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# Oxygen - the breath of life

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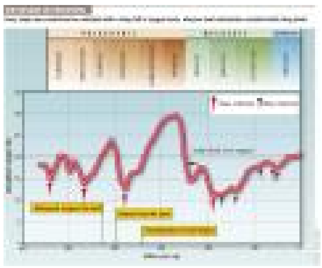
The extinction of the dinosaurs some 65 million years ago is perhaps the most celebrated scientific story of modern times. Surprisingly, though, no one pays much attention to an equally intriguing mystery. What was it that triggered the rise of the dinosaurs in the first place and then allowed them to dominate life on Earth for the next 160 million years? The answer that is emerging is a surprising one: oxygen.

It seems this gas has played a much greater role in driving evolutionary change than any meteor impact, volcanic eruption or ice age. Recent findings indicate that oxygen levels in Earth's atmosphere have fluctuated throughout its history: it may have been these variations more than anything else that have energised life to make leaps of development or forced it to retreat, in events including the colonisation of land, numerous mass extinctions - and the rise of the dinosaurs.



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The oxygen of evolution

We live in a world that is quite atypical of Earth during most of its 4.6-billion-year history, and probably its future as well. For much of the past, Earth had an atmosphere with less oxygen than it does now. Only in the past 2.2 billion years has there been free oxygen in the atmosphere at all, and probably only for the past 600 million years has there been enough to support animal life. As new methods have been developed that allow precise estimates of ancient oxygen levels, it has become clear that they also varied enormously during those 600 million years.

What has caused oxygen to rise and fall so dramatically? It seems a wide range of interacting biological, geological and chemical processes are involved. Oxygen is a highly reactive gas that rapidly undergoes chemical reactions with reduced compounds - especially carbon, sulphur and iron - on Earth's surface and crust and in the sea. These reactions trap oxygen, removing it from the atmosphere. Once out of circulation, oxygen can only be released by other reactions involving the reduction of oxidised compounds. The most important of these is photosynthesis, the reduction of carbon dioxide by plants, algae and microorganisms, which liberates free oxygen as a by-product.

This balance between oxidation and reduction dictates the level of oxygen in the atmosphere over geological timescales. So to estimate past oxygen levels we need to estimate the rates at which oxygen was being liberated and consumed. Geology plays a critical role here, in particular the interplay of erosion, sedimentation and subduction that take minerals out of contact with the atmosphere or sea, and the convulsive processes that bring others up into play.

The tectonic forces that cause the rise of mountains and the folding and buckling of Earth's crust can bring to the surface rocks that contain reduced compounds which then react with oxygen. The most important of these are dark shales, formed from mud on the bottom of stagnant oceans.

When buried, these rocks have no contact with free oxygen. If they are uplifted and then erode under the onslaught of rain, wind, cold and heat, however, vast volumes of oxygen will be consumed, causing atmospheric levels of the gas to fall.

The reverse can also occur. If large volumes of reduced compounds are rapidly removed from contact with the atmosphere - perhaps buried at subduction zones where one tectonic plate dives beneath another, or built into sedimentary rocks on the bottom of dank swamps - free oxygen levels can soar.

The best example of this occurred in the Carboniferous period, when vast forests became buried in coal swamps. Because the trees were primitive and had poor root systems, they fell over easily and piled up fast enough to cut them off from the air. Wood is rich in reduced carbon, and as a result of the removal of all this material, levels of free oxygen hit a record high.

There are other ways to change oxygen levels. During the late Permian period, the world became hot and arid. Deserts spread far and wide. The global rate of photosynthesis fell, less carbonaceous material was buried and oxygen levels plummeted.

A greater understanding of such processes has led to new models of how oxygen levels have changed. The most powerful of these models is Geocarbsulf, developed by Robert Berner of Yale University. There are still many details to be filled in, but geologists increasingly view the larger trends with confidence (see Graph).

