

Oxygen

The Molecule that made the World

Chapter 5: The Bolsover Dragonfly

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About

Dr Nick Lane is a British biochemist and writer. He was awarded the first Provost's Venture Research Prize in the Department of Genetics, Evolution and Environment at **University College London**, where he is now a Reader in Evolutionary Biochemistry. Dr Lane's research deals with evolutionary biochemistry and bioenergetics, focusing on the origin of life and the evolution of complex cells. Dr Lane was a founding member of the UCL Consortium for Mitochondrial Research, and is leading the UCL Research Frontiers Origins of Life programme. He was awarded the 2011 BMC Research Award for Genetics, Genomics, Bioinformatics and Evolution, and the 2015 Biochemical Society Award for his sustained and diverse contribution to the molecular life sciences and the public understanding of science.



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THE SMALL MINING TOWN OF BOLSOVER in Derbyshire enjoyed an unexpected fifteen minutes of fame in 1979. While working a coal seam 500 metres beneath the surface, local miners dislodged a gigantic fossilised dragonfly with a wing-span of half a metre, rivalling that of a seagull. Experts from the Natural History Museum confirmed that the fossil dated to the Carboniferous period, about 300 million years ago. The giant was dubbed the Bolsover dragonfly, but although one of the oldest and most beautifully preserved of fossil insects, it was far from unique. Similar fossils from the coal measures of Commeny in south-east France had been described by the French palaeontologist Brongniart as long ago as 1885, and giant dragonflies had since been unearthed in North America, Russia and Australia. Gigantism was unusually common in the Carboniferous.

The Bolsover dragonfly belongs to an extinct group of giant predatory flying insects, thought to have sprung from the same stock as the true dragonfly (Odonata) and known as the Protodonata. Like their modern counterparts, the Protodonata had long narrow bodies, huge eyes, strong jaws and spiny legs for grasping prey. Pride of place went to the largest insect that ever lived, the colossal *Meganeura*, which had a wing-span of up to 75 cm and a diameter across the chest (thorax) of nearly 3 cm. This prototype dragonfly differed mostly from its living relatives in the structure of its wings, which were primitive in the number and pattern of veins. The giant size and primitive wing structure led the French scientists Harlé and Harlé to propose in 1911 that *Meganeura* could never have managed to fly in our thin modern atmosphere. They argued that such a giant could only have found the power to fly in a hyperdense atmosphere containing higher levels of oxygen than the present 21 per cent. (If the extra oxygen was added to a constant amount of nitrogen, the air as a whole would be more dense). This startling

claim echoed down the corridors of 20th century science, to be repeatedly and vigorously rejected by the palaeobiological establishment. By 1966, the Dutch geologist MG Rutten could write, in a charmingly antiquated style that has passed forever from the scientific journals:

“Insects reached sizes of well over a metre during the Upper Carboniferous. In view of their primitive means of breathing, by way of trachea through the external skeleton, it is felt that these could only survive in an atmosphere with a higher O₂ level. As a geologist, the author is quite satisfied with this line of evidence, but other geologists are not. And there is no way of convincing one’s opponent.”....

.... The idea is that the size of flying insects is restricted by the need for oxygen to diffuse through the branching network of hollow tubes that makes up the tracheal system. Any increase in size increases the distance that oxygen must diffuse and so makes flight less efficient. The upper limit to passive diffusion is considered to be about 0.5 cm. According to Robert Dudley, a physiologist at the University of Texas, an elevation of oxygen to 35 per cent would increase the rate of oxygen diffusion by approximately 67 per cent, improving the oxygenation of flight muscles, allowing thicker constructions and permitting insects to grow larger. While other selective pressures, such as predation, probably drive the actual tendency to get bigger, higher oxygen levels raise the physical barrier to greater size.

So far so good, but there is one problem with this line of reasoning: the tracheal system may be primitive, but it is far from inefficient – with it, flying insects achieve the highest metabolic rates in the whole of the animal kingdom. Almost without exception, insect flight is totally aerobic, which means that their energy production is dependent entirely on oxygen. In spite of our well ventilated lungs, powerful hearts, elaborate circulatory systems and red blood cells packed with the oxygen-carrier haemoglobin, we are less efficient. Sprinters cannot breathe in enough oxygen to power their efforts and instead must resort to the less efficient process of glycolysis, which produces a mild poison, lactic acid, as a by-product. The longer we persist in violent exercise, the more lactic

acid builds up, until finally we are left half paralysed, even if we are running for our lives. Heavy-legged exhaustion is the product of a respiratory failure that does not trouble insects. If you ever thought that a housefly never grows tired of buzzing, you were probably right: unfortunately for us, it does not poison itself with lactic acid.

The limits of insect flight are not at all easy to define. In a handful of rather quirky experiments dating back as far as the 1940s, experimenters tried tethering insects, attaching tiny weights, cutting oxygen levels to a fraction of normal air, and replacing nitrogen with light-weight helium mixtures. All went to show the surprisingly wide safety margins of insect flight. Some insects are even able to fly in low-density helium mixtures with an oxygen content of just 5 per cent. In most experiments, insects gained no apparent benefit if oxygen levels were increased to 35 per cent. The broad conclusion was that insect flight is not limited by tracheal diffusion, so oxygen cannot act as a spur to greater size. This is still the opinion of many entomologists, but the tide is beginning to turn.

