Implications of the late Palaeozoic oxygen pulse for physiology and evolution

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The late Palaeozoic was marked by significant changes in atmospheric chemistry and biotic composition. Geochemical models suggest a marked increase and then decline of atmospheric oxygen and associated shifts in the concentration of carbon dioxide. Although the actual magnitude of these changes is uncertain, the pulse of oxygen concentration may have reached a maximum of 35% and then dropped to 15% (compared with the present 21%). This oxygen pulse may have influenced the evolution of major groups of organisms.

MOST models of atmospheric evolution indicate that oxygen fluctuated substantially at various times during the Phanerozoic[1][6]. The recently developed oxygen model of Berner and Canfield[6] confirms general features of several earlier reconstructions[2,4], and indicates a rise in oxygen to 35% and then a fall to 15% over the span of 120 Myr during the late Palaeozoic (Fig. 1a). Although these atmospheric oxygen fluctuations are thought to have been largely driven by biotic factors[1,7–9], there has been little consideration of how oxygen changes affected organismic physiology or biosphere evolution.

This essay focuses on the biological effects of hyperoxia and describes changes in the fossil record correlating with varying atmospheric oxygen levels. Relative to the present atmospheric level of 21% oxygen, the Palaeozoic oxygen changes shown in Fig. 1a are substantial and would have had dramatic biological consequences. An increased global oxygen supply during the Mid-Devonian to late Carboniferous would have enhanced diffusion-dependent processes such as respiration. Accordingly, certain organisms could attain a larger body size. An increased aquatic oxygen concentration and greater oxygen penetration into benthic substrates would permit greater biomass densities in most habitats. Elevated oxygen could also increase metabolic rate and turnover and resource accessibility, thereby promoting the radiation of some taxa. Associated atmospheric changes in air density and heat capacity would have affected several biological processes.

In contrast, a decline in global oxygen during the Permian (Fig. 1a) would require compensatory respiratory adaptations and might have been restrictive for some groups. The rate of oxygen decline was too gradual, however, to have been the primary cause of the end-Permian extinction. A 15% oxygen atmosphere at sea level, for example, is equivalent to the oxygen partial pressure (15 kPa in dry air) at an altitude of about 2.5 km, which is well within the adaptation limits for most extant biota[10].

Effects of changing O_2 concentration

Table 1 compares biologically important physical differences between the existing atmosphere and the estimated extremes of the late Palaeozoic oxygen pulse. In plants and most animals, respiration is entirely diffusion limited, thus tissue composition and metabolic demand as well as body shape and thickness are determined by the availability of oxygen[11–13]. Table 1 shows oxygen effects on diffusion-dependent body thickness. Relative to dimensions dictated by the present atmospheric level, organisms in 35% oxygen could have a 27% greater diffusive distance, allowing for thicker constructions, less work invested in gas exchange, and greater body size. In contrast, the estimated end-Permian atmosphere containing 15% oxygen would necessitate an 18% reduction in diffusive distance. Biological effects from changes in ultraviolet radiation during the oxygen pulse are unlikely given that all of these atmospheric oxygen levels far exceed the minimal amounts required for a biologically effective ozone shield[4,14,15].

Nitrogen partial pressures are thought to have been fairly constant throughout the Phanerozoic[15–17]. Thus, relative to present atmospheric levels, a 35% oxygen atmosphere would have a 21% greater air density and barometric pressure, whereas a 15% oxygen atmosphere would be 13% less (Table 1). A denser atmosphere would favourably influence the evolution of insect flight by offering greater lift and altering characteristics such as the Reynolds number and boundary layer thickness[18,19]. Density changes would also affect biological processes ranging from ventilatory mechanics to wind-shear resistance. Physical parameters such as viscosity, specific heat and thermal conductivity would also vary in the low and high oxygen atmospheres (Table 1). Calculations of such variation require physical constants based on standard temperature and pressure, however, which may not apply to the variable oxygen conditions of the late Palaeozoic atmosphere.

