CHAPTER THREE



Silence of the Aeons

Three Billion Years of Microbial Evolution

T IS NEXT TO IMPOSSIBLE FOR US, with our historical perspective honed to decades or centuries, to conceive of the vast tract of time that ebbed away during the Precambrian era. We are dealing with a period that spanned 4 billion years — nine-tenths of the total duration of the Earth. Imagine that we are rocketing backwards through time at a rate of one millennium per second. In two seconds, we will have returned to the time of Christ, in ten seconds to the birth of agriculture; in half a minute we will see the first cave painters, and in less than two minutes we will catch a glimpse of our ape-like ancestors shuffling across the African savanna. Rushing backwards, the catastrophe that wiped out the dinosaurs will unfold before our eyes in 18 hours time; and in 4½ days we will have prime seats for the opening drama of multicellular life in the Cambrian explosion. Then we continue our journey in silence. In 44 days time, we will have returned to the first mysterious stirrings of life, and in 53 days the Earth will condense from a cloud of gas and dust.

For 40 days and 40 nights, in our compressed time scale, the Earth was populated entirely by microscopic single-celled bacteria and simple algae. With no real fossil record to bridle the imagination, it is not surprising that most of the pioneering efforts to understand the early history of life were little better than speculation. How can we have any coherent idea today of biochemical changes taking place in microbes that left little trace

in the rocks, or of the oxygen concentration in a fleeting atmosphere long gone? The answer is indeed written in the rocks, sometimes in microscopic fossils, and sometimes in the molecular ghosts of ancient geochemical cycles. More than this, the atavistic genes of modern organisms often betray their evolutionary roots. The script written in the genes is enigmatic, although obviously meaningful. Our only guide, a molecular Rosetta stone, is the way in which the proteins encoded by the genes are used today. If a protein such as haemoglobin, the red pigment of red blood cells, is specifically designed to bind oxygen today, and we know from genetic sequences that some bacteria also have a gene for a similar protein, there is certainly a good possibility that our common ancestor had it too. If so, we can infer that they too used the haemoglobin to bind oxygen. If, instead, they used it for something else, the clue to what that was may still be hidden in the structure of the molecule.

To understand the effect of oxygen on evolution, we need to trace two stories in the rocks and the genes: the evolution of the microbes themselves, and the timing and magnitude of the oxygen build-up in the air. Before we begin, however, we will do well to bury a hatchet in a particularly subversive double-headed ghoul. This is the common misapprehension that evolution necessarily tends towards greater complexity, and that microbes, being microscopic and without brains, are at the bottom of the evolutionary pile. So many evolutionary biologists have attacked the lay concept of evolution as a progression towards a higher plane, and to so little avail, that one begins to wonder whether there is a global conspiracy to thwart them. Two cautionary tales should provide a clearer perspective on Precambrian evolution. The first challenges the assumption that evolution tends towards greater complexity, while the second argues that microbes are far from simple.

In 1967, Sol Spiegelman, a molecular biologist at the University of Illinois, reported a series of experiments designed to establish the smallest unit that could evolve by natural selection. He took a simple virus that replicated itself using only a handful of genes, which consist of a string or 'sequence' of 4500 'letters'. The protein products of these genes subverted the molecular machinery of infected cells to produce new viral particles. Spiegelman wanted to see just how simple the viral life-cycle could become if he provided the virus with all its raw materials in a test tube, instead of a host cell with its complicated molecular machinery. He gave his virus the main enzyme necessary for it to complete its life-cycle, and a free supply of all the basic building blocks needed for it to copy its genes.

The results were spectacular. For a while the virus replicated itself exactly, preserving its original gene sequence. After a period, however, a mutation caused part of one gene to be lost. Because this gene was only necessary for the virus to complete its normal life-cycle in an infected cell, and was not necessary in the test tube, the mutant virus could survive quite happily without it. More than happily, in fact: the new gene sequence was shorter than the old one, so the mutant virus could replicate itself faster than the non-mutant viruses. This faster rate of replication allowed the mutants to prevail over their competitors until they, too, were overtaken by a new mutant, an even slimmer-line virus able to replicate itself still faster. In the end, Spiegelman produced a degenerate population of tiny gene fragments, which became known as 'Spiegelman's monsters'. Each little monster was just 220 letters long. They could replicate at a furious speed in the test tube, but could not hope to survive in the outside world.

The moral of the tale is simple. Evolution selects for beneficial adaptations to a particular environment, and the simplest, fastest or most efficient solution will tend to win out, even if this means that excess baggage is jettisoned and organisms become less complicated. We now realize that many simple single-celled organisms, which we once thought were relics from a primitive age that had never evolved a complex lifestyle, have instead lost their ancient sophistication. We touched on fermentation in the last chapter. Far from being a simple energy-producing system that was later displaced by more efficient mechanisms involving oxygen, it seems that, as in the yeasts, fermentation is often a recent (in evolutionary terms) adaptation to oxygen-free environments, and such fermenters have actually lost their ancestors' ability to use oxygen.

My second cautionary tale illustrates the metabolic sophistication of supposedly simple microbes. Humans and other large animals will quickly suffocate and die without oxygen, because our bulk, a community of some 15 million million cells, precludes the use of any other type of respiration. As a result, we are rather limited in the biochemical reactions we can carry out, albeit very efficient at marshalling our limited resources. Some microbes, however, can live using oxygen to respire, but if deprived of air will simply switch to another way of satisfying their energy requirements and continue without a glitch.

The bacterium Thiosphaera pantotropha is one such, and is about as far removed as we can get from our sense of an evolutionary pinnacle: it lives on faeces. Originally isolated in 1983 from an effluent-treatment plant, it applies an extraordinary virtuosity to the extraction of energy from sewage.

When oxygen is present, it extracts energy from a wide range of organic and inorganic substrates by aerobic respiration. When conditions become anaerobic, however, it can extract energy from thiosulphate or sulphide using nitrogen oxides instead of oxygen. The only trick missing from this metabolic cabaret is an ability to ferment. Such biochemical versatility lends the bacterium great flexibility in lifestyle — it can switch from one energy-producing process to another in response to sudden chemical changes, which are brought about by the periodic injections of dissolved oxygen used to speed up the decomposition of effluent in treatment plants.

Curiously, genetic analysis of a wide range of living organisms suggests that LUCA — the hypothetical bacterium proposed as the Last Universal Common Ancestor, the greatest grandmother of all living things in the world today — may have had a similar ability to switch between different types of metabolism, nearly 4 billion years ago. Most of her descendants appear to have lost their illustrious ancestor's flexibility. We will return to this theme in Chapter 8.

