Through these processes plants have been imperceptibly removing carbon dioxide from the atmosphere and regulating climate as the millennia ticked away. Initially, early in their evolutionary history, the small and leafless early land plants had rather insignificant effects on weathering rates. But as plant life began to spread across the continents and into upland areas, things changed. The 'greening of the land' and the rise of leafy forests with deeper rooting systems enhanced rock weathering on an unprecedented grand scale, stripping carbon dioxide out of the atmosphere.[74] Falling carbon dioxide levels allowed larger leaves and promoted competition for taller trees, further entraining the evolution of large rooting systems.[75] The rhythmic dance of plants, carbon dioxide, and climate reinforced itself, building in tempo over evolutionary time as carbon dioxide levels spiralled downwards, dragging the temperature of the Earth with them as the greenhouse effect weakened. As the Earth moved towards a catastrophic snowball state, threatening the global extinction of plant life, and probably much else besides, the thermostat kicked in. Rates of rock weathering slowed in the cooling climate, and the consumption of carbon dioxide from the atmosphere halted, stabilizing the climate and preventing the suffocation of plant life.

In the end, we can see that plant life was a major beneficiary of its own activities, falling carbon dioxide levels with each generation imperceptibly preparing the world for the next by facilitating the evolution of larger leaves. It was a progression of cause and effect, without foresight or planning. Any notion that plants 'pulled' carbon dioxide out of the atmosphere to permit the evolution of leaves is deeply flawed. Plants' modifications of their own environment were unconscious and undirected. Intriguingly, plant evolution generated changes in the global environment that persisted as a legacy to modify subsequent generations.[76] Falling carbon dioxide levels saw the evolution of leafy plants, which in turn accelerated the diversification of terrestrial animals and insects. Astonishingly, these far-reaching consequences for life on Earth stem from the interaction between greenhouse gases, genes, and geochemistry.[77]

Chapter 3

Oxygen and the lost world of giants

Oxygen breathes life into all complex living organisms. For centuries, scientists peered keenly down the dimly lit half-billion-year-long corridor of Earth's past to discern whether the atmospheric content was set at the present-day level of 21% as complex life evolved. The dénouement to this mysterious puzzle emerged only recently, when a handful of pioneering scientists clarified the picture in the final decades of the twentieth century. We now believe that 300 million years ago, oxygen levels rose to a magnificent 30%, before sometime later falling to a lung-sapping 15%. Tropical swamplands played the starring role in oxygen's highs and lows and helped engender a remarkable evolutionary episode of gigantism in the animal world.

Deposition and denudation are processes inseparably connected, and what is true of the rate of one of them, must be true for the rate of the other.

Charles Lyell (1867), ***The principles of geology***

OXYGEN, in its molecular form, is the second most abundant gas in our atmosphere but second to none in courting controversy. Its discovery is often credited to the great experimenter Joseph Priestley (1733–1804), who in 1774 showed that heating red calyx of mercury (mercuric oxide) in a glass vessel by focusing sunlight with a hand lens produced a colourless, tasteless, odourless gas. Mice placed in vessels of the new 'air' lived longer than normal and candles burned brighter than usual. As Priestley noted in 1775, 'on the 8th of this month I procured a mouse, and put it into a glass vessel containing two ounce measures of the air from my mercuric calcinations. Had it been common air, a full-grown mouse, as this was, would have lived in it about quarter of an hour. In this air, however, my mouse lived a full half hour.'[1] Later experiments revealed that mice actually lived about five times longer in the 'new air' than normal air, giving Priestley an early indication that air is about 20% oxygen.

About the same time, the Swedish chemist Carl Scheele (1742–86), working in Uppsala, showed that air contained a mixture of two gases, one promoting burning (oxygen) and one retarding it (nitrogen). Like Priestley, Scheele had prepared samples of the gas that encouraged burning ('fire air') by heating mercuric oxide, and also by reacting nitric acid with potash and distilling the residue with sulfuric acid. However, by the time his findings were published in a book entitled the *Chemical treatise on air and fire* in 1777, news of Priestley's discovery had already spread throughout Europe and the great English chemist lay claim to priority. Only later did it become clear from surviving notes and records that Scheele had beaten Priestley to it, producing oxygen at least two years earlier. The harsh lesson from history, which still rings true today, is that capitalizing on a new exciting discovery requires its expedient communication to your peers. The talented Scheele died at 43, his life shortened by working for much of the time with deadly poisons

like gaseous hydrogen cyanide in poorly ventilated conditions. Nevertheless his achievements were considerable. He notched up the discovery of no less than five other gases besides oxygen that were new to science, laid the foundations for modern photography with his report of the action of light on silver salts, and was elected into the Swedish Royal Academy of Sciences in 1775.

Both Priestley and Scheele were tenacious devotees of the phlogiston theory, a concept hopelessly wide of the mark that had dominated chemistry for half a century. It was originally advanced by the German scholar and adventurer Johann Becher (1635–82), and shaped into the form in which Priestley and Scheele knew it by the German chemist George-Ernst Stahl (1660–1734). Stahl's theory maintained that air was necessary to absorb the imponderable fluid 'phlogiston' and without air the opportunity for absorption was lost—this was why things failed to burn in the absence of air. It held that burning a substance released phlogiston into the air in a form that manifested itself as a flame. After burning, the inert residue was said to have become 'dephlogisticated' while the gas driven off (oxygen) was designated 'dephlogisticated air'.

It fell to the founder of modern chemistry, Antoine Lavoisier (1743–94) (see Plate 3), to sort out the confusion. Lavoisier has been described as a man of 'conspicuous vanity, hauteur, and no little concupiscence',[2] who enjoyed the considerable advantage of starting out at the top, by being born into a wealthy French family. Lavoisier demolished the phlogiston theory in a masterly series of careful experiments showing that substances actually gained rather than lost mass after burning, stating in his *Mémoires* to the French Academy in 1786 that 'in every combustion there is an increase in weight in the body that is being burned, and this increase is exactly equal to the weight of the air that has been absorbed'. Priestley vainly attempted to repair the theory by proposing that phlogiston had negative mass, hence substances gained mass after burning, but there was no recovering from Lavoisier's awesome analytic evidence.