What are the highlights? First, at the start of the "age of animals" 542 million years ago, oxygen levels were lower than today. They fluctuated for 100 million years before rising steadily, peaking some 400 million years ago at around 25 per cent near the beginning of the Devonian period. This was followed by a steep decline, after which levels rose and rose, peaking again near the end of the Carboniferous. Quite a peak it was too: oxygen levels may have exceeded 30 per cent. From then we see a precipitous fall to a nadir of around 12 per cent at the end of the Triassic period, and then an irregular but slowly rising curve to the present day.

Many palaeobiologists now believe that these changes have had profound effects on life, especially animal life. In particular, periods of lower oxygen have coincided with every mass extinction we know of.

The aftermaths of these extinctions were times of rapid evolution, often producing novel body plans with new, more efficient respiratory systems. Palaeobiologists used to view new respiratory structures as add-ons to body plans evolved largely for movement. Some of us now think that basic designs evolved to maximise respiratory efficiency, with locomotion as a secondary benefit.

For instance, the evolution of bipedalism in reptiles may have had as much to do with allowing them to breathe while running as it did with locomotion itself. Similarly, both fish and cephalopods have changed their body shape to force larger volumes of water across their gills.

A quick thought experiment shows why this was so. Throughout their lives animals need to feed, drink, reproduce and respire. The first three of these can usually be put off for days or even years, but for the vast majority of animals respiration can be put off only for a few minutes. Evolution is prodded by natural selection, which is a euphemism for variable rates of death. And nothing kills quicker than lack of oxygen.

## Conquering the land

There is now abundant evidence that oxygen levels have fluctuated widely over the past 600 million years, but how do we know these changes had major evolutionary effects? Let's look at two important events in the history of animal life that may have been sparked by changes in oxygen levels: the conquest of land and the ascendancy of the dinosaurs.

The overall pattern of the conquest of the land is fairly well known. The first land plants appeared in the late Cambrian period, 500 million years ago, but animals did not follow for another 75 million years. What took them so long? By the time we find the first undisputed evidence of land animals - small scorpions - their relatives had been living in water for over 100 million years. That's a long time to wait for evolution to invent legs and a respiratory system suitable for breathing air.

There is some evidence to suggest, however, that evolution was not holding them back. As many as 100 living lineages of fish show some adaptation to terrestrial life, and the fossil record of these forms indicates that the evolution of the necessary body structures can occur relatively quickly, certainly in much less than 100 million years. So it appears that it was not the wait for new structures that delayed the move to land. Most probably the animals had to wait until oxygen levels rose enough to allow lungs to function.

The latest Geocarbsulf results show that oxygen exceeded modern levels for the first time near the end of the Silurian period. It was soon after this that invertebrates appeared on land. Coincidence? The subsequent history of terrestrial life suggests not.

Following the Silurian high, oxygen levels plummeted; then came the Devonian mass extinction. This seems to have had a drastic effect on the new land colonists, driving most of them back into the sea, or to extinction.

According to a recent study by myself, Robert Berner, Conrad Labandeira of the Smithsonian Institution in Washington DC and Michel Laurin of the Denis Diderot University of Paris, as oxygen levels dropped, so too did the number of terrestrial arthropods (*Proceedings of the National Academy of Sciences*, vol 103, p 16818). By the time oxygen bottomed out at 13 per cent, only a few arthropods were left on land. Studies are now under way to determine if these survivors had superior respiratory systems.

Land animals did not become common again until the early Carboniferous, around 345 million years ago. Why this second colonisation of land? Again, oxygen levels provide a possible explanation. During the late Devonian oxygen began to rise again. By the Carboniferous, levels were once again equal to today's, and once again this rise coincides with a colonisation of land: a second colonisation, quite distinct from the Silurian adventure. All in all, this pattern is consistent with the idea that rising oxygen levels had substantial evolutionary effects.