The Precambrian, then, was a time of spectacular metabolic innovation. Microbes learnt to harness the power of the Sun, as well as the oxidizing power of oxygen, and to generate energy from an array of sulphur, nitrogen and metal compounds. The chemistry of these life-giving reactions has sometimes left subtle traces — so-called carbon or sulphur signatures — in sedimentary rocks, and occasionally, not at all subtly, in the form of billions of tons of rocks. The metabolism of ancient microbes was directly or indirectly responsible for our most important reserves of iron, manganese, uranium and gold, to say nothing of the gold prospector's false nugget, iron pyrites. These rocks and ores were not deposited continuously or synchronously, but at different times and under different environmental conditions. Their sequence has been carefully reconstructed through precise radioactive dating, and together the findings open a colourful window on oxygen and life in the formative years of our planet.

The first signs of life in rocks are found in the same Greenland rocks that we discussed in Chapter 2, and take the form of an anomaly in the proportions of different carbon isotopes they contain. This important finding was reported in the journal Nature in 1996 by a NASA-funded doctoral student, Stephen Mojzsis, and his colleagues at the Scripps Institution of Oceanography at La Jolla in California. The interpretation of these carbon signatures in rocks is so important to our story that it is worth explaining what they are and why they are there. Not only do carbon isotopes preserve a record of the triumphs and tribulations of life, but their shifting proportions can permit surprisingly quantitative estimates of the changes in the atmospheric composition of the ancient Earth.

There are several different atomic forms of carbon (as opposed to molecular forms such as diamond or graphite). These atomic variants are called *isotopes*. Each carbon isotope has six protons in the nucleus, giving them all an atomic number of six. This means they are all carbon and all have exactly the same chemical properties. But the carbon isotopes differ in the number of neutrons in their nuclei and so vary in their atomic weight. The more neutrons they have, the heavier the atoms. Carbon-12, for example, has six neutrons, giving it an atomic weight of 12 (6 protons + 6 neutrons), whereas carbon-14 has 8 neutrons, giving it an atomic weight of 14 (6 + 8).

Carbon-12 is by far the most abundant carbon isotope on Earth (accounting for 98.89 per cent of the total) and has an honourable place in chemistry as the standard against which the relative weights of all other elements are measured. The carbon-12 nucleus is stable and does not decay. In contrast, carbon-14 is produced continuously in minute amounts (about 1 part in 10¹²; one part in a million million) in the upper atmosphere, through the bombardment of cosmic rays. The unstable carbon nuclei formed decay through radioactive emissions at a fixed rate. The half-life (the time taken for half the total mass to decompose) is exactly 5570 years. This short time period (in geological terms) makes radiocarbon dating useful for determining the age and authenticity of prehistoric remains or historical documents, such as the Dead Sea scrolls and the Turin shroud.¹

Fascinating as it is, carbon-14 has no further place in our story. It is the other main isotope of carbon, carbon-13, that concerns us here. Unlike carbon-14, carbon-13 has a stable nucleus and does not decay. In this respect, it is similar to carbon-12. The total amount of carbon-13 in the Earth and its atmosphere is therefore constant (1.11 per cent of the

¹ Carbon-14 is dispersed throughout the atmosphere and absorbed by living plants in photosynthesis, then eaten by animals, in proportion to its abundance in carbon dioxide. This abundance remains roughly constant because in the long term the rate of formation balances the rate of decay. When plants and animals die, however, the cessation of gas exchange or breathing means that their tissues are no longer in equilibrium with the atmosphere, so their carbon-14 content declines in proportion to the rate of radioactive decay; older organic compounds therefore contain less carbon-14.

total). This means that the overall ratio of carbon-12 to carbon-13 on or in the Earth is constant (99.89 to 1.11). In other words, if we add up the total amount of carbon in plants, animals, fungi and bacteria, and buried as coal, oil and gas, and present in the air as carbon dioxide, and dissolved in the oceans and swamps as carbonates, and petrified as carbonate rocks (such as limestone), then we will find that the overall ratio of stable carbon isotopes is 99.89 to 1.11.

Despite this fixed ratio, there are still some small but definite variations in the ratio of carbon-12 to carbon-13 in the carbon buried in the rocks. These variations are brought about by living things, and so far as we know, *only* by living things. The reason is that photosynthetic cells using carbon dioxide from the air or sea to make organic matter prefer to use carbon-12. This is because the lighter carbon-12 atoms have a slightly greater vibrational energy, which means that a smaller input of energy (activational energy) is needed for a reaction to take place. The reactions of the carbon-12 isotope are therefore catalyzed more quickly by enzymes than those of the heavier (less vibrational) carbon-13 isotope. The faster rate at which carbon-12 bonds are cracked means that organic matter becomes enriched in carbon-12 relative to carbon-13. In fact, the ratio of carbon-12 to carbon-13 is skewed towards carbon-12 by an average of 2 or 3 per cent compared with the unadulterated background ratio.

When the remains of plants, algae or cyanobacteria are buried in sediments, their extra carbon-12 is buried with them. Because the buried organic matter is enriched in carbon-12, it is impoverished in carbon-13. This means that more carbon-13 is left behind as carbonates in the oceans or rocks, or as carbon dioxide in the air. This is called the principle of mass balance – which simply says that what is buried below the ground cannot be found above the ground. The implications of this elementary idea have a surprisingly long reach. Both carbon-12 and carbon-13 are incorporated into carbonate rocks (such as limestone) in a ratio that reflects their relative concentration in the oceans. As more carbon-12 is buried as part of organic matter, more carbon-13 is left behind in the oceans, and so the carbonate rocks have a relatively high content of carbon-13. Thus biological activity is betrayed in two different ways: by an enrichment of carbon-12 in buried organic matter, such as coal, or by an enrichment of carbon-13 in carbonate rocks such as limestone.