Exulted by the victory, Lavoisier organized one of his famous *soirées* in Paris to entertain society's elite in the form of a mock trial. The event is recorded as follows:

> He invited a large distinguished party, and enacted this trial in front of them. Lavoisier and a few others presided over the judicial bench, and

> the charge was read out by a handsome young man who presented himself under the name 'Oxygen'. Then the defendant, a very old and haggard man who was masked to look like Stahl, read out his plea. The court then gave its judgement and sentenced the phlogiston theory to death by burning, whereupon Lavoisier's wife, dressed in the white robe of a priestess, ceremonially threw Stahl's book on a bonfire.[3]

Not long after this charade on 8 May 1794, Lavoisier himself conspicuously failed to navigate the dangerous political undercurrents of the French revolution and was arrested, tried in less than a day, and tragically sentenced to death by guillotine the same afternoon. A contemporary of Lavoisier's, the mathematician Joseph-Louis Lagrange (1736–1813), famously observed at the time 'it needed but a moment to sever that head and perhaps a century will not be long enough to produce another like it'.[4]

Credit for the discovery of oxygen is often shared between Priestley, Scheele, and Lavoisier. Yet it is possible alchemists knew of the 'magical' properties of air at least 170 years before this dynamic trio came along. As early as 1604, the Polish alchemist Michael Sendivogius (1566–1636) reported that 'there is in the air a secret food of life' and may have explained how to produce it to the brilliant Dutch inventor Cornelius Drebbel (1572–1633).[5] If so, it could explain how Drebbel managed to keep the passengers alive in his new invention—the submarine. For in around 1621 Drebbel built three submarines, each bigger than its predecessor,[6] based on a design involving greased leather tightly stretched over a wooden frame. The largest vessel allegedly carried 16 people and was propelled by oarsmen whose oars projected out of the sides through ports sealed with tight-fitting leather flaps. Large pigskin bladders situated beneath the rowers' seats were filled with water through pipes and emptied by the crew squashing them flat to regulate buoyancy.

Drebbel's magnificent 16-man submarine, with six pairs of oars, was demonstrated to King James I on the banks of the River Thames with a return underwater voyage from Westminster to Greenwich (~22 km) lasting three hours. Fevered speculation surrounded how the sailors and passengers were kept alive for so long. Some said there were tubes to the surface and a set of bellows in the craft to circulate air. However, the famous chemist Robert Boyle reported that one of the passengers noted that a 'chemical liquor' had been used to replace

the 'quintessence of air'.[7] We may never know for sure how it was achieved; Drebbel was notoriously secretive about his inventions, and never kept notes or diagrams of his work. The question is: did he use Sendivogius's method for producing oxygen? If he did, it was a brilliant demonstration that Drebbel understood our essential requirement for oxygen.

Nearly a century after Lavoisier brilliantly put paid to the phlogiston theory, his fellow Frenchman, the palaeontologist Charles Brongniart (1859–99), began exploring and excavating 300-million-year-old Carboniferous fossils from a quarry in Commentry, north-eastern France.[8] Charles Brongniart was the grandson of Adolphe Brongniart (1801–76), the renowned palaeobotanist and physician, who in turn was the son of Alexander (1770–1847), a chemist, mineralogist, and also, as it happens, palaeontologist. Evidently, a passion for fossils ran deeply in the Brongniart family. The quarry formed when the site was a narrow freshwater lake about 9 km long by 3 km wide. Streams and rivers from the surrounding mountains drained into the lake around its marshy shoreline, creating ideal environmental conditions for fossilizing plants and animals, especially, as it turned out, fossil insects.

In a remarkably productive collecting period between 1877 and 1894, Brongniart unearthed hundreds of previously unknown fossil insects and brought them to the attention of the scientific world. His most astonishing fossil find, announced to the world in a detailed paper published in 1894, was an ancient predatory dragonfly—*Meganeura*—with a giant wingspan of 63 cm.[9] Brongniart's *Meganeura* fossil resides today in the Muséum Nationale d'Historoire Naturelle, Paris.[10] Following the publication of this great work, other collectors soon began to turn up new specimens of giant insects in Carboniferous-aged rocks. To be sure, none were as spectacular as *Meganeura*, but some fossil mayflies rivalled the 16 cm wingspans of modern Giant Andean Hummingbirds. Before the close of the century, spectacular finds like these made it obvious to palaeontologists that diverse groups of Carboniferous insects had reached giant proportions, dwarfing their living counterparts.

Two of the most celebrated giant insect fossils turned up in the coal seam of a colliery, long since closed, near the small medieval town of Bolsover, Derbyshire in 1978. The first had a wingspan of some 20 cm; the second specimen was over twice the size of the first, with a staggering wingspan of half a metre. Bigger than any living dragonflies, these fossilized flyers are the largest and oldest known examples of monster dragonflies; their discovery hit the headlines around the world. The first specimen, dubbed the 'beast of Bolsover', is not to be confused with Bolsover's longstanding and pugnacious Member of Parliament, Dennis Skinner. *The Daily Telegraph* proclaimed 'World's oldest dragonfly found in pit' and queues formed in Cromwell Road when the specimen was displayed in the Natural History Museum, London.

Giant winged insects were only one part of the story; the fossilized remains of Carboniferous floras and faunas demonstrated that gigantism was genuinely the order of the day. Some giant forms of plant life that today are characteristically small, like clubmosses and horsetails, colonized the ancient tropical coal swamps. Trees distantly related to our modern clubmosses reached heights of 40 m, while beneath them ancestral forms of horsetails inflated to majestic heights of 15 m or more towered above the luxuriant undergrowth of ferns. The evolution of huge plants created new habitats for animals to exploit for food and shelter, and fittingly insects, spiders, and millipedes also evolved into giants. The centipedes and millipedes inhabiting swamps reached lengths of a metre or more. Only recently, in 2005, a trackway was discovered in Scotland thought to have been made by a six-legged Carboniferous water scorpion some 1.5 m long.[11] Primitive amphibians, the biological intermediates between bony fish and reptiles that conquered the land, also attained gigantic proportions. The ancestors of our newts, resembling flattened crocodiles with large skulls, truncated snouts, and stocky limbs, reached several metres in length.[12]

The ecological community of giants must have been a spectacle to behold, with airborne insects swarming through the tropical forests, as beneath them the ground bristled with the activities of the giant swamp dwellers. The most extraordinary episode of gigantism that the world has ever witnessed was no brief evolutionary experiment, either. The world's gigantic fauna flourished for 50 million years from late in the Carboniferous, 300 million years ago, to the start of the subsequent Permian Period. After the Permian, the fossil evidence dries up. No giant animals have yet been unearthed in

rocks younger than the Permian, 250 million years ago. The strange zoological oddities thrown up by the Carboniferous coal deposits are an intriguing puzzle demanding explanation.

In 1911 a French duo, Édouard and André Harlé, rose to the challenge and offered the world a controversial hypothesis about the giant insects: they argued that the flight of these giants might be explained if atmospheric pressure was higher in the Carboniferous relative to now.[13] Their rationale is straightforward. Higher atmospheric pressure increases air density (and resistance) on the wings and bodies of flying animals, allowing them to generate lift more easily. Ingenious though it was the idea had no precedent, and at the time no evidence to support it. Charles Lyell, the leading geologist of his day, for example, had earlier remarked in his 1865 book *The student's elements of geology*, that the raindrop prints he found on shale rock surfaces one day 'resemble in their average size those which now fall from the clouds. From such data we may presume that the atmosphere of the Carboniferous period corresponded in density with that now investing the globe'. After Lyell, few others followed up such observations and the questions concerning higher atmospheric pressure and the giant insects raised by the French duo remained firmly in the background.

