates the inside from the outside;
- (vi) hereditary material – RNA, DNA or an equivalent, to specify the detailed form and function.

Everything else (the kind of thing you will find in standard mnemonics for life's properties, such as movement or sensitivity) are just nice-to-have added extras from the point of view of bacteria.

It doesn't take much reflection to appreciate that all six factors are profoundly interdependent, and almost certainly needed to be from the very beginning too. A continuous supply of organic carbon is obviously central to growth, replication, ... everything. At a simple level, even an 'RNA world' involves the replication of RNA molecules. RNA is a chain of nucleotide building blocks, each one of which is an organic molecule that must have come from somewhere. There is an old rift between origin-of-life researchers about what came first, metabolism or replication. It's a barren

debate. Replication is doubling, which consumes building blocks in an exponential fashion. Unless those building blocks are replenished at a similar rate, replication swiftly ceases.

One conceivable escape is to assume that the first replicators were not organic at all, but were clay minerals or some such, as long and ingeniously argued by Graham Cairns-Smith. Yet that solves little, because minerals are too physically clumsy to *encode* anything even approaching an RNA-world level of complexity, although they are valuable catalysts. But if minerals are no use as replicators, then we need to find the shortest and fastest route to get from inorganics to organic molecules that do work as replicators, like RNA. Given that nucleotides have been synthesised from cyanamide, it's pointless to posit unknown and unnecessary intermediates; it's far better to cut straight to the chase, to assume that some early environments on earth could have provided the organic building blocks – activated nucleotides – needed for the beginnings of replication.⁴ Even if cyanamide is a poor starting point, the tendency to produce a strikingly similar spectrum of organics under disparate conditions, from electrical discharges in a reducing atmosphere, to cosmic chemistry on asteroids, to high-pressure bomb reactors, suggests that certain molecules, probably including some nucleotides, are favoured by thermodynamics. To a first approximation, then, the formation of organic replicators requires a continuous supply of organic carbon in the same environment. That rules out freezing environments, incidentally – while freezing can concentrate organics between ice crystals, there is no mechanism to replenish the building blocks needed to continue the process.

What about energy? That is also needed in the same environment. Joining individual building blocks (amino acids or nucleotides) together to form

⁴ This is an appeal to Occam's razor, the philosophical basis of all science: assume the simplest natural cause. That answer might turn out not to be correct, but we should not resort to more complex reasoning unless it is shown to be necessary. We might ultimately need to invoke celestial machinations to explain the origin of replication, when all other possibilities have been disproved (though I doubt it); but until then we should not multiply causes. This is simply a way of approaching a problem; but the remarkable success of science shows that it is a very effective approach.

long-chain polymers (proteins or RNA) requires first activating the building blocks. That in turn demands a source of energy – ATP, or something similar. Perhaps very similar. In a waterworld, as was the earth 4 billion years ago, the source of energy needs to be of a rather specific kind: it needs to drive the polymerisation of long-chain molecules. That involves removing one molecule of water for each new bond formed, a dehydration reaction. The problem of dehydrating molecules in solution is a bit like trying to wring out a wet cloth under water. Some prominent researchers have been so distracted by this problem that they have even contended that life must have started on Mars, where there was much less water. Life then hitch-hiked to earth on a meteorite, making us all Martians really. But of course life here on earth does perfectly well in water. Every living cell pulls off the dehydration trick thousands of times a second. We do so by coupling the dehydration reaction to the splitting of ATP, which takes up one molecule of water each time it is split. Coupling a dehydration to a 'rehydration' reaction (technically termed 'hydrolysis') in effect just transfers the water, while at the same time releasing some of the energy pent up in the bonds of ATP. That greatly simplifies the problem; all that is needed is a continuous supply of ATP or a simpler equivalent, such as acetyl phosphate. We'll address where this may have come from in the next chapter. For now, the point is that replication in water needs a continuous and liberal supply of both organic carbon and something much like ATP, in the same environment.

That's three out of six factors: replication, carbon and energy. What about compartmentalisation into cells? This is again a matter of concentration. Biological membranes are made of lipids, which are themselves composed of fatty acids or isoprenes (joined to a glycerol head-group, as noted in the previous chapter). When concentrated above a threshold level, fatty acids spontaneously form into cell-like vesicles that can grow and divide if continuously 'fed' with new fatty acids. Here again, we need a continuous supply of both organic carbon and energy to drive the formation of new fatty acids. For fatty acids, or for that matter nucleotides, to accumulate faster than they dissipate, there must be some sort of focusing: a physical funnelling or natural compartmentalisation that increases their concentration locally, enabling them to form larger-scale structures. When such conditions are met, the formation of

vesicles is not magic: physically, this is the most stable state → overall entropy increases as a result, as we saw in the previous chapter.

