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ATMOSPHERIC CARBON DIOXIDE/OXYGEN IMBALANCE IN THE LATE CRETACEOUS, HATCHING OF EGGS AND THE EXTINCTION OF BIOTA

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ABSTRACT

A new theory explains why dinosaurs, pterosaurs and large avian species like *Hesperornis* became extinct at the end of the Cretaceous while mammals, smaller Cretaceous birds, crocodiles, chelonians and saurians survived.

An atmospheric carbon dioxide/oxygen imbalance at the end of the Cretaceous caused by kimberlite volcanism, basalt flows and a reduction in oxygen production by marine phytoplankton is proposed.

The unfavourable area to volume ratio of large eggs for diffusion of respiratory gases compared to that of small eggs resulted in the asphyxiation of the embryos of large endothermic egg laying groups. Endothermic species, e.g. dinosaurs that covered their eggs with soil, restricted the free circulation of air and would have been first to become extinct. Smaller ectothermic species, e.g. crocodiles, chelonians and saurians with lower embryonic respiratory requirements and endothermic species like the birds that did not cover their eggs, survived.

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INTRODUCTION

The host of explanations for the extinction of biota at the end of the Cretaceous put forward before 1963 is summarized by Jepsen (1963). Since then the number of ideas has grown by the addition of new theories or by the elaboration of some of the older ideas. Three main categories of recent theories can be recognised.

Theories in the first category postulate an agent lethal or harmful to life generally, e.g. cosmic radiation (Uffen, 1963; Terry and Tucker, 1968) or physiological malfunctioning due to the reversals of the magnetic field of the earth (Crain, 1971; Hays, 1971). These factors, however, fail to explain the most puzzling aspect about the extinction, viz. the selective way in which groups were affected.

The second set of theories explains the extinction of selected groups and also ignores the spectrum of animal and plant life that was involved. As examples the theory of Bramlett (1965) which considers planktonic forms and the theory of Swain (1974) which accounts for the dinosaurs alone may be mentioned.

The third group of theories is based upon the observation that a global drop in temperature and general deterioration of climate occurred at the end of the Cretaceous. This observation, based on the sudden disappearance of warm water Foraminifera from the fossil record at the Maestrichtian–Danian boundary, is generally accepted (Russell, 1965; Bakker, 1975; Desmond, 1976; Van Valen and Sloan, 1977; Percival and Fischer, 1977). This is in contrast to the original idea that a rise in temperature occurred at this time (Colbert *et al.*, 1946).

Although a reduction in temperature is widely accepted, the magnitude of the reduction is still a point of dispute. Some authors (Stapleton, 1975; Desmond, 1976; Van Valen and Sloan, 1977) consider the reduction drastic enough to have been

directly or indirectly responsible for the extinction. Such a drop in temperature would have caused a contraction of the tropical zone and an extension of the polar and temperate regions with a gradual displacement of all forms of life towards the equator with the possible extinction of some equatorial species. However, as is acknowledged by Desmond (1976), Stapleton (1975) and Van Valen (1977), asylum areas would have remained. Additional extinction factors are therefore needed in these problematic areas to explain the disappearance of species. Some of the factors that have been mentioned are, e.g. large scale migrations with overcrowded living conditions and consequent interspecific competition. Bakker (1975), however, considers the cooling to have been insignificantly small and gradual. He also postulates interspecific competition but blames it on the creation of monotonous landscapes created by marine regressions. Cooper (1977) points out the importance of the fact that most magnetic reversals coincided with marine regressions and comes to the conclusion that life both on sea and land must have been extremely rigorous during extended periods of regression. According to him these periods were characterized by a relatively harsh continental climate with a high thermal range and increased aridity due to decreased evaporation. He relates the climatic cooling to a drop in solar radiation reaching the earth's surface due to dust veils and higher carbon dioxide (CO_2) levels. This he in turn relates to reduced photosynthesis and volcanism.

Ryan and Cita (1977), on the contrary, suggest that the cooling was due to a reduction in atmospheric CO_2 levels.

It is evident that no generally accepted explanation which accounts for the selective extinction of biota exists. It is, however, clear that the extinction was due to some change in the physical environment and the physiological or behavioural inability of some species to adapt successfully to this change. An all important fact that must be accounted for by any hypothesis on the cause of the extinction is the selective way in which groups were affected. Why did the dinosaurs perish while other archosaurs like crocodiles managed to survive and why were birds, mammals, the Sauria (lizards and snakes) and chelonians not affected?