If atmospheric pressure was higher 300 million years ago compared to now, then it can only have been brought about by a higher concentration of either or both of the two dominant gases making up the atmosphere, nitrogen and oxygen. Given that nitrogen and oxygen comprise the bulk (almost 99%) of our atmosphere between them, improbably large additions of the other constituents are required to significantly alter total atmospheric pressure. Argon, the leading player among the minor constituents, is just 1% by volume, carbon dioxide 0.04%, and methane only 0.0017%. Nitrogen is chemically far more inert than oxygen[14] and consequently its concentration has probably remained the same since reaching its current level early in Earth history. Oxygen, on the other hand, is quite reactive, making it a plausible contender for increasing atmospheric pressure.

What the question really amounts to is whether the oxygen content of our atmosphere has been fixed at 21% as the diversity of life on land and in the oceans blossomed over the past half billion years.[15] Although a challenging problem, even today, considerable scientific insight was brought to the matter as early as 1845 by the Frenchman Jacques Ebelmen (1814–52).[16] Ebelmen set out for the first time the fundamental concepts needed to understand the history of oxygen and carbon dioxide in our atmosphere in a perceptive paper in 1845. He recognized how the burial and oxidation of plant organic matter and sulfur compounds in rocks and sediments added or removed oxygen from the atmosphere over geological time. The rationale for invoking these processes will, I hope, become clear shortly. Unfortunately, as is often the case with radical ideas, the scientific world was not ready for the Frenchman's pioneering vision. In spite of the best efforts of others to draw it to the attention of a broader audience, his seminal contribution to our thinking languished unnoticed in an obscure scientific journal for over 170 years.[17]

This is not to say others hadn't given the problem of oxygen thought, too. John Ball (1818–89), Irish botanist and alpine explorer, was very struck by the significance the Carboniferous coal measures held for the oxygen content of the atmosphere. This was evidently the burial of plant matter on a grand scale, and he commented in his lecture to the Royal Geographical Society in 1879 'In the history of the earth, regarded as the scene of organic life, there is one event of transcendent importance, to which I think sufficient attention is not given. I allude to the deposition of the coal measures.'[18] Ball presciently grasped the significance of coal formation in the Carboniferous for the oxygen content of the atmosphere: 'In forming this amount of coal, the plants of that period must have set free more than 45 billions of tons of oxygen gas, increasing the quantity previously existing in the atmosphere by about 4 per cent.' With these comments echoing from the past, we cannot help but be struck by the near miss that occurred in the annals of scientific history. Between them, the trio of Ebelmen, Ball, and Brongniart, all scientific contemporaries, held the key pieces of a tantalizing scientific puzzle at their fingertips—massive carbon burial, atmospheric oxygen, and giant insects—yet fate decreed that the pieces were not yet ready to fall into place.

Earlier I casually dismissed nitrogen as a player in raising atmospheric pressure because its chemistry is too dull to cause large variations in its atmospheric content. But given that the organic debris of plants also contains small quantities of nitrogen, originally derived from the atmosphere by microbes, could the formation of the Carboniferous coal measures have altered the nitrogen content of the atmosphere significantly? Calculations suggest not. The flux into the Carboniferous coal measures is far too small relative to the very large mass in the atmosphere. Our best estimate is that the nitrogen content of the atmosphere dropped by less than one-hundredth of 1%—a trivial amount.[19]

From the very promising foundations laid by Ebelmen, the baton in the race that unfolded in the following century, to answer how Earth's oxygen content had varied as life evolved, was not so much dropped as misplaced. Lloyd Berkner and Lauriston Marshall at the Southwest Center for Advanced Study, Texas (among others) finally retrieved it in 1965 languishing in the intellectual dust, and picked it up and ran with it. At a symposium on the 'Evolution of Earth's atmosphere' convened by the National Academy of Sciences of the United States,[20] they argued that oxygen produced by land plants during photosynthesis was the primary source of oxygen in the atmosphere.[21] In other words, as plant life evolved and became more abundant leading up to the Carboniferous, 300 million years ago, it added increasing amounts of oxygen to the atmosphere. Oxygen levels were only restored to some sort of equilibrium by the subsequent decay of organic materials, a process that consumes oxygen.[22]

Here is an apparently plausible, if rather speculative, mechanism for driving up Earth's oxygen content during the rise of giant insects. Two decades later, greater scientific rigour was brought to bear on the matter by the pioneering geochemist Robert Garrels (1916–88).[23] Garrels was the son of a chemical engineer who had been an outstanding athlete: competing in the 1908 Olympics, his father came second in the 110 m hurdles and third in the shot-put. Garrels himself, though destined for a scientific career, maintained a keen interest in athletics and established an informal gang of like-minded scientists interested in swimming, rowing, and running known as the Bermuda Biological Station Athletic Club (BBSAC). We gain a glimpse of his contributions to science in the words of his protégé Robert Berner, who wrote of him as being 'among the handful of persons that over the past half century truly altered the course of geochemistry, which was his speciality, as well as that of earth science in general. Hidden within this modest, affable, kind, and considerate man was the soul of a revolutionary.'[24] Berner is no slouch when it comes to geochemistry or athletics. An outstanding BBSACer and swimmer, he is also an innovator of scientific thought and was elected to the National Academy of Sciences in North America for his accomplishments at a young age. As we shall see, Berner plays a pivotal role in discovering Earth's oxygen history (see Plate 4).

Garrels' geochemical brilliance was to recognize not only that Earth's atmospheric oxygen content is intimately tied to the evolution of plant life,[25] but also that it is intimately tied to the recycling of Earth's rocky crust. The day-to-day activities of oxygen-producing plants and microbes are linked with the very slow processes of sedimentation and carbon burial in rocks and on the ocean floor. The chain of reasoning begins with photosynthesizing plants adding oxygen to the atmosphere as they manufacture biomass. Eventually when the forests (marine or terrestrial) die, they offer rich pickings for animals, bacteria, and fungi that break down their remains, consuming oxygen in the process. Decomposition of organic matter reverses the effects of photosynthesis, reclaiming the oxygen originally released during its synthesis and returning carbon dioxide back to the atmosphere. However, a small fraction of plant biomass, less than 1%, escapes complete decomposition. We see one expression of this today in the high Arctic, where the activity of nature's decomposers is slowed by the cold climate and waterlogged conditions to promote the development of peatlands. Organic carbon also accumulates on the continental shelves that receive water discharged from the world's rivers; these are Earth's carbon superhighways transporting huge quantities of floating organic debris and dissolved organic carbon compounds out to sea. The Amazon, for example, by far the largest river system on Earth, exports a staggering 70 million tonnes of carbon to the coast every year.[26] On being flushed into the sea, much of it becomes buried in near-shore sediments containing little or no oxygen and, with rates of decomposition slowed in such circumstances, thick deposits of organic matter accumulate in the sediments of continental margins.

