8. P. Shor, *Phys. Rev. A* **52**, 2493 (1995).
9. A. Steane, *Phys. Rev. Lett.* **77**, 793 (1996).
10. D. Tolkunov *et al.*, *Phys. Rev. A* **71**, 060308 (2005).
11. K. Roszak *et al.*, *Phys. Rev. A* **73**, 022313 (2006).
12. M. Franca Santos *et al.*, *Phys. Rev. A* **73**, 040305 (2006).
13. L. Derkacz *et al.*, *Phys. Rev. A* **74**, 032313 (2006).
14. M. Yönaç *et al.*, *J. Phys. B* **39**, S621 (2006).
15. Z. Ficek *et al.*, *Phys. Rev. A* **74**, 024304 (2006).
16. K. Ann *et al.*, *Phys. Rev. B* **75**, 115307 (2007).

17. C. Pineda *et al.*, *Phys. Rev. A* **75**, 012106 (2007).
18. W. K. Wootters, *Phys. Rev. Lett.* **80**, 2245 (1998).
19. E. Schrödinger, *Naturwissenschaften* **23**, 807 (1935).
20. In Schrödinger's thought experiment, a cat is placed in a box with a randomly triggered poison. According to quantum theory, until an observation is made, the cat is in a superposition of two states, in effect both "alive" and "dead" simultaneously.
21. A. Einstein, B. Podolsky, N. Rosen, *Phys. Rev.* **47**, 777 (1935).

22. T. Yu, J. H. Eberly, http://arxiv.org/abs/quant-ph/0503089.
23. T. Yu, J. H. Eberly, *Phys. Rev. B* **66**, 193306 (2002).
24. F. Mintert, A. R. R. Carvalho, M. Kus, A. Buchleitner, *Phys. Rep.* **415**, 207 (2005).
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EVOLUTION

# Oxygen and Evolution

**Robert A. Berner, John M. VandenBrooks, Peter D. Ward**

Changes in atmospheric oxygen concentration may be linked to key evolutionary events during the past 550 million years.

The rise of atmospheric oxygen ($O_2$) concentration during the Precambrian eon (~4500 to ~550 million years ago) was closely tied to biological evolution. Additional changes in atmospheric $O_2$ concentrations over the past ~550 million years (the Phanerozoic eon) have probably also been intertwined with biological evolution. Here we examine the evidence for changes in $O_2$ concentrations and their biological causes and effects during the Phanerozoic.

Evidence for variations in atmospheric $O_2$ concentrations over Phanerozoic time comes mainly from the geochemical cycles of carbon and sulfur. The weathering of organic carbon and pyrite sulfur results in $O_2$ consumption, and their burial in sediments results in $O_2$ production (*1*); organic burial represents an excess of global photosynthesis over global respiration. Existing combined carbon-sulfur-oxygen models all show distinct variation of $O_2$ over time, with a maximum centered around 300 million years ago, but with differences between models for the past 200 million years (*1*). They are based on either the abundance of reduced carbon and sulfur in sediments, the $^{13}C/^{12}C$ and $^{34}S/^{32}S$ values for the oceans, or the interaction of the carbon and sulfur cycles with cycles of other elements such as phosphorus.

The model shown in the figure is the most detailed for the entire Phanerozoic and lends itself readily to the discussion of evolutionary phenomena. Note the large rise in $O_2$ prior to 300 million years ago. The primary cause of this rise is believed to be the evolution of large vascular land plants (*1*). The plants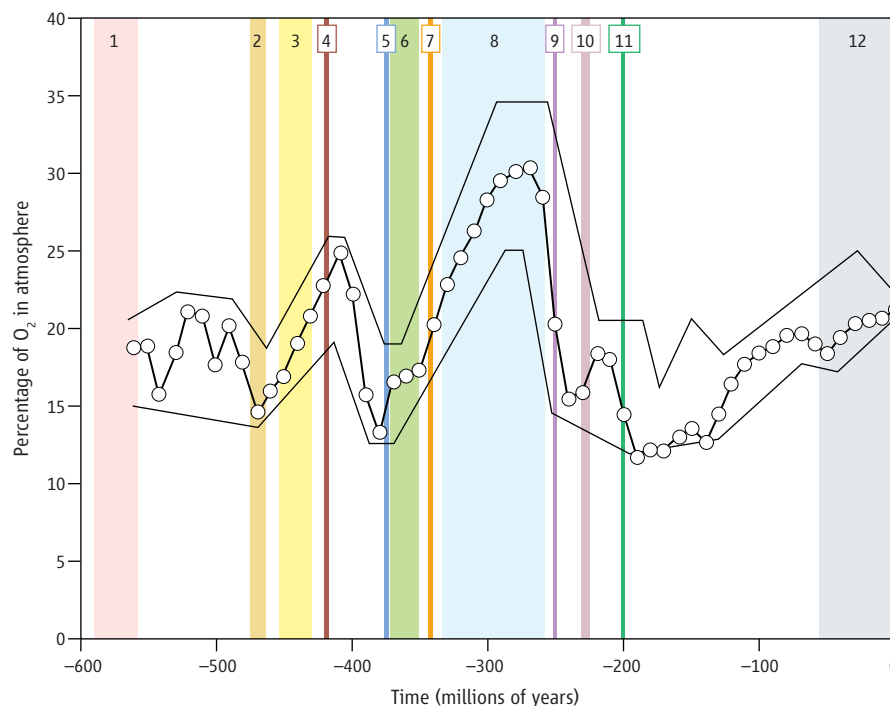 caused increased burial of organic matter (and hence increased $O_2$ production) because of the introduction of a new bio-degradation-resistant substance, lignin. The excessive burial of lignin and other plant debris in swamps during the late Paleozoic (~360 to 260 million years ago) led to the formation of vast coal deposits and to increased wildfires, as evidenced by abundant fossil charcoal (*2*). The drop in $O_2$ concentration across the Permian-Triassic boundary (~260 to 245 million years ago), and the relative lack of coal deposition during the last 5 million years of this time span, are believed to have been due mainly to a substantial reduction in the geographic extent of lowland forests and swamps. This resulted in a drop in global organic matter burial and in $O_2$ input to the atmosphere (*3*).