If reactive building blocks are indeed supplied continuously, then simple vesicles will grow and divide spontaneously, as a result of surface-area-to-volume constraints. Imagine a spherical vesicle – a simple 'cell' – enclosing various organic molecules. The vesicle grows by incorporating new materials: lipids in the membrane and other organics inside the cell. Now let's double in size: double the membrane surface area, and double the organic contents. What happens? Doubling the surface area more than doubles the volume, because the surface area increases by the square of the radius, while the volume increases by its cube. But the contents only doubled. Unless the contents increase at a faster rate than the membrane surface area, the vesicle will buckle into a dumb-bell, which is already halfway to forming two new vesicles. In other words, arithmetic growth introduces an instability that leads to division and doubling, rather than simply getting bigger. It's only a matter of time before a growing sphere divides up into smaller bubbles. So a continuous flux of reactive carbon precursors entails not only a primitive cell formation but also a rudimentary form of cell division. Such budding, incidentally, is also how L-form bacteria, which lack a cell wall, divide.

The problem of surface-area-to-volume ratio must set a limit to the size of cells. This is just a matter of the supply of reactants and the removal of waste. Nietzsche once observed that humans will not mistake ourselves for gods so long as we need to defecate. But in fact excretion is a thermodynamic necessity, binding even for the godliest. For any reaction to continue in a forward direction, the end product must be removed. This is no more mysterious than the build-up of a crowd at a railway station. If passengers can't get on to a train as fast as new people arrive, there will soon be a blockage. In the case of cells, the rate at which new proteins are formed depends on the rates of delivery of reactive precursors (activated amino acids) and removal of waste (methane, water, CO₂, ethanol – whatever the energy-releasing reaction may be). If these waste products are not physically removed from the cell, they prevent the forward reaction from continuing.

The problem of waste removal is another fundamental difficulty with the

idea of a primordial soup, in which reactants and waste marinate together. There is no forward momentum, no driving force for new chemistry.⁵ Likewise, the larger a cell becomes, the closer it approximates to soup. Because the volume of a cell rises faster than its surface area, the relative rate at which fresh carbon can be delivered and waste removed across its bounding membrane must fall as the cell gets larger. A cell on the scale of the Atlantic ocean, or even a football, could never work; it is just soup. (You might think that an ostrich egg is as big as a football, but the yolk sac is mostly just a food dump – the developing embryo itself is much smaller.) At the origin of life, natural rates of carbon delivery and waste removal must have dictated a small cell volume. Some sort of physical channelling would also seem to be necessary: a continuous natural flow that delivers precursors and carries away waste.

That leaves us with catalysts. Today, life uses proteins – enzymes – but RNA also has some catalytic capabilities. The trouble here is that RNA is already a sophisticated polymer, as we have seen. It is composed of multiple nucleotide building blocks, each of which must be synthesised and activated to join together into a long chain. Before that happened, RNA could hardly have been the catalyst. Whatever process gave rise to RNA must also have driven the formation of other organic molecules that are easier to make, notably amino acids and fatty acids. Thus any early 'RNA world' must have been 'dirty' – contaminated with many other types of small organic molecules. The idea that RNA somehow invented metabolism by itself is absurd, even if RNA did play a key role in the origins of replication and protein synthesis. So what did catalyse the beginnings of biochemistry? The probable answer is inorganic complexes, such as metal

⁵ A familiar example is the alcohol content of wine, which cannot rise above about 15% by alcoholic fermentation alone. As alcohol builds up, it blocks the forward reaction (fermentation), preventing the formation of any more alcohol. Unless the alcohol is removed, fermentation grinds to a halt: the wine has reached thermodynamic equilibrium (it has become soup). Spirits such as brandy are produced by distilling wine, thereby concentrating the alcohol further; I believe we are the only life form that has perfected distillation.

sulphides (in particular iron, nickel and molybdenum). These are still found as cofactors in several ancient, and universally conserved, proteins. While we tend to think of the protein as the catalyst, in fact the protein only speeds up reactions that happen anyway – the cofactor determines the nature of the reaction. Stripped of their protein context, cofactors are not very effective or specific catalysts, but they are much better than nothing. How effective they are depends, yet again, on the throughput. The first inorganic catalysts just began the channelling of carbon and energy in the direction of organics, but they cut the need for a tsunami back down to a mere river.

And these simple organics (notably amino acids and nucleotides) also have some catalytic activity of their own. In the presence of acetyl phosphate, amino acids can even join together, to form short 'polypeptides' – little strings of amino acids. The stability of such polypeptides depends in part on their interactions with other molecules. Hydrophobic amino acids or polypeptides that associate with fatty acids should persist longer; and charged polypeptides that bind to inorganic clusters such as FeS minerals could also be more stable. Natural associations between short polypeptides and mineral clusters may enhance the catalytic properties of minerals, and could be 'selected' for by simple physical survival. Imagine a mineral catalyst that promotes organic synthesis. Some of the products bind to the mineral catalyst, prolonging their own survival, while at once improving (or at least varying) the catalytic properties of the mineral. Such a system could in principle give rise to richer and more complex organic chemistry.