Palaeoatmospheric models for carbon dioxide[7,8] show that this gas underwent large and sometimes inverse fluctuations compared to those for oxygen (Fig. 1b). The high carbon dioxide levels occurring in the Ordovician and Silurian resulted from tectonic activity[4,8,15]. During the late Carboniferous oxygen peak, atmospheric carbon dioxide concentration was similar to PAL (0.036%) but was about three times greater at the end of the Permian. Carbon dioxide shifts of this magnitude affect a number of atmospheric properties (Table 1), aquatic pH, as well as animal and plant physiology (see below).

Late Palaeozoic biological correlations

The mid- to late Palaeozoic (Devonian–Permian) saw major shifts in the diversity and complexity of nearly all groups of plants and animals throughout the biosphere[20–29]. The Permian saw a dramatic restructuring punctuated by the end-Permian extinction[23–25].

These biotic changes and shifts in divergence of major groups proceeded in parallel with the rise and then fall of oxygen availability. However, the late Palaeozoic was also characterized by changes in physical factors such as climate, tectonics and geochemical cycling[7,23][25]. Some workers have linked localized oxygen reductions during the Permian to the decline and disappearance of taxa[9,30]; however, the most likely effect of global atmospheric hypoxia (Fig. 1a) was elimination of species specialized for the permissive hyperoxic atmosphere.

Terrestrial invertebrates. Insects and other arthropod groups provide spectacular examples of the expansive and contractive influences associated with the oxygen pulse. There was a marked Carboniferous diversification of insects on the basis of feeding specializations[23,25] and the origin of flight, and many species exhibited gigantism relative to extant forms. Predatory defence is the usual explanation offered for insect gigantism[31]. However,

FIG. 1 *a*, Palaeoatmospheric oxygen concentration model[6] showing the estimate (solid line) and its range (dashed lines), based upon sensitivity analysis. Between the mid-to-late Devonian (380–360 Myr), oxygen increased from ~18 to 20%, and then rose sharply to ~35% by late Carboniferous (286 Myr). The present atmospheric level (PAL) of 21% is indicated. Oxygen steadily declined throughout the Permian (286–250 Myr) and dropped to about 15% by the end of the Palaeozoic (250 Myr). Model is based on the exchange rate of fixed carbon between the atmosphere, ocean and sediments[4,6,7] and on various assumptions[6,9,83]. *b*, Palaeozoic atmospheric carbon dioxide model[7-9]. This gas was present in relatively large amounts in the Ordovician–Silurian, fell precipitously during the Devonian–Carboniferous, and increased in the late Permian. The minimum value shown for the late Carboniferous and early Permian approximates PAL for carbon dioxide (about 0.036%; dotted line). Model is based on estimates of fixed carbon exchange and transfer processes within the inorganic, carbonate–silicate cycle[1,7,8].
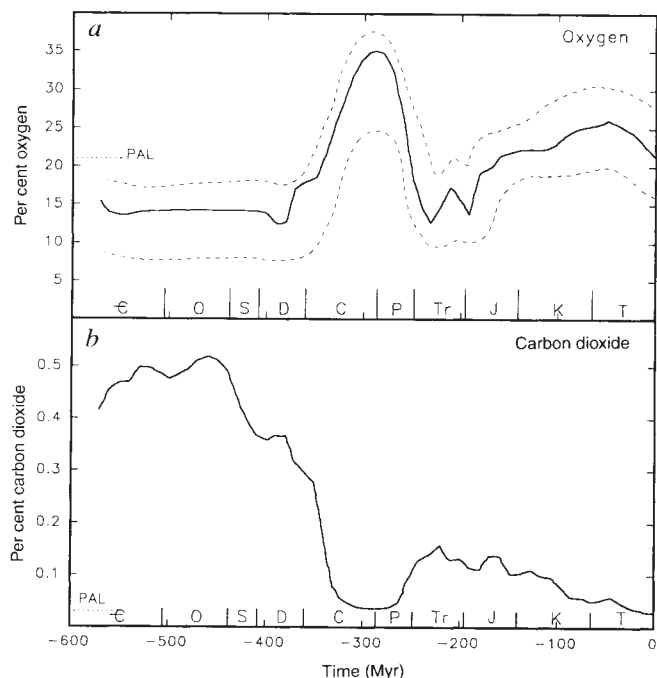
by increasing diffusive permeation, increased oxygen concentration would have permitted insects to become larger. Insects have a tracheal gas-exchange system, a branching network of tubes extending from the body surface to the small tracheoles within respiring cells. This system is primarily, if not exclusively, diffusion dependent, with 0.5 cm suggested as an upper limit to passive diffusion[32,33].