This paper attempts an explanation by taking into account the geological, palaeontological and meteorological factors involved in relation to the differences in expected physiological responses of organisms that could have led to the extinction of the different groups.

THE CRETACEOUS ENVIRONMENT

In order to discuss the change in the environment at the close of the Cretaceous period it is necessary to review what we know about the climate prior to and during the Cretaceous.

The Late Triassic, Jurassic and Cretaceous periods were marked by an absence of polar ice and hot to temperate climates (Robinson, 1971; Desmond, 1976; Van Valen and Sloan, 1977). During the Cretaceous, subtropical forests grew as far north as present-day Alaska (Van Valen and Sloan, 1977) and dinosaurs occurred inside the Cretaceous arctic circle (Desmond, 1976).

One agent that could have caused the mild climate and absence of polar ice for such a long period is the hothouse-effect of a high atmospheric PCO_2. Indirect evidence does point to a high CO_2 content of the Cretaceous atmosphere, e.g. the abundance of carbonate rocks which led to the term "Cretaceous" for this particular period in the history of the earth. These carbonate rocks were formed from the waters of the Cretaceous oceans that were saturated or supersaturated with calcium carbonate ($CaCO_3$) (Fairbridge *et al.*, 1967). To replenish the $CaCO_3$ that was being locked up in the carbonates, vast amounts of atmospheric CO_2 must have been available. In addition two equally vast CO_2 sinks existed in the formation of oil and black muds.

The majority of the oil reserves of the world are of Cretaceous age and recent deep-sea drilling projects have revealed the existence of extensive deposits of sapropelic black muds of this age. Ryan and Cita (1977) remark that more carbon is locked up in the muds formed during this period than in any geological period since the Precambrian. For this reason they conclude that the Cretaceous should rightly be looked upon as the carboniferous period in the history of the earth. The removal of CO_2 from the atmosphere for the formation of the black muds according to them led to a drop in the CO_2 levels of the atmosphere and a subsequent drop in temperature.

If, however, the carbonate rocks and oil are also taken into account it becomes clear that a source of CO_2 to replenish the atmospheric CO_2 which was being locked away in these sinks must have existed. The atmosphere itself (if present PCO_2 values are taken as a standard) would have held too little CO_2 even for the formation of the muds (Ryan and Cita, 1977).

A steady supply of CO_2 from volcanic and other sources and the consequent high atmospheric CO_2 levels could have stimulated the population explosion of the $CaCO_3$ fixing foraminifera in the Cretaceous.

The reducing conditions that prevailed in the sediments of shallow seas at the time of the extinction (Percival and Fischer, 1977) may be the result of a rise in CO_2 and a drop in oxygen (O_2) levels of the atmosphere and biosphere at that time. The presence of large deposits of bauxite formed during this period is interpreted by Tappan (1968) as indicative of a humid climate, increased CO_2 and carbonated ground water.

A drop in O_2 production by photosynthesis, in-

creased oxidation of newly exposed rocks and the fixing of O_2 by bacteria coincided with an outpouring of CO_2 from various volcanic sources and this may have caused a serious CO_2/O_2 imbalance in the Late Cretaceous atmosphere.

CARBON DIOXIDE SOURCES

Volcanism as a CO_2 source

The carbon in carbonaceous rocks (and oil and black muds) primarily entered the sea as atmospheric CO_2 derived from volcanic action (Rodgers, 1957). There may be more than a grain of truth in the seemingly outdated statement of Goldschmidt (1958) that the volcanism of the present day is mostly confined to the shrunken remnants of much larger regions of volcanism.

Not only the intensity but also the nature of the volcanism varied appreciably over geological time (Rutten, 1966). Because of the limited extent and predominantly acid nature of the most familiar of our present-day volcanoes we are easily misled by Hutton's principle of uniformitarianism into a biased picture of the possible impact volcanism can have on the biological environment.