Geological periods conducive to carbon burial, such as the Carboniferous (about 300 million years ago) with its huge, low-lying swamps and

massive coal seams, leave robust carbon-12 signatures in organic inclusions such as coal in the rocks. The farther back in time we go, the harder it is to read carbon signatures, if only because less and less organic matter survives intact. Eventually, the samples shrink to the size of grains and require sophisticated equipment to read them. With this in mind, Steven Mojzsis and colleagues set about studying the ancient Greenland rocks, determined to think small. Their approach brought swift rewards: they found minute carbon residues trapped inside grains of a calcium phosphate mineral called apatite. Apatite can be secreted by microorganisms, but can also crystallize inorganically from the oceans, so the association of carbon with apatite is, in itself, no more than suggestive of life. When the Scripps team examined the carbon-isotope ratios, however, the results were startling. The carbon inclusions were enriched in carbon-12 by as much as 3 per cent over the normal background ratio. As a leading geochemist, Heinrich Holland, remarked in the journal Science: "the most reasonable interpretation of the data is surely that life existed on earth more than 3.85 billion years ago." Not only this, but life may even have discovered the trick of photosynthesis, which is, after all, the main source of carbon signatures today.

Is this credible? Other pieces of evidence fit the same story. Moving forward a mere 300 million years, to the 3.5-billion-year-old rocks in Warrawoona in Western Australia, we find microscopic fossils that resemble modern cyanobacteria. Throughout the Precambrian period, most cyanobacteria lived in communal structures called stromatolites: great domes of living rock, which grew to heights of metres. A few living stromatolites are still found today in the right conditions — in Shark Bay in Western Australia, for example. Nearby, shapes resembling modern stromatolites are imprinted in rocks 3.5 billion years old. There is little evidence of geothermal activity, past or present, in these bays, so it seems likely that the microbes living in these ancient stromatolites gained their energy from photosynthesis, just as they do today. While none of these findings is conclusive on its own, when taken together, the carbon signatures, microfossils and fossil stromatolites do make it look as if photosynthetic bacteria were already colonizing the early Earth at least 3.5 billion years ago.

The earliest definitive evidence for the existence of cyanobacteria must wait another 800 million years. We are now 2.7 billion years before the present, floating in the shallows of an ocean that was soon to precipitate some of the largest iron-ore formations in the world. Today we can visit these iron formations in the Hamersley Range, near Wittenoom in Western Australia. For such old rocks, they have suffered relatively little chemical and physical change, called metamorphosis by geologists. Heat and pressure, the twin forces of metamorphosis, tend to destroy flimsy biological molecules. Because the Hamersley Range had suffered so little metamorphosis, Jochen Brocks and his colleagues at the Australian Geological Survey and University of Sydney, held out hope that a few ancient molecules — characteristic biological fingerprints called biomarkers might have survived intact in the shales underlying the iron formations. After conducting a painstaking series of extractions and laboratory tests to eliminate the possibility of contamination with more recent molecules, their hopes were rewarded in full when they discovered a rich mixture of recognizable biomarkers. Their work was promptly published in Science in August 1999, with a flurry of commentary. Not only had the Australian surveyors found fingerprints diagnostic of cyanobacteria — that is, molecules found only in cyanobacteria — they also found a large number of complex steranes, a family of molecules derived from sterols such as cholesterol, which have only ever been found in the cell membranes of our own direct ancestors, the single-celled eukaryotes.

The finding was a double whammy: proof that oxygen-producing cyanobacteria and the first representatives of our own eukaryotic ancestors coexisted not less than 2.7 billion years ago. The earliest known fossils of eukaryotic cells date to about 2.1 billion years ago, so Brocks and his colleagues had pushed back the evolution of the eukaryotes 600 million years. This is significant in terms of the environment that must have existed to support these cells. Apart from anything else, the biosynthesis of sterols is an oxygen-dependent process, requiring more than a trace of oxygen in the atmosphere. Modern eukaryotes can only synthesize sterols if given at least 0.2 to 1 per cent of the present atmospheric levels of oxygen, and there is no reason to suppose that their ancestors were any different. If the cyanobacteria had indeed evolved between 3.5 and 3.85 billion years ago, as was suggested by the fossil evidence in the Warrawoona rocks and the carbon signatures, it is quite plausible that some free oxygen could have accumulated in the atmosphere by this time. But did this increase in oxygen correspond exactly in time to the evolution of the eukaryotes? And if so, did the rise in oxygen in fact stimulate their evolution?

Trends in carbon-isotope ratios can be used, in principle, to calculate changes in atmospheric oxygen. This is because the burial of organic matter prevents the complete oxidation, by respiration, of the carbon produced by photosynthesis. As photosynthesis and respiration are essentially reverse reactions, the one generating and the other consuming oxygen, any increase in the amount of carbon buried should lead to an equivalent increase in the amount of free oxygen left over in the air. If we know exactly how much carbon was buried at any one time, then, in principle, we can calculate how much oxygen must have been left in the air. In practice, however, unless we can be certain that the rate of oxygen removal by volcanic gases or the erosion of land masses remains constant, all we can say is that there was a qualitative increase in oxygen. During recent geological history, the younger rocks preserve a detailed history of environmental change, and we are sufficiently familiar with most of the important parameters to calculate oxygen levels on the basis of carbon burial, as we shall see in Chapter 5. Unfortunately, this approach is unreliable when dealing with the very ancient Precambrian period — there are so many uncertainties that, at best, we only get a sense of the direction of change. For a more quantitative estimate, we must employ other methods.

One clue to oxygen levels during this period is to be found in the very same iron formations that overlie the shales of the Hamersley Range. Massive sedimentary iron formations were deposited here and around the world in alternating bands of red or black ironstone (haematite and magnetite, respectively), and sediment, typically flint or quartz. The individual bands range in depth from millimetres to metres, while the formations themselves can be up to 600 metres [approximately 2000 feet] thick. Most of these formations were deposited between 2.6 and 1.8 billion years ago, but sporadic outcrops range in age from 3.8 billion to 800 million years.

Today, after the exhaustion of most premium ore deposits, the banded iron formations are by far the world's richest source of low-grade iron ore. According to the US Geological Survey, world iron-ore resources still exceed 800 billion tons of crude ore, containing more than 230 billion tons of iron, much of which comes from Australia, Brazil and China. Of this total, at least 640 billion tons were laid down between 2.6 and 1.8 billion years ago. The Hamersley formation alone contains 20 billion tons of iron ore, with 55 per cent iron content.