The reason the tracheal system is so efficient is that oxygen remains in the gas phase and need not pass into solution until the last possible moment, as it enters the flight muscles themselves. As a result, the ability of the tracheal system to deliver oxygen typically exceeds the capacity of the tissues to consume it. The only real inefficiency is the blind endings of the trachea, which branch into fine tubules in much the same way as the blind bronchioles in our own lungs. Just as we suffocate if we cannot physically draw breath, so too insects are limited by the diffusion of gases in the blind alleys of the tracheal system. Most insects get around this difficulty, as we do ourselves, by actively ventilating their trachea.

For insects, there are two ways of ventilating the trachea, known as abdominal pumping and autoconvective ventilation. Most 'modern' insects, including wasps, honeybees and houseflies, rely on abdominal pumping, in which the insects contract their abdomens rhythmically to squeeze air through the tracheal network. The rate of pumping changes in response to the amount of oxygen available. If honeybees are placed in low-oxygen

air, for example, their metabolic rate remains constant – they continue to get through the same amount of oxygen as they fly – but the rate of water loss by evaporation may increase by as much as 40 per cent, implying that the bees compensate for the low oxygen by pumping their abdomens more vigorously, thereby increasing the rate of tracheal ventilation, and so evaporation. The efficiency of this process allows most insects to keep an even keel in changeable conditions.

Dragonflies, locusts and some beetles rely on the second, more primitive, means of ventilation, autoconvective ventilation. This is a splendidly opaque way of saying that they create drafts when they flap their wings. Insects that depend on autoventilation can increase airflow in their trachea by increasing the frequency or amplitude of wing beats – they flap their wings harder. There is of course a catch here: beating wings demands energy, and the harder they beat the more energy is needed. Since energy production requires oxygen, and the availability of oxygen can only be increased by beating, which consumes the extra oxygen, dragonflies and other autoventilating insects may be uniquely susceptible to fluxes in oxygen levels.

In principle, a rise in oxygen levels should enable dragonflies to beat their wings less actively to achieve the same flight performance; or, for a constant rate of beating, the body size might be increased. In a detailed study published in the *Journal of Experimental Biology* in 1998, Jon Harrison and John Lighton put these ideas to the test, and finally produced solid evidence that dragonfly flight metabolism is sensitive to oxygen. They measured carbon dioxide production, oxygen consumption and the thoracic temperature of free-flying dragonflies kept in sealed respiratory chambers. Raising the oxygen content from 21 to 30 or even to 50 per cent increased the metabolic rate. This means that, in today's atmosphere, dragonfly flight is limited by oxygen insufficiency. If dragonflies can fly better in high-oxygen air, then presumably larger dragonflies, that could not generate enough lift to become airborne at all in today's thin air, would have been able to fly in the postulated oxygen-rich mix of the Carboniferous. It seems that the Bolsover dragonfly really was only able to fly, and so survive, in an oxygen-rich atmosphere.

DRAGONFLIES WERE NOT THE ONLY GIANTS of the Carboniferous – many other creatures attained sizes never matched again. Some mayflies had wingspans of nearly half a metre, millipedes stretched for over a metre, and the *Megaranea* spider, with a leg-span of nearly half a metre, would have chilled the marrow of Indiana Jones. Even more terrifyingly, scorpions reached lengths of a metre, dwarfing their modern cousins, the largest of which barely manages a fifth of that length. Among the terrestrial vertebrates, amphibians grew from newt-like proportions to reach body lengths of five metres. They left some of the oldest footprints in England, at Howick in Northumberland, with dimensions of 18 cm in length and 14 cm across. In the plant world, ferns turned into trees, while the giant lycopods reached perpendicular heights of nearly 50 metres. Their only survivors today are the diminutive herbaceous ground or club mosses, such as the ground pine (*Lycopodium obscurum*), which rarely attain heights of over 30 cm.

Was all this rampant gigantism related to oxygen? It is certainly possible. Like the dragonfly, each of these organisms depends on the passive diffusion of gases in one way or another. The size of amphibians, for instance, is restricted by their capacity to absorb oxygen by diffusion across their skin, whereas the height of plants depends on the thickness of their structural support, which in turn is limited by the need for gas exchange. On the other hand, while it is plausible that high oxygen levels might enable greater size, it is hard to back the claim with direct evolutionary evidence. There is one tantalising suggestion from modern ecosystems, however, that this is indeed the case.

Tucked away in the correspondence section of *Nature* in May 1999 was a short letter on the size of crustaceans – the class that includes shrimps, crabs and lobsters – in polar regions. The correspondence pages of *Nature* present brief descriptions of research, rather than detailed papers, but the conciseness of the format makes it the perfect arena for good old-fashioned understatement – this, after all, was where Watson and Crick chose to publish their proposal in 1953 for a possible solution to the structure of the salt of deoxyribonucleic acid, based on their interpretation of x-ray photographs – the famous double helix. The more recent letter is admittedly less momentous, but it too solves a longstanding riddle rather neatly: the relationship between gigantism and

oxygen availability.