Abundant evidence exists for the presence of large-scale basic volcanism in the past. It has been calculated that in excess of 1 million cubic miles (about $4{,}2 \times 10^6$ km^3) of basalts have been transferred to the surface during the last 180 million years (Holmes, 1965). If the amount of gas released by these lavas is calculated on the basis of a gas fraction of one per cent of the basalt mass (Sg=2,9. Holmes, 1965) and if it is assumed that 30 per cent by volume of the gas fraction, as in some present-day lavas, was CO_2, a total of about 2×10^5 metric tons of CO_2 was released *annually*. The production of CO_2 would have fluctuated with peaks coinciding with great lava flows, e.g. in the Indian Deccan (Late Cretaceous, Early Tertiary 700 000 km^3), the Paraná (Early Jurassic 200 000 km^3), Siberia (Jurassic 250 000 km^3) and southern Africa (Jurassic).

During these peak periods the production of CO_2 could have equalled or exceeded the amount of CO_2 poured annually into the atmosphere by the burning of fossil fuel (1×10^9 metric tons) which has raised the CO_2 content of the atmosphere by about 10–12 per cent since the beginning of the century and which has caused considerable concern among climatologists (Budyko, 1974; Baes *et al.*, 1977).

Plateau lavas were, however, only one of a number of sources. Other contributions probably came from acid volcanism and mid-oceanic basalt flows associated with seafloor spreading. Layers of ash from Cretaceous acid volcanism occur over vast areas of North and South America, Asia, Antarctica and Africa. Sulphur and CO_2 from these volcanoes probably contributed to reducing conditions and pyrite formation in the sediments of shallow seas at the time of the extinction (Percival and Fisher, 1977). It is also interesting to note that the presence of vast uninterrupted accumulations of ash have in fact been used as an indication that no extraordinary changes took place at the Cretaceous–Tertiary boundary (Russell, 1965).

The major contribution of CO_2, however, probably came from kimberlite and perhaps carbonatite volcanoes. Peak periods of these exclusively continental types of volcanism coincided with major mid-oceanic subsidence and marine regressions (Cooper, 1977). From the Permian to the Early Tertiary extensive provinces of alkaline, carbonatite and kimberlite volcanoes developed in Siberia, Africa, South and North America and India (Du Toit, 1954; Holmes, 1964).

Determination of a definite peak in kimberlitic volcanism is not possible at present due to the few radiometric datings available on kimberlites and the unreliability of some of these determinations (Barrett and Allsop, 1973). By implication, however, it is generally accepted that a peak in kimberlitic volcanism occurred at the end of the Cretaceous in southern Africa (Holmes, 1965; Barrett and Berg, 1973; Boyd and Nixon, 1973; Moore, 1973; Fesq *et al.*, 1973).

The abundance of these pipes in southern Africa can be illustrated from the Platbakkies–Aggenys swarm with about 270 pipes concentrated in an area of only 8 400 km^2. To this Cornellisen and Verwoerd (1973) add "Without any doubt many more remain to be discovered". This swarm forms part of one of two large igneous provinces in Angola, South West Africa and South Africa (Prins and Verwoerd, personal communication).

The presence of huge blocks of unmetamorphosed coal in a Transvaal pipe far below the coal seams from which they were derived (Holmes, 1964) proves that no hot lavas flowed through the pipe. Kimberlites are thought to have been gas volcanoes extremely rich in CO_2.

Kimberlitic eruptions have been compared to the process of fluidization used in industry to mobilize solid particles in a stream of fast moving gas. According to Holmes (1964) "Kimberlite pipes are magnificent demonstrations of the effect of long continued fluidization". In some cases the unweathered rock from kimberlite pipes contains 10 per cent water and CO_2. This is a striking indication of the immense proportion of gas that must have been available when the pipes were being drilled to the surface (Holmes, 1964).

MARINE REGRESSION AND THE CO_2/O_2 IMBALANCE

Tappan (1968) has pointed out that marine transgression favours phytoplankton growth, while Haq (1973) has also noted a close correlation in time between phytoplankton maxima and marine transgression. It is likely that episodes of marine

transgression would have been accompanied by a build-up of atmospheric oxygen and a reduction in CO_2 levels for, as Tappan (1968) has pointed out, phytoplankton photosynthesis has controlled the atmospheric O_2/CO_2 balance since early Permian times. The opposite would also be true for periods of marine regression, and a relative increase in PCO_2 with a reduction in O_2 levels can be expected with regressive episodes (Tappan, 1968; Cooper, 1977). Increased oxidation of newly exposed rocks would further reduce atmospheric O_2 levels (Rutten, 1966).