Exactly how these iron formations came into being, or why they should be banded, is a mystery. Or rather, there are so many possible explanations, and so little evidence to support one theory over another, that few geologists would be bold enough to attempt a categorical explanation. There have nonetheless been some imaginative attempts. Ancient superstition held that large deposits of haematite (from the Greek 'bloodlike') formed from the streams of blood that flowed into the ground after great battles. More scientifically, the banding of ironstones has been attributed to cyclical extinctions of algal populations, overcome by their own toxic oxygen waste. Neither theory has much credence. In fact, there is no reason to suppose that all the formations were produced in the same way, especially those separated by deep gulfs of time. But some general principles do apply to them all, and these reveal something of the conditions under which they must have formed. Most importantly, no banded iron formations have been deposited since atmospheric oxygen approached modern levels. Because iron does not dissolve in the presence of oxygen, the immediate implication is that the oceans were oxygen-free before the deposition of the banded iron formations, and too well aerated to support their formation in later times. To tease the truth out of this implication, we will need to look at the behaviour of iron in a little more detail.

Only the Earth's core, and meteorites, contain pure iron. Tools made from meteoritic iron are an expensive curiosity. All iron in ores from the Earth's crust is oxidized to some extent, although we shall see that iron in the oxidized state does not always imply the presence of oxygen. There are two main forms of iron in nature, ferrous iron (Fe²⁺), which tends to be soluble, and the more highly oxidized ferric iron (Fe³⁺), best known in the guise of rust (ferric oxides), which is insoluble.² In the presence of oxygen, soluble ferrous iron is oxidized to insoluble rust. Not surprisingly, there is very little iron dissolved in today's well-ventilated oceans, as oxygen snatches electrons from dissolved iron and the ferric oxide compound precipitates out as rust before any iron build-up can occur. One exception is the poorly ventilated floor of the Red Sea, where dissolved iron is enriched to 5000 times normal levels, and only bacteria can survive. The early Precambrian oceans must have been similar in this respect: in the absence of oxygen, dissolved iron from volcanic emissions and erosion could have accumulated to very high levels.

 $^{^2}$ The two forms differ in their degree of oxidation, ferric iron (Fe $^{3+}$) being more oxidized than ferrous iron (Fe $^{2+}$).

A second modern example gives an idea of what might have happened next. The Black Sea is the largest body of poorly oxygenated water in the world, and is stratified into two layers. The surface waters are well oxygenated to depths of about 200 metres [656 feet], and if not fished to oblivion support a teeming ecosystem, including the famous caviar sturgeon. In contrast, the deeper waters, which account for 87 per cent by volume of the Black Sea, are stagnant and cannot support animal life (with the sole exception, it seems, of nematode worms, the only known animal that can complete its life cycle in the absence of oxygen). The current state of the Black Sea seems to have developed about 7500 years ago, several thousand years after the end of the last ice age, in an event that has been linked to Noah's Flood by the marine geologists William Ryan and Walter Pitman of Columbia University. As the great land glaciers melted, the sea level around the world rose by several hundred feet. The Black Sea, however, was isolated in its own basin by a land bridge across the Bosphorus, and the glacial meltwater did not affect its depth as much as that of the surrounding seas. The basin was left low and dry, so to speak, well below sea level, as is the Dead Sea today.

Whether as the consequence of an earthquake, or stormy weather, or the pressure of the rising Mediterranean, the land bridge spanning the Bosphorus finally collapsed with a roar that must have sounded like the wrath of God. This, say Ryan and Pitman, was the reality of Noah's flood. Salt water poured into the low Black Sea basin at an estimated rate of 10 cubic miles [42 million cubic metres] per day — a cascade 130 times greater than the Niagara Falls. The villages clinging to the shores were drowned beneath the Mediterranean waters, they say, in a catastrophe whose memory reverberated around the ancient world. An area the size of Florida was added to the existing lake.

Since biblical times, the shallow, tideless straits of the Bosphorus have impeded mixing of the brackish Black Sea water with the saline water of the Mediterranean. The denser saline sinks to the bottom, and the undisturbed bottom waters rarely come into contact with the air. The only living things that thrive in these depths are anaerobic (oxygen-hating) bacteria. Many of these are sulphate-reducing bacteria, which generate the noxious gas hydrogen sulphide as a waste product. Because hydrogen sulphide reacts with any oxygen percolating down, the depths remain anoxic and the stratified system, once established, sustains itself. The build-up of hydrogen sulphide makes the deep waters of the Black Sea stink of rotten eggs, and stains the mud on the bottom black, giving the

sea its modern name. Its ancient name, the Euxine, lends itself to the term euxinic, which refers to any foul-smelling sulphidic body of water, lacking oxygen, movement and animal life in the depths.

The Black Sea, although the largest, is not the only euxinic body of water on the planet. Similar conditions occur in some Norwegian fjords that are separated from the open ocean by shallow glacial sills. Even the oceans occasionally develop euxinic conditions. Climatic conditions sometimes conspire to cause an upwelling of nutrient-rich bottom waters to the surface. Here, the combination of plentiful nutrients and bright sunlight stimulates an algal bloom, leading to a massive but transient increase in biomass. As the nutrients are exhausted, the algae die and sink to the bottom. Their decay consumes oxygen faster than it can be replenished by currents or diffusion from the oxygen-rich surface waters. These oxygen-poor conditions stimulate a second bloom, this time of oxygenhating sulphate-reducing bacteria, which release hydrogen sulphide as they break down the organic matter. Stagnant conditions may set in for periods of months until the supply of decaying organic matter is exhausted. Occasionally, the stagnant waters well up to the surface, releasing hydrogen sulphide gas into the atmosphere. One such upwelling occurred in St Helena Bay near Cape Town in South Africa in 1998, provoking furious and misguided complaints about the smell of rotten sewage in the air.

Such combinations of circumstances may explain the genesis of banded iron formations. Back in Precambrian times, the low levels of atmospheric oxygen must have kept the oceans permanently euxinic. The surface waters, however, were home to photosynthetic bacteria at least 2.7 billion years ago, and perhaps as long as 3.8 billion years ago. As happens today, there must have been frequent upwellings of the bottom waters, bringing dissolved nutrients and iron into contact with the photosynthetic bacteria living in the surface layers. If these bacteria were cyanobacteria, as suggested by the biomarkers in the Hamersley Range, then they would have been producing oxygen as a waste product of photosynthesis. In such oxygen-rich waters, dissolved iron welling up to the surface would have precipitated out as rust, and sunk to the bottom of the ocean to form beds of red haematite and black magnetite.

If this was the case, the banding of ironstones with flint or quartz could have been produced by seasonal influences, such as higher rates of photosynthesis (and therefore oxygen production) in the summer than in the winter, or seasonal upwellings according to climatic variations. The seasonal fluctuations in iron deposition would have been set against a

steady precipitation of silica. This could not happen today. There is little dissolved silica in the modern oceans: it is extracted by some algae and lower organisms for use in their 'skeletons'. However, in the days when bacteria ruled the waves, silica was not used in this way, and so must have continuously exceeded its solubility limit of about 14–20 parts per million. It would have precipitated in a steady rain to form thick beds of flint or quartz, alternating with seasonal beds of ironstone.