The authors, Gauthier Chapelle of the Royal Institute of Natural Sciences in Belgium, and Lloyd Peck of the British Antarctic Survey, examined length data for nearly 2,000 species of crustaceans from polar to tropical latitudes and from marine to fresh-water environments. They focused on a single group, known as amphipods, which are cold-blooded, shrimp-like creatures, ranging in length from a couple of millimetres to about 9 cm. The amphipods are not exclusively marine, and are best known to most of us as sand-hoppers, or the shiny brown animals that leap about when pot plants are moved in the garden.

The thousands of marine species of amphipod are a cornerstone of polar food chains, being the staple diet of juvenile cod, which are in turn preyed upon by seals, and the seals by polar bears. In some bottom waters, amphipods are found at an extraordinary density of 40,000 per square metre. These tiny creatures offer even more of a square meal in polar waters: the largest Antarctic species are some five times larger than their tropical cousins – true giants by amphipod standards. In this respect, amphipods are not alone. For the last hundred years or so, scientists have catalogued numerous giant species in polar seas. Although polar gigantism is usually ascribed to the low temperatures and the reduced metabolic rates of cold-blooded animals, the relationship is not straight-forward. Surprisingly, polar gigantism had never been satisfactorily explained. The trouble is that the inverse correlation between size and temperature is curved rather than linear, and has a number of puzzling exceptions. In particular, many species achieve far greater sizes in freshwater environments than they ought to on the basis of temperature alone. Freshwater amphipods from Lake Baikal in Russia, for example, are twice as large as those in the sea at the same temperature.

Then Chapelle and Peck had a clever idea and applied it to their amphipod data. What if the true correlation was not with water temperature at all, but with the dissolved oxygen concentration? Oxygen dissolves better in colder water and is nearly twice as soluble in

polar seas than in tropical waters. The salt content also affects the solubility of oxygen, which dissolves 25 per cent better in fresh water than in saline. The highest oxygen saturation is therefore in large freshwater lakes verging on the Arctic tundra, such as Lake Baikal – and this is where the largest crustaceans are to be found. When Chapelle and Peck re-plotted their length data against the oxygen saturation of the water, they got a nearly perfect fit [FIGURE 5]. While it is true that a correlation says nothing about mechanism, it seems likely that inadequate oxygen availability limits size in many species, or conversely that high oxygen raises the barrier to gigantism.

Of course the dependence of giants on high oxygen means that they are perilously susceptible to falling oxygen levels. In a stark closing line, Chapelle and Peck predict that giant amphipods will be among the first species to disappear if global temperatures rise, or if oxygen levels decline. We can hardly begin to imagine what effect this might have on the rest of the food chain.

THE CASE FOR CHANGEABLE OXYGEN levels in the atmosphere is not easy to dismiss. This conclusion stands in opposition to Lovelock's Gaia theory, which argues that the living biosphere has regulated the levels of oxygen in the atmosphere over the last 500 million years. While this may be true for much of the time, there have surely been periods when the biosphere lost control over oxygen levels. If anything, the possibility that Gaia cannot always maintain the physiological balance that Lovelock ascribes to her only strengthens his concerns about our impact on the planet. Given the unequivocal evidence of global glaciation punctuating the Earth's history, it is plain that Gaia does not have a tight control over temperature. Something similar seems to be true of oxygen. We have a tenuous grasp of the factors that control oxygen or carbon dioxide levels, but the fact that there have been times when they have tipped out of balance means that it can happen again, perhaps with our help. The feedback mechanisms postulated by Lovelock and others have the power to resist change for a period. If we are to judge from the case of oxygen, they do not have indefinite flexibility and cannot resist catastrophic change. We should beware.

With the exception of fire there is remarkably little evidence that high oxygen levels are in any way detrimental to life. On the contrary, high oxygen may have opened evolutionary doors that are closed to us today. Falling oxygen closes these doors, and the species left outside are unlikely to survive. Most of the giants of the Carboniferous, for example, failed to survive until the end of the Permian period, when Robert Berner's calculations suggest that oxygen levels plummeted to 15 per cent, as the climate became cooler and drier.

We must conclude that high oxygen is good, low oxygen is bad. At the end of such a lengthy and detailed analysis, this platitude may seem a bit of a lame conclusion. And yet. We saw in Chapter 1 that high levels of oxygen are toxic, causing lung damage, convulsions, coma and death, and we are assured that oxygen free radicals are at the root of ageing and disease. What is going on: is oxygen toxic or not? This paradox did not escape the notice of Barry Halliwell and John Gutteridge, authors of the standard text on free radicals in biology and medicine, who remarked laconically that 'the plants and animals existing in the Carboniferous times must presumably have had enhanced antioxidant defences, which would be fascinating to study if these species could ever be resurrected.' Yes indeed! How did they overcome oxygen toxicity? Might there be some way that we can imitate them to protect ourselves against free radicals in disease? It is time to look in a little more detail at the strange spectre of oxygen toxicity, and what life does about it.

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