Gigantism occurred in the Protodonata (dragonflies; wing span up to 71 cm), the Ephemeroptera (mayflies, 9–20 cm),

the Palaeodictyoptera (1–43 cm) and in the Diplura and Thysanura[34-37]. For example, the giant Carboniferous dragonfly *Meganeura monyi* had a thoracic diameter of about 2.8 cm[38]. By contrast, thoracic width of the largest (10-cm wingspan) extant dragonflies (*Anax, Aeshna*) is about 1 cm[38,39] (M. May, personal communication). Most of the various insect taxa that attained exceptionally large body sizes during the Carboniferous did not persist after the Permian, when 27–30% of the known insect orders were lost (Fig. 2)[40-42]. Gigantism also characterized some

TABLE 1 Comparison of physical properties of the present oxygen atmosphere (21% O_2) with those of the relatively hyperoxic late Carboniferous (35% O_2) and the relatively hypoxic end-Permian (15% O_2)

	21% O_2 (present)	35% O_2 (285 Myr)	15% O_2 (250 Myr)	Biological importance
Respiratory gases				
Oxygen				
O_2 partial pressure (kPa)	21.2	35.3	15.1	Respiration, lignin biosynthesis
Krogh's maximum radius (cm)*	0.11	0.14	0.09	Size limit for diffusion dependence
Water O_2 content (ml l^{-1})†	6.9	7.4	4.9	Aquatic respiration
Carbon dioxide†‡				
CO_2 partial pressure (kPa)	0.03	0.03	0.09	Effects on photosynthesis, moisture content and global energy balance
Water CO_2 content (ml l^{-1})	0.31	0.31	0.9	Aquatic pH effects, acid–base balance and ion regulation
Air properties				
Density (kg m^{-3})	1.29	1.56§	1.12§	Flight and respiratory mechanics, wind shear
Dynamic viscosity kg (m^{-1} s^{-1})	18.2×10^{-6}	+	−	Boundary layer thickness
Specific heat (Jg^{-1} deg^{-1})	1.006	+	−	Heat capacity and relative humidity
Thermal conductivity (Js^{-1} m^{-1} deg^{-1})	2.4×10^{-2}	+	−	Earth thermal budget, climate

For values not calculated, the plus and minus symbols represent an increase and decrease, respectively, relative to the present 21% oxygen atmosphere.
 * The equation for the maximum radius of a diffusion-dependent animal is $r \leqslant (6KpO_2/vO_2)^{-2}$, where pO_2 is oxygen partial pressure at its surface, vO_2 is oxygen-consumption rate, K is Krogh's diffusion constant, and 6 is a geometric shape constant[13,14].
  † Values calculated for fresh water at 20 °C and constant pH.
  ‡ Palaeozoic CO_2 changes partly in and out of phase with those for O_2 (see Fig. 1 and text).
  § Calculation assumes nitrogen and trace gas partial pressures similar to present atmosphere.

FIG. 2 Stratigraphic ranges of 30 insect orders[41] and 16 tetrapod morphotype lineages[68] in relation to the late Palaeozoic oxygen pulse[6]. Record extends from the Lower Devonian (400 Myr) to the Lower Triassic (240 Myr). The Carboniferous diversification of both the insects and vertebrates correlates with the rise in atmospheric oxygen. A correlation also exists for the end-Permian (250 Myr) disappearance of members of both groups and the fall in atmospheric oxygen. Insect data are from ref. 41 modified according to ref. 37 (see also refs 40 and 84). Estimates for insect extinctions at the close of the Permian range from 8 of 30 orders (27%)[41] to 8 of 27 orders (30%)[40]. The 75% extinction rate shown for end-Permian tetrapods in this figure parallels other estimates (67% of amphibian families and 78% of reptilian families[25]).
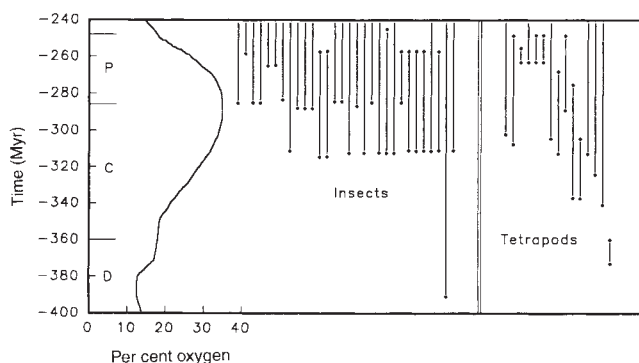
other Carboniferous arthropods (such as diplopods, arthropleurids and scorpions)[26,36,43-46], extant relatives of which are diffusion dependent[47].