Total present atmospheric oxygen is estimated to return through the biological respiratory-photosynthetic cycle approximately every 2 000 years (Tappan, 1968). A drop in phytoplankton abundance due to a major regressive episode decreases the available organic matter for oxidation by bacteria and would have forced the bacteria to turn to oxidation of sulphides and could have caused a further depletion of atmospheric O_2 (Tappan, 1968).

Increased atmospheric CO_2 levels would be in part compensated for by the resultant increased cloudiness (and in the presence of large scale volcanism also by a dust veil) which in turn would further tend to reduce photosynthesis and oxygen production. Under cloudy conditions, plant respiration approaches oxygen production; thus terrestrial plants would not necessarily have prevented the development of a CO_2/O_2 imbalance caused by a phytoplankton depletion (Tappan, 1968) and high volcanic production of CO_2.

THE EFFECT OF THE CO_2/O_2 IMBALANCE

At the end of the Cretaceous, peak CO_2 production by kimberlites and basalt flows (e.g. southern Africa and Indian Deccan) coincided with a major marine regression. This could have caused a final drastic increase in atmospheric CO_2 levels with a subsequent profound effect on the climate and directly and indirectly also on the biological world.

The temperate climate of the Cretaceous and the absence of polar ice might have been caused by the hothouse effect of the high CO_2 levels of the atmosphere. It could also have created the niches for the population explosion of organisms by providing the carbon for the formation of the chalk, oil and black muds. The dust veil at the peak of the explosive kimberlitic volcanism could have screened off most of the incoming solar radiation. In much the same way the solid component of man's pollutive activity is reversing the hothouse effect of the CO_2 fraction of pollution (Razool and Schneider 1971).

A diminishing production and gradual extraction of CO_2 could have escalated the drop in temperature induced by the dust veil. This could have culminated in the generally accepted gradual deterioration of the climate since the upper Tertiary. (Russell, 1965; Chiarelli, 1973).

The influence on marine life

As Cooper (1977) has pointed out, the end of the Cretaceous saw a major marine regression with disastrous consequences for marine organisms in general.

Drying-up of shallow seas sharply reduced phytoplankton photosynthesis with a resultant sharp drop in O_2 production and relative increase in atmospheric CO_2 levels. By the decrease in biomass of the plankton fauna due to the drying up of shallow seas and the deterioration of the climate, the base of the oceanic food pyramid was removed. This, in turn, would have endangered all other marine species dependent on the primary producers. Subsequent competition for the remaining food could have caused the elimination of groups like the ammonites and belemnites.

The influence on amniotes

Each species is adapted to a particular range of environmental conditions. If these conditions should change, as would be the case when long-term build up of CO_2 in the atmosphere occurs, species may find the changing situation marginal for survival and eventually lethal. A population may cease to be viable by the direct influence of adverse conditions on all or any of the stages present in the animal's life history. It is possible that drastic changes in CO_2/O_2 levels could affect the eggs (especially if they were only marginally able to cope with respiratory stresses) without directly influencing the ability of the adults to survive.

The metatherian and eutherian mammals are the only amniotes that do not reproduce by cleidoic eggs, contrary to speculations by Desmond (1976) on the possible viviparity in Late Cretaceous dinosaurs. The possibly viviparous ichthyosaurs were extinct before disaster struck at the end of the Cretaceous (Desmond, 1976) and can be ignored for the sake of this argument.

It is safe to accept that the dinosaurs were oviparous. This assumption is confirmed by the reproductive physiology of living archosaurs (the crocodiles) and the dinosaur descendants, the birds. In these animals the embryos are dependent on the eggshell for the supply of $CaCO_3$ for calcification of the bones (Packard *et al.,* 1977). The crucial transition from oviparity to viviparity which involves the loss of the eggshell and development of a placenta is thus not possible in these groups. In all probability the same applied to the dinosaurs. In chelonians, where most of the $CaCO_3$ is derived from the eggshell, viviparity as well as ovoviviparity is also unknown.

This is in contrast to the Sauria where the material for bone calcification is derived, not from the shell, but from the yolk. The transition from oviparity to ovoviviparity for this reason is common amongst the Sauria and both states are often found in different species of the same genus.

Convincing arguments in favour of an endothermic metabolism in the dinosaurs and pterosaurs have been recently advanced by various authors, e.g. de Ricqlés (1974), Bakker (1975), and Desmond (1976) to name but a few. The general increase in body mass of dinosaurs and the absence of small species at the end of the Cretaceous is ascribed to the necessity for endothermic animals, which lack an insulating layer of fur or feathers, to reduce the ratio of body area relative to body mass as much as possible (Desmond, 1976). The insulated mammals and birds of the Late Cretaceous could, however, afford to remain small.