Although this is, perhaps, the most widely accepted model of banded iron formation, there are still some difficulties with it. The oldest iron formations, 3.8 billion years old, were surely formed before oxygen began to accumulate. Furthermore, most of the ironstones around the world do not consist of simple iron oxides such as haematite, as might be expected if oxygen levels were genuinely high and the reactions were no more than bucket chemistry. There are other biological mechanisms that can oxidize iron without any requirement for free oxygen. One was described in 1993 by Friedrich Widdel and his colleagues at the Max Planck Institute for Marine Microbiology in Bremen. They isolated a strain of purple bacteria from lakeside sediments which could use the energy from sunlight to produce iron ores without requiring free oxygen. The main product of the bacterial reaction is a brownish rust-like deposit, ferric hydroxide, which is commonly found in banded iron formations. Widdel argued that the same seasonal upwellings that brought nutrients and iron to the sunny surface waters could have stimulated great bursts of iron-ore formation by purple bacteria. Thus, while the presence of cyanobacteria and rusting iron in banded iron formations suggests that free oxygen may have played a role in their genesis, Widdel and his colleagues have shown that some iron formations could have been formed by purple bacteria in the absence of oxygen. Despite their promise, then, banded iron formations cannot give us a quantitative estimate of oxygen levels in the air during this period.

One possible solution to the problem of exactly when oxygen levels rose has been put forward by Donald Canfield of the University of Southern Denmark, a leading authority on Precambrian oxygen levels, in a series of papers published in *Science* and *Nature*. Canfield turned, rather elliptically at first sight, to the oxygen-hating sulphate-reducing bacteria that produce hydrogen sulphide under stagnant conditions, to estimate the timing of the increase in atmospheric oxygen. His rationale was founded on two observations.

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First, sulphate-reducing bacteria gain their energy from a reaction in which hydrogen reduces sulphate to produce hydrogen sulphide. Although sulphate (SO₄²⁻) is found at high levels in modern sea water (at about 2.5 grams per litre) it should not have been plentiful in the early Precambrian period, as its formation requires the presence of oxygen. This premise is supported by the absence of sulphate evaporites, such as gypsum, from the early Earth. If sulphate can only form in the presence of oxygen, then the sulphate-reducing bacteria could not have established themselves until there was some oxygen in the atmosphere. We can go further: because low sulphate is a rate-limiting factor for sulphatereducing bacteria, virtually precluding their growth in freshwater lakes, their activity depends on the concentration of sulphate. This in turn depends on the concentration of oxygen. Put another way, even though sulphate-reducing bacteria are strictly anaerobic — they are actually killed by oxygen — they cannot exist in a world without oxygen, and their activity is ultimately governed by oxygen availability.

The second observation applied by Canfield relates to sulphur isotopes. Just as photosynthesis leaves a carbon signature in the rocks, the sulphate-reducing bacteria similarly discriminate between the two stable isotopes of sulphur, sulphur-32 and sulphur-34. As with carbon isotopes, the lighter sulphur-32 atoms have a slightly greater vibrational energy, and so their reactions are catalyzed more quickly by the action of enzymes. Sulphate-reducing bacteria therefore produce hydrogen sulphide gas enriched in sulphur-32, leaving more sulphur-34 behind in the oceans. In some conditions, both the hydrogen sulphide and sulphate can precipitate from the oceans to form rocks. Sulphur signatures can be read in these rocks. In particular, and perhaps surprisingly for those who still do not associate minerals with life, hydrogen sulphide reacts with dissolved iron to form iron pyrites, which then sinks to the bottom sediments. Iron pyrites can be formed by either volcanoes or bacteria. Against the consistent, unadulterated ratio of sulphur isotopes from volcanoes, the hand of biology signs off with a clear signature — in other words, a distortion in the natural balance of isotopes.

Canfield examined the sedimentary iron pyrites deposited during the Precambrian period for sulphur signatures, and found them. The first signs of a skewing in the sulphur-isotope ratios date to about 2.7 billion years ago, implying there was a build-up of oxygen at this time. Interestingly, this is very close to the date given to the first eukaryotic cells in the Hamersley shales by Jochen Brocks and his colleagues. After this, little

changed for half a billion years. Then, around 2.2 billion years ago, there was an abrupt rise in the sulphur-32 content of iron pyrites, suggesting that the amount of sulphate in the oceans must have risen to the point where they could support a much larger population of sulphate-reducing bacteria. This, in turn, indicates that much more oxygen must have been available to produce the sulphate. Thus Canfield's work implies that there was a small rise in oxygen levels 2.7 billion years ago, followed by a much larger rise about 2.2 billion years ago.

Unequivocal evidence of free oxygen in the air and oceans requires proof of oxidation on land, as changes wrought by the thin air cannot be obscured or confounded by the rich biology and chemistry of the oceans. More than a billion years before the invasion of the land by plants and animals, the terrestrial populations of microbes could not have compared in abundance or diversity with their marine cousins. The widespread rusting of iron minerals on land is therefore the most tangible evidence we have for oxygen in the atmosphere. These rusting iron minerals are found in fossil soils (palaeosols), and in the so-called continental red-beds.

In a classic series of measurements, the geochemists Rob Rye and Heinrich Holland from Harvard University examined the iron content of ancient fossil soils, and used these measurements to estimate the period when oxygen built up in the air. Their reasoning was as follows. Because iron dissolves in the absence of oxygen, but is insoluble in the presence of oxygen, iron could leach out of very ancient soils (when there was no oxygen in the air) but became trapped in more recent soils (when oxygen was present in the air). By measuring the iron content of fossil soils, Holland and Rye estimated that a large rise in atmospheric oxygen took place between 2.2 and 2 billion years ago. From the amount of iron left in the fossil soils, as well as its rustiness — its oxidation state — they estimated that the concentration of atmospheric oxygen at this time probably reached 5 to 18 per cent of present atmospheric levels.