The gradual and continual burial of the fragmentary remains of plants on land, and in the sea, means that a fraction of the oxygen produced during its synthesis cannot be reclaimed by chemical or biological processes. Instead, it is free to accumulate, adding tiny amounts of oxygen to our atmosphere from year to year. Over millions of years, these marginal increments accrue. Unlikely though

it seems, the swamplands and continental shelves are the lungs of the Earth on a geological timescale of millions of years, slowly exhaling oxygen into the atmosphere.

Garrels and colleagues' further revelatory insight was to recognize that the natural cycling of sulfur through the oceans, atmosphere, and crust by chemical and biological processes adds oxygen to, and removes it from, our atmosphere. Heterotrophic bacteria are unable to manufacture biomass from simple chemical compounds and instead consume other organisms—living or dead. Some of these bugs are strict anaerobes that specialize in metabolizing sulfur compounds. They obtain energy by feasting on dead plant material and dissolved sulfur (sulfate) to make hydrogen sulfide. Under the right conditions, the hydrogen sulfide precipitates out as the common mineral known as iron pyrite or fool's gold.[27] The microbial conversion of organic matter to pyrite takes place in the oxygen-free intertidal mudflats around the coastlines of the world. Because the organic matter consumed was synthesized by photosynthesis, the net effect is to release oxygen.[28] Via this route, the burial of pyrite at sea also slowly adds oxygen to the atmosphere.

Eventually, over the eons, sediments containing the obliterated remains of plants, and pyrite, are heated and compressed until their transformation into sedimentary rocks is complete. These newborn rocks sit tucked within the Earth's crust until tectonic upheavals or retreating seas expose them as mountain ranges or the coastal cliffs of newly formed continents. Weathered by wind and rain, they slowly erode, giving up their cargo of organic matter and pyrite, which come under chemical attack.[29] Organic matter is oxidized with oxygen back to carbon dioxide and water and iron pyrite is oxidized back to iron oxide and sulfate. Slowly, the cycle of burial and oxygen production is reversed by exposure and oxygen consumption. In a surprise recent discovery, scientists have found that microbes, too, participate in the leg of the cycle that converts organic matter back to carbon dioxide while consuming oxygen. Laboratory experiments revealed super-bugs capable of digesting 365-million-year-old organic matter present in shale, a common sedimentary rock.[30] It is too early to say how important shale-eating microbes are for accelerating oxygen consumption; for now we can marvel at their amazing metabolic versatility.

We can see now that the daily activities of plants and microbes are locked in a very slow dance to the rhythmic cycling of the Earth's crust. The burial of organic matter and pyrite in rocks adds oxygen to the atmosphere, while the uplift, exposure, and weathering of those same rocks removes it. Garrels realized that the astonishing significance of this usually unhurried dance is that it controls the oxygen content of the atmospheric over geological time. In elucidating all this, he rediscovered what Ebelmen had glimpsed 130 years earlier. Rarely is anything new in science. Today, humans are artificially accelerating the 'weathering' of organic matter by burning our fossil fuel reserves of coal and gas. Like the natural weathering processes, our combustion of fossil fuels is consuming atmospheric oxygen.[31] We are, however, in no danger of even denting our oxygen reserves, let alone consuming them and driving ourselves to extinction. At the present glacial-paced rate of oxygen consumption it would take 70 000 years for that disastrous scenario to unfold, and our fossil fuel reserves are estimated to last only the next 1000 years or so.[32]

With a solid theoretical foundation for unravelling the evolution of Earth's oxygen content through the ages in place, the next task was to retrieve it from the rock record. That aim required drawing up an inventory of changes in the abundance of sedimentary rocks rich in organic matter and pyrite over geological time. The technique, pioneered in the late 1980s, is called the 'rock abundance' approach and involves determining the cycling—the birth and death—of rocks over millions of years. Robert Berner and his then-graduate student Donald Canfield were the architects of the approach.[33] A glimpse of Canfield's unusually modest personality surfaced in an anecdote after he moved to the NASA Ames Research Center in California. While at the NASA Ames, Canfield was known to wear a shirt discarded by a Kroger grocery store employee named Chuck. Naturally, on his office door in one of NASA's most prestigious research institutes was not Donald Canfield but a certain Chuck Kroger. Few people got the joke.

Although drawing up an inventory of the abundance of sedimentary rocks for each slice of geological time, and the average carbon and sulfur content each type contains may seem like a tall order, much information was already available from oil companies who had exhaustively scoured the world for fossil fuels over the last century. Armed with what amounted to a geological history

of the relevant rocks of our planet, Berner and Canfield simulated changes in the Earth's atmospheric oxygen content over the past 540 hundred million years (Fig. 3). The curve they obtained showed a major oxygen pulse created as levels rose sharply to peak at around 35% in the middle of the Carboniferous, 300 million years ago, and then fell to around 15% 200 million years ago. Remarkably, this rise and fall in oxygen was beautifully synchronized with the

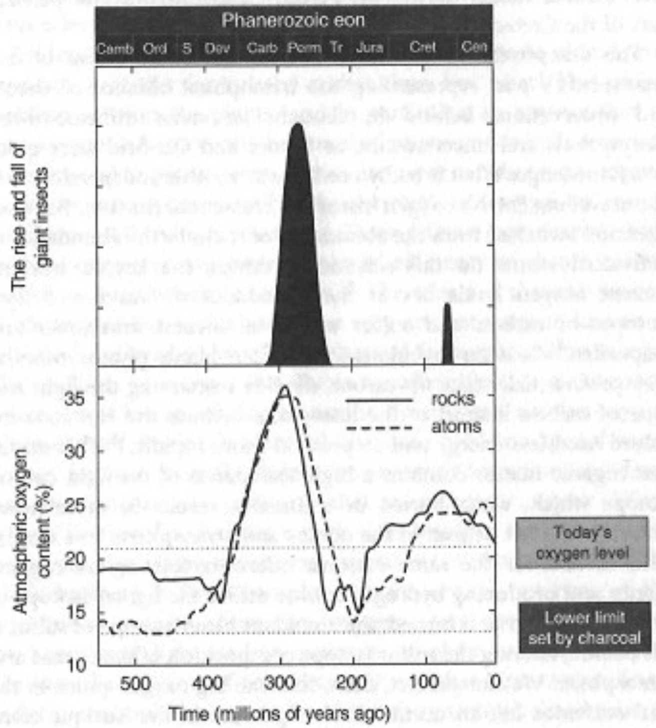

Fig. 3 Changes in the Earth's atmospheric oxygen content and giant insect abundance over the past 540 million years. The lower graph depicts two curves, one calculated using the 'rock abundance' approach, the other using the 'atomic abundance' approach. The lower horizontal line indicates the minimum level for oxygen set by the presence of fossil charcoal. Camb = Cambrian, Ord = Ordovician S = Silurian, Dev = Devonian, Carb = Carboniferous, Perm = Permian, Tr = Triassic, Jur = Jurassic, Cret = Cretaceous, Cen = Cenozoic.

evolution and extinction of Brongniart's gigantic insects, and the other animals that came to light subsequently (Fig. 3). The curve also hinted at a second minor oxygen pulse during the Cretaceous. Other than these two features, the general picture at most other times during the last half billion years was one of stability. In other words, oxygen production and consumption, inexorably linked to the life cycle of sedimentary rocks, have been finely balanced for a very long time indeed, except during the Permo-Carboniferous and perhaps part of the Cretaceous.