What then was the factor that discriminated between the dinosaurs and pterosaurs on the one hand and birds, crocodiles, mammals, chelonians and the Sauria on the other? The answer may perhaps be supplied by a study of the influence of a CO_2/O_2 imbalance in the atmosphere on the reproductive success of some of the groups involved.

The influence on the reproduction of amniotes

As the flux of O_2 and CO_2 across the shell of an egg depends on the concentration gradient, a change in atmospheric CO_2/O_2 levels, as has been postulated, could have led to a potentially lethal accumulation of CO_2 and a lack of O_2 in developing embryos of those forms laying cleidoic eggs. In view of this the reproduction of Cretaceous land vertebrates should be investigated and two factors of dinosaur reproduction should be mentioned.

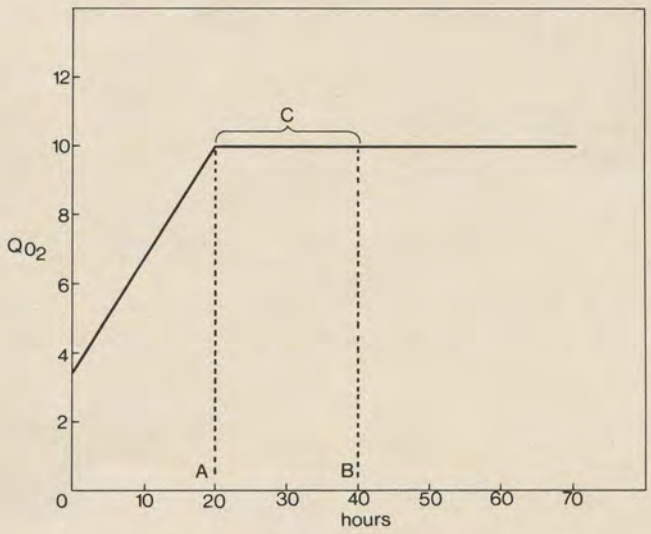
Firstly, the scarcity of juvenile dinosaurs (Richmond, 1965) and secondly the thinning of and increase in porosity of Late Cretaceous dinosaur eggshells as has been observed (Erben, 1972). Like *Protoceratops* (Colbert, 1969), all dinosaurs had in all probability retained the reptilian habit of covering the eggs with soil or vegetable matter whereas birds as a group (the only other major endothermic egg-laying group) have in general abandoned this practice. This probably indicates that dinosaur embryos never attained a metabolic rate quite as high as that of avian or mammalian embryos, as otherwise incubation of the eggs by the adults would have been necessary even in a hot Cretaceous climate.

However, with altered CO_2/O_2 levels during development, the large buried dinosaur eggs would have had a distinct disadvantage compared to the smaller eggs of crocodiles and other ectothermic reptiles as large eggs have a less favourable surface to volume ratio. Moreover, the respiratory requirements of the dinosaur embryos would have been considerably higher, if an endothermic physiology for dinosaurs is accepted, than those of the embryos of the ectothermic reptiles.

The largest eggs of endotherms will, therefore, be the first to show reduced hatchability with altered CO_2/O_2 levels and this disadvantage centres around the respiratory needs of the embryos which have to be met by diffusion alone (as is the case in the chicken egg) (Wagensteen and Rahn, 1970/71). Diffusion through the eggshell and membranes is subject to Fick's law by which, if known gas requirements are used, the maximum distance gas can diffuse to meet the demands of a metabolising cell can be calculated as 0,5 mm. This limits the maximum diameter of spherical organisms to 1,00 mm in the absence of a transport system to supplement diffusion (Wood, 1969). This calculation holds true for all organisms with the possible exception of an embryo inside the eggshell. In this case respiratory gases have to traverse not only the eggshell but also the shell membranes and a layer of albumen. Wood (1969) comments that in organisms where the distance of 0,5 mm is exceeded, supplementary transport mechanisms like cytoplasmic streaming or aqueous channels are present. Wagensteen and Rahn (1970/71), however, have shown that no supplementary systems exist in the egg and that the respiratory needs are met by diffusion alone.