How has the variation in atmospheric $O_2$ concentration through the Phanerozoic affected the evolution and development of life on Earth? In 1970, McAlester (*4*) noted that to understand these effects, it is necessary to first run "long-term experiments on the effects of abnormally high or low $O_2$ partial pressures on the living representatives of the many groups which exist today."

Unfortunately, few scientists have heeded this call, and the effects of the modeled $O_2$ concentrations (~13 to 31%) on modern physiology and development are still poorly understood, especially in the hyperoxic range

R. A. Berner is in the Department of Geology and Geophysics, Yale University, New Haven, CT 06520, USA. E-mail: robert.berner@yale.edu ]. M. VandenBrooks is in the School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA. P. D. Ward is in the Department of Biology, University of Washington, Seattle, WA 98195, USA.

**A possible link.** The atmospheric $O_2$ curve is taken from (*23*). The upper and lower boundaries are estimates of error in modeling atmospheric $O_2$ concentration. The numbered intervals denote important evolutionary events that may be linked to changes in $O_2$ concentration (see text).

(>21% $O_2$, the current atmospheric $O_2$ concentration). Furthermore, most studies have focused on the effect of $O_2$ on insect development, and even those limited studies examined $O_2$ levels outside the range of geologic variation (5). However, the existing studies point to a substantial effect of this range of $O_2$ variation on development and evolution.

Many studies have used *Drosophila melanogaster* to study these effects. For example, it has been shown that hyperoxia causes an increase in body size in *D. melanogaster* through multiple generations (6), whereas hypoxia decreases body size (7); $O_2$ concentration is negatively correlated with tracheal diameter in insects of the same body size (8), and hypoxia causes a decrease in cell size (9).

Fewer studies have investigated the effects of $O_2$ concentrations on vertebrates. For example, hyperoxia (35% $O_2$) induces regression of the external gills in tree frogs (*Agalychnis callidryas*) and causes early hatching when the frogs are subsequently exposed to air levels of $O_2$ (21%) (10). When juvenile trout (*Oncorhynchus mykiss*) are exposed to hyperoxia (38% $O_2$), their body weight increases compared to those at 21% $O_2$ (11).

One of us has studied the embryonic development of *Alligator mississippiensis* under seven different $O_2$ concentrations between 16 and 35% (spanning the entire Phanerozoic $O_2$ range) (12). The results show a positive effect of $O_2$ on body size, developmental rate, and bone composition, with a developmental optimum at ~27% $O_2$, beyond which the negative effects of increased $O_2$ concentration begin to play a larger role and cause increased mortality.

Four major events in the history of life illustrate the effects of rising, or high, concentrations of $O_2$ on evolution. First, the origin of the first animal body plans (see the figure, interval 1) coincided with a rapid rise in atmospheric $O_2$ concentration (13).

Second, the conquest of land by animals occurred during two independent phases of high $O_2$ concentration (14). The earliest, ~410 million years ago (interval 4), involved mainly arthropods; the other, which followed the Devonian mass extinction and a period of stasis (Romer's Gap, interval 6), involved both arthropods and vertebrates (interval 7).

Third, with increasing $O_2$ concentrations through the Carboniferous and Permian (interval 8), gigantism developed in several arthropod groups, and body size increased across primitive reptile-like animals and their descendants (12, 15, 16). The gigantism has classically been attributed to an increase in diffusive capacity caused by an increase in atmospheric $O_2$ concentration. This may explain the effect seen in egg-laying vertebrates, because diffusion across the eggshell will be increased and have an effect on hatchling and therefore adult body size. Alternatively, in some insects, body size is limited by the amount of their body that can be allocated to trachea. Because tracheal diameters decrease with increased $O_2$ concentration, a higher maximal body size can be achieved in times of higher $O_2$ concentration (17).

Lastly, the increase in mammalian body size in the Tertiary has been linked to rising $O_2$ concentrations (18) (interval 12), although the direct mechanism remains unclear, and community diversification occurred during the Ordovician rise in $O_2$ (interval 3).