The deceptively simple curve is now an iconic image of our atmosphere's past representing the triumphant alliance of theory and observation. Behind it, though, lie some difficult-to-test assumptions and uncertainties, as Berner and Canfield were quick to acknowledge. What it badly needed was another independent way of unravelling Earth's oxygen history to crosscheck the first. For that, attention switched from the abundance of rocks to the abundance of individual atoms. In this scheme of things, the key to tracking ancient oxygen levels lies in the abundance of heavy and light isotopes of carbon and sulfur atoms in ancient limestones and evaporites.[34] It is an ingenious idea. When plants photosynthesize they preferentially take up carbon dioxide containing the light isotope of carbon instead of the heavy one because the reactions involved need less energy and so proceed more rapidly.[35] This means that organic matter contains a high abundance of the light carbon isotope which, when buried in sediments, results in more heavy carbon being left behind in the oceans and atmosphere. In a similar fashion, and for the same reasons, microbes feasting on organic matter and producing hydrogen sulfide utilize the lighter isotope of sulfur. When pyrite is buried, the abundant heavy isotope of sulfur is left behind, altering the sulfur isotope composition of the oceans and atmosphere. We can predict, then, that the big oxygen pulse in the Carboniferous left an unmistakable signature in the isotopic composition of both limestones and gypsum deposits left over from the ancient oceans.

Even though the theory appeared sound, all attempts to exploit it and reconstruct a history of atmospheric oxygen over the past 540 million years foundered. It produced curves which had large catastrophic swings in oxygen levels incompatible with life on Earth. Some simulations, for instance, gave a negative amount of oxygen in the atmosphere—problems echoing Priestley's attempts to patch up his beloved phlogiston theory. Others implied very low oxygen levels that did not square with the known facts. Fossil charcoal is a valuable geological indicator of the minimum amount of oxygen in the atmosphere because charcoal is produced by forest fires burning in an atmosphere with a minimum of 13% oxygen (see Plate 5).[36] So the presence of charcoal in rocks and sediments dating back over the last half billion years tells us that atmospheric oxygen levels probably didn't dip below 13%.[37]

Evidently, something was wrong with the 'atomic abundance' approach as it was formulated at that time, but what? The critical problem lay with the plants, and in particular, an appreciation of how oxygen influences the business of photosynthesis. It was only uncovered after plants were grown in modern laboratory experiments in atmospheres artificially enriched in oxygen to mimic conditions 300 million years ago. During these experiments, high levels of oxygen greatly lowered plants' efficiency to absorb carbon dioxide and manufacture biomass.[38] The reason is that the process of photosynthesis is catalysed by a very ancient enzyme known as Rubisco,[39] believed to have been inherited from cyanobacteria some 2700 million years ago. But Rubisco suffers from a biochemical indecision: it has an affinity for carbon dioxide and also for oxygen. When carbon dioxide is plentiful, the issue holds no special significance, because it easily claims the enzyme's attention and feeds into the biochemical pathways that manufacture sugars. When oxygen is plentiful, Rubisco's dark side emerges, with its affinity for oxygen disrupting the smooth operation of photosynthesis. The whole business is fairly complex but the critical outcome of the experiments was to show that oxygen alters the abundance of the heavy and light carbon isotopes of plant organic matter.[40] The logical extension of this discovery was that high oxygen levels in the past should leave a distinctive carbon isotopic fingerprint in the fossilized remains of plants.[41]

When these previously hidden details of oxygen's influence on plants were fed into the 'atomic abundance' model, they allowed the isotopic fractionation of plants to change as oxygen changed. This new feedback between plants and the atmosphere brought stability to the calculations, and saw a fresh curve depicting a change in Earth's atmospheric oxygen emerge. This time it closely tracked that obtained from the 'rock abundance' method (Fig. 3): each history of oxygen supported the other.[42] Plants had picked the lock of the 'atomic abundance' method, and both methods (rocks and atoms) revealed a prominent oxygen pulse 300 million years ago.

If the conclusions of experiments with living plants are robust, they point to another means of testing the contentious Carboniferous oxygen pulse by searching for its fingerprints in the isotopic composition of fossil plants. Indeed, modern geochemical techniques revealed its signature in 300-million-year-old fossils collected from rocks around the world.[43] It may seem like a giant leap of faith to move from laboratory experiments on modern plants to predicting what we might find in fossil plants sandwiched into rocks some 300 million years old. Yet plants back then, as now, employed the same enzyme, Rubisco, to catalyse photosynthesis, and this biochemical similarity between the past and the present offers a basis for optimism in such an enterprise. Giant insects, the matching histories of atmospheric oxygen, and shifts in the isotopic composition of fossil plants—the evidence to win over the critics begins to mount.

Another, more direct, means of inferring the oxygen content of the ancient atmosphere also surfaced when scientists analysed tiny samples of 'fossil air' trapped in bubbles of fossil resin (amber).[44] These tiny time capsules reportedly contained samples of the Cretaceous atmosphere with 30% oxygen. Inevitably, in spite of a number of careful precautions and crosschecks, the results came under fire. Doubts arose over the capacity of the amber bubbles to effectively seal-off a pristine sample of air for such a long period of time; oxygen is a reactive gas and amber is a porous resin.[45] Some suggested that the bubbles leaked the gases trapped inside. The effect of this leakage could be that very slowly, over the millennia, the original gaseous composition of the bubble becomes distorted, giving potentially misleading conclusions concerning composition of the ancient atmosphere. Still, all of these points have been rebuffed and it remains to be seen if the amber bubbles will one day yield up reliable secrets about the oxygen content of the past atmosphere.