In terms of timing, these findings are corroborated by the appearance of continental red-beds between 2.2 and 1.8 billion years ago. These sandstone rock formations were probably formed by free oxygen reacting with iron in the rocks during the erosion of mountain ranges. Rivers must have run red as they flowed over the barren surface of the Earth, a scene that conjures up images of nuclear winter. Rather than being washed out to sea, some eroded minerals deposited in valleys and alluvial

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plains, ultimately forming the beds of red sandstone. Because the red-beds were formed from eroded minerals, however, we cannot use them to estimate the concentration of oxygen in the air, only the timing.³ The timeline from the first carbon signatures in Greenland rocks to the formation of the red-beds is shown in Figure 2.

A bizarre microbial relic also attests to a rise in free oxygen around 2 billion years ago: the natural nuclear reactors at Oklo, in Gabon, West Africa. The solubility of uranium, like iron, depends on oxygen. But unlike iron, uranium becomes more soluble, rather than less, in the presence of oxygen. The chief uranium mineral found in rocks older than about 2 billion years is uraninite, but this ore is very rarely found in younger rocks. The sudden transition is associated with the rise in oxygen. What seems to have happened is that, as the oxygen levels increased, oxidized uranium salts leached out of uraninite ores in the rocks and washed away in streams. Their concentration cannot have been higher than a few parts per million.

In Gabon, 2 billion years ago, several streams converged on shallow lakes encrusted with bacterial mats, similar to the mats that still exist today in the geyser pools at Yellowstone National Park in the United States and elsewhere. Some of the bacteria that lived in these mats had a penchant for soluble uranium salts as an energy source. They converted the soluble uranium back into insoluble salts, which precipitated out in the shallow water beneath them. Over the next 200 million years or so, the bacterial mats deposited thousands of tons of black uranium ore in their lakes.

There are two main isotopes of uranium, both radioactive, as most of the Cold War generation knows. Uranium-238 has a long half-life of 4.51 billion years. Half the uranium-238 that was present when the Earth condensed from its cloud of radioactive dust is still out there somewhere. Its sister isotope, uranium-235, decays much faster, with a half-life of about 750 million years. Most uranium-235 has therefore already decayed into its daughter elements, by emitting neutrons. If one of these neutrons hits a nearby uranium-235 nucleus, however, the effect is to split the nucleus into one or more additional neutrons, plus large fragments of roughly equal mass, with a liberation of energy equal to the total loss of

³ The red colour of the continental red-beds shows that the iron was completely oxidized, as would be expected for deposits of eroded debris that had been exposed to the air for an indeterminate, but probably lengthy, period. Because there is no spectrum of oxidation, we cannot estimate the atmospheric oxygen levels from the red-beds.

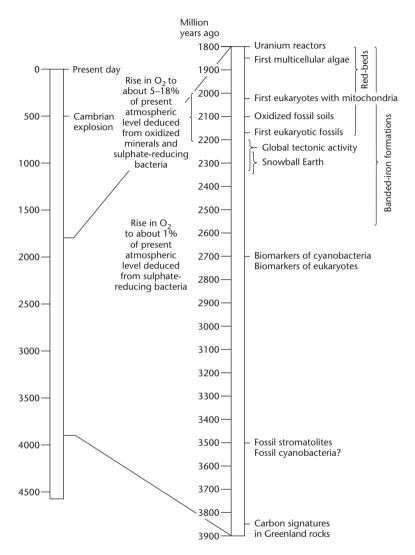


Figure 2: Geological timeline expanding the mid-Precambrian period (Archaean and early Proterozoic). Note the burst of evolutionary activity in the period 2.3 to 2 billion years ago, as oxygen levels rose to about 5–18% of present atmospheric levels.

mass. (Energy is related to mass according to Einstein's famous equation $E = mc^2$.) If the uranium-235 atoms are closely packed together, there is a good chance that the newly emitted neutrons will hit more uranium-235 nuclei. In these circumstances, a chain reaction — nuclear fission — can take place, potentially causing a nuclear explosion.

For nuclear fission to take place, uranium-235 must be enriched to at least 3 per cent of the total mass of uranium. Today, uranium-235 accounts for only 0.72 per cent of uranium by mass, so we must enrich it ourselves if we wish to build a nuclear power station or an old-fashioned uranium atom bomb. Two billion years ago, however, less uranium-235 had already decayed. Its content in uranium ores would have been higher — in fact about 3 per cent. The uranium-loving bacteria in Gabon therefore stockpiled enough ore enriched in uranium-235 to start a nuclear fission chain reaction. This, at any rate, was the conclusion of the French secret service in 1972. There had been something of a panic when uranium ores mined along the Oklo River, near the border with the Congo Republic, turned out to be depleted in uranium-235. Some consignments had less than half the expected 0.72 per cent uranium-235. In an Africa still emerging from colonial rule and beset by civil unrest, the implication that some tribal group had stolen enough uranium to make a nuclear bomb did not bear thinking about. The French threw everything at the problem, and it was not long before a large team of scientists from the French Atomic Energy Commission solved the case.

Samples of the Oklo ores showed clear relics of spent radioactive fission, even when they were extracted from undisturbed seams. Instead of decaying naturally, tons of uranium-235 had fissioned away in half a dozen separate locations, producing a million times the power of natural decay. The natural reactors in Gabon had apparently been sustained for millions of years by a steady flow of water from the streams that fed into the ancient uranium lakes. Water slows the speed of neutrons, reflecting them back into the core of the reactor, so instead of quelling the inner fires, water actually promotes nuclear fission. The streams did more than this, however — they also acted as safety valves against nuclear explosion. Whenever the chain reactions approached danger levels, water boiled off, allowing neutrons to escape. This scuttled the chain reactions and shut down the reactors until flow was re-established. There is no evidence of a nuclear explosion. The entire system was finally buried beneath sediments where it remained undisturbed until the arrival of the French, a testament to the ingenuity of bacteria 1.8 billion years before Enrico

Fermi and his Chicago team applied their genius to making the first manmade atomic bomb; and indeed a testament to the potential long-term safety of burying nuclear waste.

What of the catastrophic mass extinction, the oxygen holocaust described by Lynn Margulis (see Chapter 2, page 19)? There is no trace of a holocaust in the rocks. Far from being a profound and debilitating challenge, the appearance of oxygen seems to have driven the evolution of new forms of metabolism, and new branches in the tree of life, as argued by Preston Cloud in the 1960s (see Chapter 2). But why did it take so long for oxygen to accumulate, despite more than a billion years of continuous production by cyanobacteria? To put it into context, this interlude is twice as long as the entire modern era of plants and animals (the Phanerozoic), or for that matter 15 times as long as the period since the demise of the dinosaurs. Is this long gestation perhaps hidden evidence of a difficult adaptation, concealing the throes of life as it struggled to cope with a poisonous gas? It seems unlikely. A number of speculations can explain the delay; for example, iron-loving bacteria may have dominated the ecosystem until the iron ran out, or the cyanobacteria may have been restricted to shallow-water stromatolite communities that absorbed as much oxygen as they produced, because of the presence of non-photosynthetic oxygen-respiring bacteria. The most likely explanation is simply that there was no change for a billion years because a stable equilibrium persisted for that time.