The greater density of the hyperoxic atmosphere facilitated insect flight by enabling relatively small articulated winglets to provide lift[46], albeit with suboptimal aerodynamics. Although the Devonian may have seen the first apterygote insects[48], winged forms diversified extensively throughout the Carboniferous[40,49]. The earliest proto-wings possibly had a respiratory function and were used secondarily for locomotion and predator escape[39,41]. The need to power flight would have required ever-more sustained and higher levels of oxidative metabolism, which would be facilitated by higher levels of atmospheric oxygen. The ability of some Recent flying insects to ventilate the tracheal system minimizes diffusive limitations; however, mechanical ventilation does not mitigate diffusion limitation in the terminal tracheoles[39,47]. Schidlowski[50] argued that the tracheal system of *Meganeura* would have been inadequate for sustaining flight metabolism in oxygen at present atmospheric levels, and predicted a hyperoxic Carboniferous atmosphere.

Flight became the decisive agent for insect dispersal and diversification. The improvement of flight and its association with smaller species may have ensured its persistence in numerous pterygote taxa through the Permian. But as already noted, large fliers did not survive beyond the Permian[37,40].

Aquatic invertebrates. The majority of aquatic invertebrates lack well-developed respiratory and ventilatory systems and depend upon diffusion-mediated respiration[12,51]. Increased oxygenation of Devonian and Carboniferous fresh waters would have increased their utility as nursery grounds for eggs and larvae, thereby expanding life-history options for the rapidly diversifying terrestrial arthropods. Beyond this, global atmospheric hyperoxia would have reduced the limitation of seasonal aquatic hypoxia, favoured infaunal penetration of marine sediments, allowed denser aggregations, and increased the body size of some groups.

Size increases have been recorded for a number of taxa throughout geological time, and have been proposed to reflect multiple biotic factors[27,52,53]. The observed correlation between size increases in marine invertebrates (bryozoans[54], foraminiferans[27], rugose corals[27] and brachiopods[26,27]) and atmospheric hyperoxia is notable because these forms have a primarily diffusion-dependent respiration. Specific examples include the largest known brachiopod (*Gigantoproductus*, with a shell 300 mm wide) of the early Carboniferous, and the radiation of the large fusilinid Foraminifera (Mid-Carboniferous–Permian).

The evolutionary transition from a 'brachiopod-dominated late Palaeozoic marine fauna' to the modern, 'mollusc-dominated Mesozoic–Cenozoic fauna' occurred at the end of the Permian[55]. Associated with this was the end-Permian extinction of several dominant members of the sessile, epifaunal filter-feeding community of the Palaeozoic, including the rugose and tabulate corals, and numerous families of brachiopods, bryozoans, crinoids and others. A number of factors, including changes in sea level and reduced temperature, may have contributed to this extinction and faunal transition[24,25]. Whereas we do not regard Permian reductions in global oxygen as a major causal factor in either of these events, hypoxia probably contributed to the decline of many of the diffusion-dependent faunal elements. The bivalves, which had a relatively greater Permian survival than did the brachiopods, and which became dominant in the Triassic[56], had numerous specializations that allowed ventilation, mobility and sediment penetration[26,57,58].