Regardless of the amber resin issues, it seems quite clear that the delicate balance between oxygen production and consumption was upset during the Carboniferous. The traditional explanation is that slow tectonic movements over millions of years altered the continental configurations to create and destroy conditions suitable for waterlogged basins favouring the formation of swamplands. But another intriguing possibility is that the plants themselves were responsible.[46] The leading theory argues that, by the start of the Carboniferous, plants had evolved the ability to synthesize a tough molecule called lignin. Lignin provided plants with much needed structural support as they grew ever taller, but it presented the microbial world with a new challenge. Its complex molecular structure required a special suite of enzymes to break it down, and some scientists believe that nature's decomposers, fungi and bacteria, lacking this biochemical pathway, struggled to digest the rain of lignin-rich forest debris.[47] If correct, then global indigestion might have ensued. Swamplands bulged and the Earth's atmospheric oxygen content rose upwards. After microbes and fungi had risen to the metabolic challenge of digesting lignin, they could begin consuming the vast reservoirs of organic matter embedded in sedimentary rocks as it became exposed over millions of years by uplifting continents and falling sea levels. Only then could oxygen's status quo be slowly restored. To be sure, this elegant version of events may even be true, but it remains highly speculative and leaves several questions unanswered. Why, for example, did it take microbes, with large populations and short generation times, millions of years to evolve the trick of digesting lignin?

Whatever the reason, the Carboniferous coal measures testify to the enormous amount of carbon that was once buried and the models indicate their formation pushed oxygen levels upwards. Brongniart's giant insects that had once swarmed the air space of the ancient tropical swamps probably had enjoyed a higher atmospheric pressure and denser atmosphere due to more oxygen. In fact, in an atmosphere containing 35% oxygen air density increases by a third over today's value, permitting larger animals to fly more easily.[48] As I outlined earlier, this is in part because a wing 'pushing' against a denser atmosphere generates lift more effectively. The same reasoning explains why few modern helicopters can fly above 4 km—the air is too 'thin'. The downside to a dense atmosphere is a greatly diminished top speed as it increases air resistance on the wings and bodies of flying animals. The drag created by greater resistance effectively slows the forward motion of the animal and limits maximum speed and acceleration. Given these considerations, we should imagine our Carboniferous giants cruising majestically through the tropical swamplands; swarming now seems inappropriate.

A century on and the Harlé brothers' speculative hypothesis that an increase in atmospheric pressure aided the flight of the giant insects looks more reasonable. But better aerodynamic lift generated by a higher atmospheric pressure is only part of the story. Bathing creatures in an oxygen-rich atmosphere also benefits their respiration and physiology, because powered flight is a costly business and oxygen is the currency that counts when it comes to paying for it. Insects obtain oxygen to power their flight tissues through a branching system of rigid tapering tubes (the tracheae) penetrating into the abdomen. Ventilation of the network of tubes in modern insects generally occurs around the openings of this branching network, but is also achieved in the deeper system of tubes by body movements that cause tracheal compression and expansion in a fashion analogous to the inflation and deflation of vertebrate lungs.[49] Even so, it is not a very efficient means of 'breathing' and air trapped in the narrowest interior regions is replenished only slowly by diffusion, which can limit the supply of oxygen to the muscles. So it may be that the tiny terminal tubes limit how long insects can fly around for and how big they can grow.[50] For giant dragonflies with correspondingly longer tracheae, refreshing the air of the respiratory system might have been difficult. Living in an oxygen-rich atmosphere probably provided a means of overcoming this physiological barrier for supplying fuel to demanding flight muscles.[51] Oxygen also fuels energy production in the power plants of cells—the tiny organelles called mitochondria—and more oxygen means more energy.

Based on this line of reasoning, it is tempting to speculate that an oxygen-rich atmosphere permitted larger flying insects by relaxing the physiological constraints imposed on today's insects. So, if evolution was given another shot, would more oxygen and a denser atmosphere see insect gigantism happen again? In fact, this evolutionary experiment may have been repeated, when a second, less dramatic pulse occurred later in the Cretaceous, around 70 million years ago (Fig. 3). Remarkably, sparse fossilized Cretaceous insects, especially mayflies, suggestively hint that once again gigantism was adopted as a way of life at a time when oxygen rose to a more modest high of around 25%.

A Carboniferous atmospheric oxygen pulse could also help explain the unusual evolutionary patterns of gigantism in other animals. Amphibians benefited because they breathe through their skin and more oxygen in the air means more can diffuse into their bodies to fuel their energy requirements. Many amphibians and arthropods on land, new to the game of breathing air, used a combination of primitive gills and lungs. More oxygen improves the efficiency of primitive lungs that struggle to get rid of waste carbon dioxide produced by respiration. Air-breathing creatures benefited from the Carboniferous pulse in oxygen in other ways. It enabled muscles to recover more quickly after a sudden turn of speed used to capture prey or evade capture. Perhaps it is even possible that reptiles evolved from amphibians thanks to an oxygen-rich atmosphere. Land-conquering reptiles appeared in the Carboniferous and, unlike their amphibious cousins, reproduced with hard-shelled eggs. Could the high oxygen content of the atmosphere have facilitated diffusion of oxygen through the hard protective shell to the developing embryo inside?

Fascinating though these ideas are, they are also worryingly circumstantial. Direct evidence linking oxygen to body size comes from investigations of natural variations in the size of amphipods, small shrimp-like creatures found in the world's oceans, lakes, and river systems. In these different habitats, they experience varying amounts of oxygen because the solubility of the gas depends on temperature and salinity. Saltwater holds less oxygen than freshwater, cold water holds more oxygen than warm water. So in the cold waters of Antarctica, amphipods experience an oxygen-rich environment, but in the warm tropical seas off the coast of Madagascar they dwell in an oxygen-poor environment. And it appears amphipod size is directly related to the amount of oxygen dissolved in the water: Antarctic amphipods reach five times the size of their tropical cousins.[52] The world's largest amphipods live in the freshwaters of Lake Baikal, enjoying even more oxygen than their Antarctic relations. In fact, the identification of giant marine animals in polar regions is easily explained by oxygen, for there is a very strong relationship between the amount of dissolved oxygen in the water and maximum body size of amphipods.[53] The ability of oxygen to account for worldwide differences in amphipod size elegantly points to its capacity to raise the bar on body size.

The conclusion we reach from all this is profound. Earth's atmospheric oxygen content has had a guiding hand on the evolution of terrestrial animals in the Carboniferous, and possibly also at other times in Earth history as well. And plants played the starring role. But it is important to recognize that oxygen by itself will not necessarily cause larger animals to evolve. It simply offers the environmental opportunity for it to happen by relaxing physiological constraints and, for flying animals, aerodynamic limitations as well. The ability of nature to exploit that capacity when given the chance is admirably demonstrated in a series of ingenious experiments conducted by Robert Dudley when at the University of Texas. Dudley investigated how fruit flies responded to an oxygen-rich atmosphere typical of the Carboniferous and made a breathtaking discovery. After just five generations flies that had bred in the oxygen-rich air grew larger by 14%.[54] Oxygen, it seems, really did alleviate constraints on body size.[55] Furthermore, when the flies originally grown in a higher-pressure atmosphere were withdrawn and bred under normal atmospheric conditions, the male offspring were 14% larger than normal. In other words, oxygen relaxed the genetic control of body size, allowing the trait to be inherited and passed from one generation to the next. If this actually happened during the Carboniferous, it is easy to picture how competition between individuals could have set in train an upward spiral in body size. Rising oxygen entrained in biology an inevitable march towards gigantism.