The long stasis was finally shattered by an apocalyptic climate change about 2.2 to 2.3 billion years ago. The Earth plummeted into the first ever ice age. This was no trivial ice age, to be compared with the recent Pleistocene cold snap, but a global freeze that may have covered the tropics in glaciers a kilometre [3280 feet] thick — in Joseph Kirschvink's memorable phrase, a 'snowball Earth'. What made the pleasant Precambrian climate collapse so violently is not known. One theory, argued by the sometime NASA geochemist James Kasting, is that the appearance of free oxygen itself brought about the freeze. As it built up in the air, oxygen would have reacted with methane (produced in large amounts by bacteria), and so removed this important greenhouse gas from the early atmosphere. As the greenhouse effect was undermined, temperatures plummeted and the Earth succumbed to the grip of an ice age. Kasting's theory has been advocated by James Lovelock among others, who claims an important role for methane-producing bacteria in his books on Gaia, but at present the theory suffers from lack of strong supporting evidence.

Whatever the reason, there is no doubt that the Earth plunged into a serious ice age about 2.3 billion years ago. It was to last for 35 million years. Hard on the heels of this ice age the planet was racked by a period of heightened tectonic activity, leading to major continental rifting and the uplift of mountain belts on a scale comparable with the Andes.

Joseph Kirschvink, a specialist in palaeomagnetism at Caltech (the California Institute of Technology) is a leading advocate of the snowball Earth theory, and one of its most thoughtful commentators. He argues that, after the glaciers finally melted, the stones and mineral dust scoured out by glacial erosion would have filled the oceans with minerals and nutrients, stimulating a cyanobacterial bloom and a rise in oxygen. As evidence for this claim, Kirschvink and his co-workers cite a huge deposit of manganese ore in the Kalahari desert in southern Africa, dated to right after the end of the snowball Earth. The Kalahari manganese field contains some 13.5 billion tons of manganese ores, or about 4 billion tons of manganese, making it by far the world's largest economic reserve of this element.

In comparison with iron, manganese is not easily oxidized, so manganese oxide ores are unlikely to have deposited from the oceans until the dissolved iron had already been exhausted; and indeed, the Kalahari manganese field overlies a rich bed of haematite, the most highly oxidized iron ore, in the Hotazel iron formation. Such a complete deposition of iron and manganese seems to demand a surplus of oxygen. In modern waters, manganese deposition is almost invariably brought about by algal or cyanobacterial blooms, which can generate very high levels of oxygen in a short period. Considered together then, Kirschvink argues, the nutrients from the melting snowball Earth stimulated a cyanobacterial bloom, followed by a precipitate oxidation of the surface oceans, ultimately aiding the accumulation of free oxygen in the atmosphere.

The drama is in the speed. If the underlying rate of change is less than the buffering capacity of the environment to absorb that change, the system as a whole can maintain a pernicious chemical equilibrium. The tendency to approach a stable equilibrium is antithetical to life, which might almost be defined as a state of dynamic disequilibrium. In Chapter 2, we saw that the Earth was saved from the sterile fate of Mars by

an injection of oxygen from photosynthesis into the atmosphere, preventing the oceans from ebbing away into space with the loss of hydrogen gas. After this, however, the world sank into a second period of stasis, in which the oxygen produced by cyanobacteria was balanced by the uptake from bacterial respiration, and reaction with rocks, dissolved minerals and gases. This new equilibrium lasted from about 3.5 billion years ago until 2.3 billion years ago, nearly a quarter of the Earth's history. Life on Earth was saved from an interminable ecological balance between iron-loving bacteria, stromatolites and cyanobacteria by the sudden punctuation of the snowball Earth, a shock that rocked it from slumbering complacency with a second big injection of oxygen.

The history of the next billion years lends support to this view of life: not a lot happened, at least to the naked eve. After the deposition of the vast banded iron formations, the dramatic climate swings, the tectonic movements, the oxidation of the surface oceans and the rusting of the continents, Earth seems to have settled down once more to a period of equilibrium, in which a new balance was established. If isotope ratios and fossil soils are to be believed, oxygen levels remained more or less constant at 5 to 18 per cent of present atmospheric levels throughout this period — more than enough for oxygen metabolism to become widespread among our ancestral eukaryotic cells. Better oxygenation would also have increased the concentration of sulphate, nitrate and phosphate in the oceans, lifting these particular brakes on growth. We begin to see simple multicellular algae in the fossil record, and a better preservation of a wider range of eukaryotic cells, suggesting that there may have been a blossoming of genetic variety.

The evolutionary success of our eukaryotic ancestors may well have been linked directly with the higher oxygen levels. We shall see in Chapter 8 that eukaryotes are a hotchpotch of different components. Each individual cell is crammed with hundreds or even thousands of tiny organs, known as organelles, which carry out specialized tasks such as respiration or photosynthesis. Modern life would be unthinkable without these organelles, yet they are aliens within. Some of them show signs of independent origins. One type, called *mitochondria*, evolved from a strain of purple bacteria. They are the sites at which the oxygen-requiring steps of respiration are carried out in all eukaryotic cells, including those of plants and algae. Photosynthesis in plant and algal cells takes place in another organelle — the *chloroplast* — which is derived from cyanobacteria.

Eukaryotic cells are thought to have developed from their primitive precursors into a kind of internal marketplace during the long period of environmental stability beginning around 2 billion years ago. Small bacteria were engulfed by the primitive eukaryotic cells, but somehow survived inside the larger cells like Jonah in the whale. As a result, the eukaryotes eventually became a community of cells within cells. The stalemate must have encouraged the trading of metabolic wares in exchange for shelter. This intimate symbiotic relationship was ultimately so successful that the internalized bacteria are now barely recognizable as once-independent entities. The long-term success of the relationship, however, conceals an interesting paradox. Let us take the mitochondria as an example.