The terrestrial flora. The Carboniferous and early Permian flora included ferns and primitive gymnosperms, as well as sphenopsids and lycopods[59-64], which were arborescent and grew to considerable height[23]. Increased plant height and arborescence required thicker support structures, particularly as a greater atmospheric density elevated wind stress. Heightened atmospheric oxygen facilitated these morphological changes by allowing diffusion through thicker support elements and by enhancing the oxygen-dependent[59] biosynthesis of lignin, a dominant structural material of many Carboniferous plants[7,23,64]. An increased oxygen level may not, however, have been entirely advantageous for plants, particularly when it occurred simultaneously with a decline in carbon dioxide (Fig. 1b). Changes in the carbon dioxide to oxygen ratio can lessen plant productivity by photorespiration[65]. However, the rarefaction of atmospheric carbon dioxide over the Carboniferous may have established a selective advantage for new, more effective carbon-fixation pathways in some plants[66].

Terrestrial vertebrates. The diversification of tetrapods began in the Devonian and was accelerated during the Carboniferous, when at least eleven of sixteen known basal lineages (including the three primary classes of amniotes: Synapsida, Diapsida and Anapsida) all appeared[23 25,67,68] (Fig. 2). In the Permian, 75 per cent of these tetrapod lineages went extinct[25,67,68] (Fig. 2).

Global atmospheric hyperoxia possibly aided the vertebrate invasion of land[2]. Breathing hyperoxic air reduces the ratio of evaporative water loss to oxygen uptake, and thus increases aerial gas exchange efficiency by lowering desiccation[47]. Although the early tetrapods had both gills and lungs[69-71], gills are not effective for aerial gas exchange, particularly carbon dioxide discharge, which is a more acute constraint for aerial respiration than oxygen uptake[47,71]. As many early tetrapods were sizeable and had a thick body armour[72], aerial cutaneous respiration could not compensate for the reduced respiratory capacity of gills in air. Tetrapods were thus heavily dependent on lung exchange[22,67,72-74]. The rise in atmospheric oxygen coupled with the reduction in carbon dioxide would have elevated primitive lung effectiveness. Subsequent changes in these gas ratios could also have influenced the transition from pulse pumping to aspiration breathing and perhaps even the shift from an oxygen to a carbon dioxide-modulated respiratory control mechanism. The reduced ratio of water loss to oxygen uptake achievable in

hyperoxic air may have also been critically important in the evolution of the cleidoic egg.

Hyperoxia would have also enhanced tetrapod metabolic capacity and thus contributed to the sustained power production required to overcome gravity. Increased metabolic performance opened new ecological options within the rapidly expanding terrestrial biosphere. Although tetrapod diversity decreased in the Permian, the synapsids underwent a pronounced diversification, proceeding from the pelycosaurs to the therapsids, a diverse assemblage of herbivores and carnivores[22,24,67,74] known as the mammal-like reptiles[22]. The diversification of synapsids seems to be partially attributable to the effects of hyperoxia and a denser atmosphere on activity enhancing specializations such as metabolic heat retention. The large 'sails' of pelycosaurs such as *Dimetrodon* are thought to have functioned in heat transfer[22,74]. The capacity to regulate heat gain and loss was an important precursor for endothermy[75].

Conclusion

Attempts to correlate atmospheric oxygen with biosphere evolution have included the origin of the ultraviolet–ozone shield and the early radiation of plants[1,4,14,15], the evolution of the diffusion-limited Ediacaran fauna[76-79], the Cambrian explosion[80], the correlation of patterns of extinction and metabolic requirements among various taxa[2,81], and regional or even mass extinction events[9,30,82].

We propose that a pulse in atmospheric oxygen spanning the mid-Devonian, Carboniferous and Permian periods influenced the contemporaneous biosphere. The rise in oxygen during the Devonian and Carboniferous favourably influenced diffusion-dependent features. Increased oxygen availability may have also fuelled the diversification and ecological radiation of late Palaeozoic groups by acting as a substrate for the evolution of behavioural, physiological and ecological adaptations, permitting greater exploitation of aquatic habitats and the newly evolving terrestrial biosphere. The fall in global atmospheric oxygen during the Permian was restrictive and modified or eliminated some taxa that radiated in hyperoxia, but was not a primary cause of the end-Permian extinction. □

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