Certainly, further imaginative experiments with modern insects will continue to yield deeper insights into the effects of the ancient oxygen pulse on animals. It is well known that oxygen is a double-edged sword: it is required to fuel energy production but is at the same time a source of toxic compounds known as reactive oxygen species. Reactive oxygen species are a major threat to the survival of cells because they damage DNA, proteins, and fats and perhaps even underlie ageing and death.[56] Organisms strive to critically maintain cellular oxygen levels sufficient for power production and yet as low as possible to minimize damage by reactive oxygen species. How did giant insects protect themselves from the seemingly inevitable onslaught of reactive oxygen species as oxygen levels ramped upwards to 30% 300 million years ago? Again experiments with living insects offer some tantalizing clues. Resting moth pupae experiencing atmospheric oxygen concentrations of up to 50% maintain levels inside their tracheae at a constant value close to 4%. As oxygen levels rise, pupae limit oxygen uptake by closing the endings of the tracheae

for as long as possible, only opening them to get rid of waste carbon dioxide that has accumulated in the meantime.[57] Moth pupae have a minimum requirement of 4% oxygen, far below the modern atmospheric concentration of 21%, implying higher concentrations are noxious. Whether giant insects behaved in a similar fashion is unknown. Many modern insects are unable to close their tracheae and only avoid suffering from oxygen toxicity because the higher metabolic activity required by flying consumes it fast enough to prevent accumulation. Evolution surely coordinated breathing-system design and metabolic activity to match the demands and capabilities of each other in giant dragonflies.[58]

Pursuing the logical connection between oxygen and animal size to its extreme leads to an obvious question: what happened when oxygen levels plunged to perilously low values at the end of the Permian, 250 million years ago (Fig. 3)? The same issue—extinction by asphyxia—had in fact been raised some 30 years earlier, long before an accurate history of oxygen was established.[59] Palaeontologists noted that, coincidentally, living representatives of certain groups of animals susceptible to extinction also had the highest demand for oxygen. In the history of life on Earth available to them at the time, extinction rate and oxygen requirement were highest in squids and amphibians and declined through a series of animal groups by way of corals, starfish, and ending with anemones. Novel though it is, the oxygen-extinction hypothesis only really began to take hold much later with the realization that all forms of giant insects and animals went extinct after oxygen levels plunged from a heady 35% to a lung-sapping 15%. By the close of the Permian, the global phenomenon of gigantism was over.

We are unsure how the insect giants met their demise during the end-Permian oxygen crisis. It is often suggested that the beneficial effects of high oxygen on insect inhalation through tracheae were reversed as the atmospheric supply dwindled; oxygen delivery through the body of giant insects slowly became less and less efficient. Yet observations on modern grasshoppers question this simple notion because adults experiencing atmospheric starvation simply ventilate their breathing systems more vigorously to compensate.[60] Juvenile grasshoppers, though, seem quite unable to respond in this way, and this increases their susceptibility to asphyxia. It is interesting to speculate from this, that giant insects survived dwindling oxygen levels, only to be doomed to extinction by the failure of their young to do the same.

Prompted by the realization that oxygen starvation took hold at the close of the Permian, palaeontologists have taken another look at whether it was implicated in the extinction of animals at that time.[61] The starting point is the observation that every animal has a minimum requirement for oxygen and this sets the maximum altitude it can survive at. Humans, for instance, live and reproduce in the Peruvian Andes at their altitudinal limit of 5 km above sea level.[62] For lowland animals living during the end of the Permian, the oxygen crisis is equivalent to being transported to the thin altitude found 5 km above sea level. Falling oxygen levels through the Permian forced the mountain dwellers to migrate to the lowlands or risk asphyxia. The ensuing mass migration is proposed to have led to overcrowding, and even extinction, as burgeoning animal populations outstripped the food supply. Is extinction by overcrowding really a credible idea? Without more evidence, many scientists are understandably reluctant to embrace it just yet, even if it apparently sheds some light on a number of seemingly odd facts about the end-Permian extinction. One of the main surviving vertebrates, for example, was a pig-like creature called *Lystrosaurus*, with a barrel-chest that perhaps gave it an increased capacity for deeper breathing. Did *Lystrosaurus* owe its survival to being fortuitously well adapted to low oxygen conditions? Also, fossils of surviving vertebrates have been found 'crowded' up in the high latitudes where they experienced a cooler climate. Again, it is possible to interpret what appears to be animal migration to a cooler climate as a response to low oxygen. The cooler climate slows an organism's metabolism and reduces its oxygen demand.

We should recognize the pioneering nature of both the 'rock abundance' and 'atomic abundance' approaches for reconstructing the history of atmospheric oxygen as multicellular life blossomed. As I have described, before the advent of these methods we had little idea of what really went on. Afterwards, the models clarified the picture by using a mathematical framework to describe those processes regulating Earth's atmospheric oxygen content over millions

of years. The skill is to reduce the complexity of the real world to the minimum number of fundamental processes required to open a realistic window on the history of oxygen. Of course, aspects of many natural phenomena will be lost in this kind of simplification. But we can glimpse the possible role of other feedbacks between the different components of the Earth system by taking a step back from this reductionist philosophy and relaxing some of the underlying simplifying assumptions.

Fire was one of the most controversial of these sorts of feedback.[63] It was put forward by James Lovelock and Andrew Watson when at the University of Reading, and the microbiologist Lynn Margulis at the University of Massachusetts in 1978. When suggesting a role for fire in regulating the oxygen content of the atmosphere, the trio had the Gaia hypothesis uppermost in their minds. Named after the Greek Goddess of the Earth, it proposes that 'the climate and chemical composition of Earth's surface are kept in homeostasis at an optimum by and for the biosphere'.[64] To support the notion that life maintains the Earth in a condition favourable for itself, they were looking for a way to keep oxygen levels constant over time; or put another way, to show self-regulation of the Earth's atmospheric oxygen content.