Imagine: 2 billion years ago a small purple bacterium was engulfed by a larger cell, which then had a case of indigestion. Whether the larger cell was predatory, or the invading cell infective, is immaterial. The fact that the insider deal persisted at all means that it was never seriously detrimental. The fact that it finally dominated, to the extent that virtually all eukaryotes have mitochondria, means that it must ultimately have been beneficial. The advantage is obvious in today's world: mitochondria use oxygen to generate energy, by far the most efficient means of biological energy generation known. In those days, though, it ought to have been a different matter. The problem is as follows. The energy currency of all cells is a compound called ATP (adenosine triphosphate). Cells use ATP either directly or indirectly to power most of the metabolic reactions that maintain life and make new material for the cell to grow. Both the symbiotic bacteria and their hosts would have produced ATP independently, by fermentation in the case of the eukaryotes, and by burning carbohydrate 'fuel' using oxygen in the case of the bacteria. The bacterial method was much more efficient, so they could produce much more ATP. Like all currencies, ATP is exchangeable. Any ATP produced by the bacteria could in principle be consumed by the host. For the host to benefit in this way, though, the bacteria would have had to export ATP to the

⁴ There is some dispute about whether the eukaryotes were produced in a single fusion event between different types of bacteria, or whether a series of engulfments took place. With the exception of chloroplasts, evidence is beginning to favour a single event, or concentrated series of events, which occurred before the deepest evolutionary branches of the eukaryotes.

host cell. Modern mitochondria have pores in their bounding membranes that enable this to happen; but free-living bacteria do not have an ATP export mechanism. On the contrary, free-living bacteria are protected by membranes and cell walls specifically designed to keep the outside world out and the inside world in. Genetic studies indicate that the ATP-export mechanism in mitochondria evolved later, albeit before the major evolutionary branches of the eukaryotes. But if the hosts could gain no extra energy from their guests, how did they benefit? Why did this symbiosis flourish?

Evidence from similar symbiotic relationships today suggests that, while the host cell may have gained no energetic benefit, it might instead have been protected from within by its oxygen-guzzling guests. By converting oxygen to water, the symbiotic bacteria would have protected their hosts from potentially toxic oxygen. This acquired immunity to oxygen poisoning would have enabled the early eukaryotes to inhabit the shallow waters where oxygen levels were highest, and so exploit the benefits of light — either by photosynthesis in the case of algae, or by grazing off the freshest pickings in the case of consumers. Over time, the success of this early pact would have encouraged an even closer union, in which the host cell spoon-fed its guests with nutrients, and they in return exported ATP into the cell.

The idea that cells might protect themselves against oxygen by associating with other cells is borne out at a looser level, which may have had even more profound consequences in the long run. When modern oxygen-hating eukaryotes such as the ciliate protozoa are placed in oxygenated water, their first impulse is to swim away to water with less oxygen. The more oxygen there is, the faster they swim. But what if there is no escape? When their surroundings are equally well oxygenated and flight is futile, the ciliates institute plan B: they clump together in a mass. Even anaerobic cells have some capacity to consume oxygen. When cells clump together in this way, each cell benefits from the oxygen consumption of its neighbours. Other communally living cells also seem to have benefited from spreading the burden in this way. For example, stromatolites, those great domed communities of cyanobacteria, are known to have contained many other types of cells, including anaerobic bacteria. Only the top few millimetres of most stromatolites are composed of oxygen-producing cyanobacteria, whereas the deeper levels are home to billions of anaerobic cells, despite high oxygen levels during the daylight hours. Again, each cell benefits from sharing the oxygen load.

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Rising oxygen levels may therefore have favoured confederations of cells, from which grew the most efficient energy system for powering life — numerous mitochondria per cell⁵ — and the first stirrings of multicellular organization. If so, it is quite possible that a tendency to huddle together as clumps of cells, to alleviate the toxicity of oxygen, was an impetus to the evolution of multicellular life. Certainly, it is a fact that all true multicellular organisms contain mitochondria. Of the thousand or so simple eukaryotes that lack mitochondria, not one is multicellular. People are thus confederates of cells and of cells within cells. We shall see in Chapter 8 that the design of the human body actually restricts oxygen delivery to individual cells: multicellular organization still serves the same purpose in us that it did for our single-celled ancestors.

The Precambrian is drawing to an end. We have travelled down 3 billion years. There has been little to see but much has changed. Without these changes, the explosion of multicellular life that is soon to follow would have been impossible. I have argued that the changes were linked with rises in atmospheric oxygen.

In summary: the first signs of life, the carbon signatures in the rocks of western Greenland, date back to 3.85 billion years ago. By 3.5 billion years ago we find microscopic fossils, resembling modern cyanobacteria, and large stromatolites. If appearances are not deceptive, these cyanobacteria were already producing oxygen. However, it is not until nearly a billion years later, 2.7 billion years ago, that we have the first definitive evidence of cyanobacteria, as well as the first signs of our own ancestors, the eukaryotes, in the form of tell-tale biochemical fingerprints in the rocks. These eukaryotes made sterols for their membranes, a task that requires oxygen. From the activity of sulphate-reducing bacteria we know that oxygen levels rose at this time, perhaps to around 1 per cent of present atmospheric levels. Another 500 million years later, 2.2 billion years ago, oxygen levels rose again, following hard on the heels of the snowball Earth. In the period of geological unrest that followed, huge banded iron formations precipitated from the oceans all around the world. Free oxygen was probably needed for the genesis of at least some of

 $^{^5}$ Just as a car might be 100 horse-power, so a eukaryotic cell with 100 mitochondria could be said to be 100 bacteria-power.

these formations. At the same time, around 2.1 billion years ago, we see the earliest fossils of eukaryotes. By 2 billion years ago, we have rock-hard evidence of oxygen accumulating in the air: fossil soils, continental red-beds and uranium reactors. Oxygen levels reached around 5 to 18 per cent of present atmospheric concentration. In the rocks, we see a sudden explosion of diversity in fossil eukaryotes. Many have mitochondria. All the elements of the modern world, bar true multicellular organisms, are in place.

Then little changed. For a billion years, oxygen levels remained steady at 5 to 18 per cent of present atmospheric levels. The prolonged period of tranquillity saw a number of quiet developments in the history of life — the flourishing of the eukaryotes, genetic diversification, colonization of new habitats, and, in the shape of the algae, the first tentative steps towards multicellular life. And yet: in the face of all these quiet advances, nothing more complicated than a few slimy green tendrils evolved in the course of a billion years. None of this prepares us for what happens next. In a geological blink of an eye, 543 million years ago, the whole of creation as we know it exploded into being. Whatever happened?