In the chicken embryo, O_2 consumption per unit mass of embryonic material initially increases for about 20 hours whereafter it becomes constant (Boell, 1955) but the omphallomesenteric circulation is established only after about 40 hours. This period between 20 and 40 hours is potentially dangerous as the individual cells have reached maximum O_2 consumption which has to be met by diffusion alone (fig. 1).

Even after the embryonic circulation has developed the embryo is in constant danger of asphyxiation. Wagensteen and Rahn (1970/71) conclude: "It would appear that during the course of evolution birds have been able to adapt to a wide variety of nesting conditions by adjusting the thickness and



A point where max O_2 uptake is reached

B point where circulation is established

C max O_2 uptake without supplementary transport mechanism

Q_{O_2} µl O_2 per mg dry weight per hour (respiring tissues only)

Figure 1. Diagram to illustrate the critical period of potential asphyxiation (C) of embryos of cleidoic eggs (adapted from Boell, 1955).

porosity of the eggshell to provide the optimal permeability for a species in a particular environment. Any significant change in either the micro-environment around the egg or the gas permeability of the shell itself must have a deleterious effect upon the embryo and the survival of the species."

This danger increases as the surface to volume ratio decreases in large eggs. In addition, the greater distance which the gas has to diffuse through the thick shell membranes and albumen, will result in necessary suitable adaptations, e.g. in the ostrich egg a branching pore system developed to enhance diffusion (Tullett and Board, 1977).

The respiratory pores of dinosaur eggs in general are described as small and few in number (Müller, 1968). Tortoise eggs, that develop in conditions that must be quite similar to those where dinosaur eggs presumably developed, have twice the amount of pores in the shell as chicken eggs (Packard *et al.*, 1977).

The need for more efficient diffusion with an atmospheric CO_2/O_2 imbalance could have induced selection to act in three possible ways:

Firstly, an increase in porosity by decreasing the surface-to-volume ratio of the egg (or the total functional pore area/volume of egg), which would have led to the production of smaller eggs. This would have been limited by the observed trend for increase in mass of the dinosaurs as a group which would have led to an increase in egg and hatchling size.

The second possible change would have been an increase in shell porosity, a trend that was present in dinosaur eggshells towards the end of the Cretaceous (Erben, 1972).

The third possibility, a thinning of the shell, was also selected for, as was shown by Erben (1972) from observations on shell fragments of Late Cretaceous age.

The increase in porosity and thinning of the shell could have countered the deleterious effects of a CO_2/O_2 imbalance to a limited extent.

In order to verify the assumption that large eggs with reduced air circulation and rarified atmosphere will show reduced hatchability some experiments with chicken eggs have been undertaken.

These experiments have shown that with reduced PO_2 (16,7 kPa (125 mm Hg) O_2) small eggs have significantly higher hatchability rate than large eggs ($P \geq 0{,}001$) and that small eggs that developed in a free circulation have a significantly higher hatchability rate than large eggs that developed under a cover of "Perlite" to cut down circulation ($P \geq 0{,}001$) (Chi squared).

If these results are applied to the upper Cretaceous situation when atmospheric CO_2 levels were rising and O_2 was being depleted, the following deductions may be made. Small uncovered eggs (= avian and prototherian eggs?) and the small covered eggs of slow metabolizing ectotherms (= crocodiles, tortoises and saurians) would have had a significantly better chance of surviving asphyxiation than the large covered eggs (= dinosaur eggs which were enormous in comparison to the eggs of crocodiles and other contemporary lizards according to Bakker (1971)).

However small this disadvantage might have been, initially, a CO_2/O_2 imbalance could have affected the viability of the embryos of the largest species, e.g. the dinosaurs. Eventually the survival of the smaller species would have become marginal until the eggs of the Pterosauria and even the larger avian species like *Hesperornis* were affected.

The embryos of eutherian and metatherian mammals were not subject to this danger as placental circulation develops early and supplies the necessary transport for gases. Moreover physiological adaptations like the Bohr effect (shift of oxygen dissociation curve) would have counteracted the effect of rising CO_2 levels.

More experiments with chelonian and crocodile eggs will be valuable and future experiments will have to be carried out with different CO_2/O_2 mixtures to get a direct comparison with the hypothetical situation at the end of the Cretaceous.

However, a rise in CO_2 and a drop in O_2 appears to have acted as a selective biological filter which affected the dinosaurs and pterosaurs, while crocodiles, birds, chelonians, saurians and mammals survived into the Tertiary.

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