The question is: how might fire influence the oxygen content of the atmosphere over millions of years? Lovelock's idea was that as oxygen levels crept up, forests became increasingly flammable when struck by lightning. It followed from experiments showing that when paper tape is lit with a spark it ignites and burns more readily in a high-oxygen atmosphere.[65] He conceived of a negative feedback tightly constraining oxygen levels whereby too much oxygen leads to wildfires that devastate plant life. As we have already seen, less vegetation means, in the long run, less carbon burial, reducing the addition of oxygen to the atmosphere. Based on this reasoning, Lovelock and colleagues proposed that the very existence of forests throughout the Carboniferous implied that oxygen levels never rose above 25%. Lovelock himself later claimed that if oxygen levels went 'above 25 per cent very little of our present land vegetation could survive the raging conflagration which would destroy tropical rainforests and arctic tundra alike'.[66]

Obviously, an atmospheric oxygen content of around 35% in the Carboniferous is at odds with the fire feedback invoked by the

Gaians. The reason for the discrepancy seems to lie in Lovelock's extrapolation from laboratory-controlled fires using paper tape to actual 'real world' forest fires. Paper tape is a poor substitute for natural bits of forest like bark, leaves, and wood, because they tend to be thicker and hold more water, giving them different combustion characteristics. Later investigations burning more realistic forest-floor materials showed that the spread of fires is unaltered in an atmosphere with 30% oxygen compared to one with 21%.[67] For drier fuels, an oxygen-rich atmosphere did seem to promote ignition. So, while the ignition of forest fires following lightning strikes appears to be more likely in an oxygen-rich atmosphere, the subsequent spread of fire will be curtailed by the overriding influence of fuel moisture. Support for the notion that, in Lovelock's memorable words, a 'raging conflagration which would destroy tropical rainforests and arctic tundra' during the Carboniferous now seems rather thin.

Other intriguing feedbacks between biology, geology, oceanography, and the oxygen content of the atmosphere are also emerging. Another team of scientists pointed out that rising levels of oxygen increase the concentration of it dissolved in seawater, thereby chemically locking up phosphorus in sediments.[68] Phosphorus is an important nutrient for marine phytoplankton but frequently limits its growth because it is always in short supply. Higher oxygen levels, it is argued, meant fewer nutrients, less growth, reduced burial of organic matter on the seafloor, and a slowing in the rate of oxygen production. This chain of events—more oxygen, less phosphorus, less phytoplankton growth, less carbon burial, less oxygen—forms a negative feedback loop that might act to slow down the rise in oxygen. In fact, phosphorus supply to the oceans and fire on land may themselves be linked through a chain of events that is postulated to end with rising oxygen levels promoting more forest fires.[69] After a fire, decimated forests fail to break down the minerals in soils to release phosphorus. So fire could retard the delivery of phosphorus into the rivers and the oceans, which in turn limits phytoplankton growth and the burial of organic carbon at sea. The net effect is a reduction in oxygen production. It all sounds a neat way of connecting events on land and in the sea, but suffers from the problem that rapidly regenerating forests recovering from fires actually develop more roots to support their expanding biomass. This effect increases, rather than decreases, the amount of phosphorus

being weathered out of soils. Also, the production of charred forest remains leads to burial of microbially-resistant charcoal, creating another positive feedback pushing oxygen upwards.[70]

Interesting though feedbacks of this sort may be, their speculative nature makes it hard to incorporate them in a realistic way into the simple class of Earth system models represented by the 'rock abundance' or 'atomic abundance' approaches. However, one attempt modelled a feedback allowing more forest fires as oxygen levels began to rise, this curbs the burial of organic matter and slows oxygen production. Encouragingly, the resulting reconstruction of Earth's oxygen history is similar to that obtained from the earlier approach, although the inclusion of a fire feedback damps the Carboniferous oxygen pulse to 27%. In this more moderate form, the negative feedback of fire is gaining credence. After all, the trunks of Carboniferous plants were protected from fire by very thick bark, and the abundance of fossil charcoal in Carboniferous sediments testified to outbreaks of forest fire even in swampy environments.[71]

Speculation has long surrounded oxygen's role in the evolution of life on Earth. In the middle of the nineteenth century the Victorian scientist Richard Owen (1804–92) argued that the 'Creator' had chosen the Mesozoic era for the dinosaurs because it was deficient in oxygen. This suited them because as reptiles they had a slower metabolism than the mammals that evolved later on. Owen then argued that oxygen levels rose throughout the Mesozoic to make the atmosphere more 'invigorating' and that this rise in oxygen was the ultimate cause of the extinction of dinosaurs and the other prehistoric reptiles.[72] Owen had no evidence for any of this and merely advanced the notion believing a benevolent Creator matched living things to suitable physical environments.

The present situation could hardly be more different. As the weight of evidence accumulates, a significant rise and fall in the oxygen content of the atmosphere during the Carboniferous and Permian is getting harder to refute. Sceptics are finally being won over, persuaded to accept the idea that the oxygen content of the air we breathe is not fixed at 21%. Indeed, it is remarkable that every time scientists tax their ingenuity to look at something different, one more piece of supporting evidence falls into place. In palaeontology, for example, researchers are incubating alligator eggs in atmospheres containing up to 35% oxygen. Oxygen is found to cause distinctive changes in the bone structure of the developing alligators, with those from higher oxygen growing faster and larger. If correct, it casts the growth rings in the fossil bones of long-extinct reptiles in a new light—as another source of information on the oxygen content of the ancient atmosphere.[73]

We have seen a remarkable alliance of evidence from the disparate fields of geology, physiology, palaeontology, and atmospheric chemistry. It points to the exciting possibility that the oxygen content of the atmosphere played a role in the evolution of large complex animals. Once furnished with reconstructions of oxygen's highs and lows over the last half billion years, palaeontologists have creatively generated hypotheses linking evolutionary novelty with oxygen's influence on animal physiology and ecology. Ebelmen laid the foundations for understanding oxygen over a century and a half ago. He remarked in his 1845 paper, 'many circumstances none the less tend to prove that in ancient geological epochs the atmosphere was denser and richer in carbon dioxide and oxygen, than at present. . . . The natural variations in the air have probably been always in keeping with the organisms that were living at each of these epochs.'[74] Only now are we finally beginning to appreciate the deeper significance his comments hold for how life in an oxygenated world evolved.

Chapter 4

An ancient ozone catastrophe?

The stratospheric ozone layer shields Earth's surface-dwelling life forms from the damaging effects of harmful excess ultraviolet radiation. Its apparent fragility was emphasized all too clearly with the shock announcement in 1985 of the discovery of an ozone 'hole' above Antarctica. Could, then, natural phenomena such as massive volcanic eruptions, asteroid impacts, and exotic cosmic events like supernova explosions have damaged the biosphere's Achilles heel in the distant past? If so, are lethal bursts of ultraviolet radiation penetrating a tattered ozone layer implicated in mass extinctions? Definitive evidence of an ultraviolet radiation catastrophe is hard to come by. But contentious claims that mutated fossil plant spores point to exactly that possibility during the greatest mass extinction of all time, 251 million years ago, are now under close scrutiny.

We are all agreed that your theory is crazy. The question which divides us, is whether it is crazy enough to have a chance of being correct.
Niels Bohr (1958), *Scientific American*