Dropping $O_2$ or relatively low $O_2$ concentrations also had evolutionary consequences. Several extinctions appear to coincide with dropping $O_2$ concentrations superimposed on global warming from increased greenhouse gas concentrations (19, 20). Three of the major extinctions—in the Late Devonian (interval 5), Permian-Triassic (interval 9), and Triassic-Jurassic (interval 11)—were also followed by an extended period of low atmospheric $O_2$ concentration. The aftermath of a major extinction is often a time of rapid evolution, potentially producing novel body plans. Many of these new body plans may have supported more efficient respiratory systems, which may have been selected for under low-$O_2$ regimes that coincide with postextinction time periods.

For example, late Cambrian/Ordovician lineages of fish and cephalopods evolved anatomical structures that took advantage of their swimming ability to force larger volumes of water across their gill surfaces, which in turn allowed for increased $O_2$ uptake (interval 2). Adaptations for more efficient respiration also occurred among terrestrial organisms. During the latter part of the Triassic (interval 10), a time of low modeled $O_2$ concentrations, the evolution of the dinosaur body plan involved a novel air-sac system (21), which was inherited in modified form by its descendants, the birds. Air-sacs allow highly efficient respiration even at high altitude (22). They may similarly have conferred a respiratory advantage to early dinosaurs as compared to other contemporary terrestrial animals.

In the past, respiratory structures were viewed as add-ons to body plans evolved largely to allow movement. Yet, the evidence discussed above suggests that the basic designs of many animals seems to maximize respiratory efficiency, with locomotion or protection (as with a mollusk or arthropod shell) as a secondary benefit.

To further this research, a better understanding of the effect of varying $O_2$ concentration on the physiology of present-day animals is needed. Multigenerational studies on a wide range of animals (both vertebrates and invertebrates) are necessary to accurately infer responses of fossil taxa to $O_2$ variation, to test evolutionary impacts of varying $O_2$ concentrations, and to understand the long-term effects of living under hyperoxic and hypoxic conditions. The results could be used to develop proxies for past $O_2$ concentrations, thereby improving $O_2$ modeling (which also needs constant updating based on better isotopic measurements). Once better modeling and more modern physiological studies have been carried out, we can begin to move from simple correlation to causation and truly test the hypotheses presented in the figure.

**References and Notes**

1. R. A. Berner, *The Phanerozoic Carbon Cycle: $CO_2$ and $O_2$* (Oxford Univ. Press, Oxford, 2004).
2. A. C. Scott, I. J. Glasspool, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 10861 (2006).
3. R. A. Berner, *Geochim. Cosmochim. Acta* **69**, 3211 (2005).
4. A. L. McAlester, *J. Paleontol.* **44**, 405 (1970).
5. J. Harrison et al., *Respir. Physiol. Neurobiol.* **154**, 4 (2006).
6. R. A. Berner, D. J. Beerling, R. Dudley, J. M. Robinson, R. A. Wildman Jr., *Annu. Rev. Earth Planet. Sci.* **31**, 105 (2003).
7. M. R. Frazier, H. A. Woods, J. F. Harrison, *Physiol. Biochem. Zool.* **74**, 641(2001).
8. J. R. Henry, J. F. Harrison, *J. Exp. Biol.* **207**, 3559 (2004).
9. M. Farzin, S. A. Blatch, J. F. Harrison, paper presented at the Annual Meeting of the Society for Integrative and Comparative Biology, Pheonix, AZ, 5 January 2007.
10. K. M. Warkentin, *Physiol. Biochem. Zool.* **75,** 155 (2002).
11. K. Dabrowski, K. J. Lee, L. Guz, V. Verlhac, J. Gabaudan, *Aquaculture* **233**, 383 (2004).
12. J. M. VandenBrooks, thesis, Yale University (2007).
13. D. E. Canfield, S. W. Poulton, G. M. Narbonne, *Science* **315**, 92 (2007).
14. P. Ward, C. Labandeira, M. Laurin, R. A. Berner, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 16818 (2006).
15. J. B. Graham, R. Dudley, N. Aguilar, C. Gans, *Nature* **375**, 117 (1995).
16. R. Dudley, *J. Exp. Biol.* **201**, 1043 (1998).
17. A. Kaiser et al., paper presented at the Comparative Physiology Meeting: Integrating Diversity sponsored by the American Physiological Society, Virginia Beach, VA, 10 October 2006.
18. P. Falkowski et al., *Science* **309**, 2202 (2005).
19. L. Kump, A. Pavlov, M. Arthur, *Geology* **33**, 397 (2005).
20. P. D. Ward, *Out of Thin Air* (Joseph Henry, Washington, DC, 2006).
21. P. M. O'Connor, L. P. A. M. Claessens, *Nature* **436**, 253 (2005).
22. Y. Jammes, *Poumon Coeur* **31**, 165 (1975).
23. R. A. Berner, *Geochim. Cosmochim. Acta* **70**, 5653 (2006).
24. The research of R.A.B. and J.M.V. was supported by the U.S. Department of Energy (grant DE-FG02-01ER15173) and that of P.D.W. by the NASA Astrobiology Institute.

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