So how could a cell be built from scratch? There must be a continuously high flux of reactive carbon and usable chemical energy, flowing past rudimentary catalysts that convert a modest proportion of that flux into new organics. This continuous flux must be constrained in some way that enables the accumulation of high concentrations of organics, including fatty acids, amino acids and nucleotides, without compromising the outflow of waste. Such a focusing of flow could be achieved by a natural channelling or compartmentalisation, which has the same effect as the channelling of flow in a water mill – it increases the force of a given flux in the absence of enzymes, so lowering the total amount of carbon and energy required. Only if the

synthesis of new organics exceeds their rate of loss into the outside world, enabling their concentration, will they self-assemble into structures such as cell-like vesicles, RNA and proteins.⁶

Plainly this is no more than the beginnings of a cell – necessary, but far from sufficient. But let's put aside the details for now, and focus on just this one point. Without a high flux of carbon and energy that is physically channelled over inorganic catalysts, there is no possibility of evolving cells. I would rate this as a necessity anywhere in the universe: given the requirement for carbon chemistry that we discussed in the last chapter, thermodynamics dictates a continuous flow of carbon and energy over natural catalysts. Discounting special pleading, that rules out almost all environments that have been touted as possible settings for the origin of life: warm ponds (sadly Darwin was wrong on that), primordial soup, microporous pumice stones, beaches, panspermia, you name it. But it does not rule out hydrothermal vents; on the contrary, it rules them in. Hydrothermal vents are exactly the kind of dissipative structures that we seek – continuous flow, far-from-equilibrium electrochemical reactors.

Hydrothermal vents as flow reactors

The Grand Prismatic Spring in Yellowstone National Park reminds me of the Eye of Sauron in its malevolent yellows, oranges and greens. These remarkably vivid colours are the photosynthetic pigments of bacteria that use hydrogen (or hydrogen sulphide) emanating from the volcanic springs as an electron donor. Being photosynthetic, the Yellowstone bacteria give little real insight into the origin of life, but they do give a sense of the primal

⁶ I don't really mean proteins, I mean polypeptides. The sequence of amino acids in a protein is specified by a gene, in DNA. A polypeptide is a string of amino acids joined together by the same type of bond, but is usually much shorter (perhaps just a few amino acids) and their sequence does not need to be specified by a gene. Short polypeptides will form spontaneously from amino acids, in the presence of a chemical 'dehydrating' agent such as pyrophosphate or acetyl phosphate, which are plausible abiotic precursors of ATP.

power of volcanic springs. These are plainly hot spots for bacteria, in otherwise meagre environments. Go back 4 billion years, strip away the surrounding vegetation to the bare rocks, and it's easy to imagine such a primal place as the birthplace of life.

Except that it wasn't. Back then, the earth was a waterworld. Perhaps there were a few terrestrial hot springs on small volcanic islands protruding above tempestuous global oceans, but most vents were submerged beneath the waves in deep-sea hydrothermal systems. The discovery of submarine vents in the late 1970s came as a shock, not because their presence was unsuspected (plumes of warm water had betrayed their presence) but because nobody anticipated the brutal dynamism of 'black smokers', or the overwhelming abundance of life clinging precariously to their sides. The deep ocean floor is mostly a desert, nearly destitute of life. Yet these tottering chimneys, billowing out black smoke as if their lives depended on it, were home to peculiar and hitherto unknown animals – giant tube worms lacking a mouth and anus, clams as big as dinner plates, and eyeless shrimp – all living at a density equivalent to tropical rain forests. This was a seminal moment, not only for biologists and oceanographers, but perhaps even more for those interested in the origin of life, as the microbiologist John Baross was quick to appreciate. Since then, Baross more than anyone has kept attention focused on the extraordinary vigour of chemical disequilibria in vents down in the bible-black ocean depths, far away from the sun.

Yet these vents, too, are misleading. They are not really cut off from the sun. The animals that live here rely on symbiotic relationships with bacteria that oxidise the hydrogen sulphide gas emanating from the smokers. That is the principal source of disequilibrium: hydrogen sulphide (H_2S) is a reduced gas that reacts with oxygen to release energy. Recall the mechanics of respiration from the previous chapter. Bacteria use H_2S as an electron donor for respiration, and oxygen as the electron acceptor, to drive ATP synthesis. But oxygen is a side-product of photosynthesis, and was not present on the early earth, before the evolution of oxygenic photosynthesis. The stunning eruption of life around these black smoker vents is therefore completely, albeit indirectly, dependent on the sun. And that means these vents must have been very different 4 billion years ago.