Now look at a second example, one in which falling oxygen levels may have stimulated the evolution of a new body plan. This could provide an answer to the often-neglected question we began with: why did dinosaurs evolve in the first place, and why were they so successful?

The time just before the dinosaurs appeared was a time of very low oxygen - the lowest during the entire age of animals. Berner has estimated that oxygen levels may have been as low as 12 per cent, which is thin air indeed, equivalent to being about 4400 metres above sea level today.

This oxygen nadir in the late Triassic must have had a major impact on reptiles, the dominant land animals of the time. Reptiles first appeared about 300 million years ago, during an oxygen high, and their lungs were adapted accordingly. They are called septate lungs and are small, rigid and sac-like. In a world with 30 per cent oxygen, septate lungs were perfectly adequate. By the end of the Triassic, however, those small and simple lungs were not so great. We know this because of the effect of increasing altitude on modern lizards. Lizards have septate lungs and their respiratory system fares poorly in thin air. They do not thrive at higher elevations and are rarely found above 2500 metres.

Declining oxygen surely had a similar impact on Triassic reptiles, and we would expect new kinds of respiratory structures to have evolved in response. Sure enough, about 230 million years ago, a brand new respiratory system appeared in what until then had been an obscure and not overly successful group. The secret was to add a system of supplementary air sacs next to the lungs, and the group that invented it was the dinosaurs.

We can see the same air-sac system today in the sole surviving descendants of the dinosaurs: birds. Like reptiles, birds have septate lungs that are small and rigid. But unlike today's reptiles, they also have air sacs, and the resultant system of respiration is much more efficient than a lizard's.

When a bird breathes in, air does not go directly into the lungs. Instead, it enters the air sacs, where it is stored briefly before passing into the lungs at the next inhalation. In this way, air enters and exits a bird's lungs at different points - in via the air sacs, out via the windpipe - allowing them to maintain near-constant, one-way airflow through their lungs. This allows a countercurrent system to be set up between the air and the bloodstream, with air passing in one direction and blood in the other. The result is far more efficient gas exchange between air and blood than is possible in lizards, or even mammals.

The differences between animals that use air sacs and those that don't are striking. Birds extract more oxygen from the air than any other animal of comparable size. At sea level they are 33 per cent more efficient at extracting oxygen than mammals. At 1500 metres a bird may be 200 per cent more efficient. This gives birds a huge advantage over mammals at altitude. It also explains why geese can migrate over the Himalayas at an altitude that would kill a human.

How do we know that Triassic dinosaurs also had air sacs? The answer lies in their bones. To save valuable space in the body cavity, much of a bird's air-sac system is tucked away inside its bones. That is well known, but it wasn't until 2005 that its full extent was discovered. Patrick O'Connor of Ohio University College in Athens and Leon Claessens of Harvard University injected birds' air sacs with latex, revealing for the first time each tiny incursion of air sac into the skeleton. They found that the system is much more voluminous and intricate than anyone had suspected (*Nature*, vol 436, p 253).

They then turned their attention to some early dinosaur bones - and found exactly the same kind of holes. It strains scientific credulity that two such intricate structures with such extraordinary similarity evolved for different purposes. There is good evidence that air sacs enabled the dinosaurs to survive and flourish through the late Triassic mass extinction. Recent work by Ken Williford of the University of Washington, Seattle, has shown that of all the land animals present at the end of the Triassic, only dinosaurs with air sacs came through unscathed.

The examples above are just two of many that appear to link changes in atmospheric oxygen with major evolutionary transitions. What of the future? Will oxygen levels change again? That is a certainty, whether as a result of desertification, tectonic activity, or something else. What we don't know is what evolution will do about it.

Peter Ward is professor of biology at the University of Washington in Seattle. This article is adapted from his book *Out of Thin Air: Dinosaurs, birds, and Earth's ancient atmosphere* (Joseph Henry Press, ISBN 0309100615)

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