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Source: *Journal of Paleontology*, Vol. 44, No. 3 (May, 1970), pp. 405-409

Published by: [SEPM Society for Sedimentary Geology](#)

Stable URL: <http://www.jstor.org/stable/1302577>

Accessed: 05-04-2015 17:31 UTC

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JOURNAL OF PALEONTOLOGY

*A publication of THE SOCIETY OF ECONOMIC PALEONTOLOGISTS
AND MINERALOGISTS and THE PALEONTOLOGICAL SOCIETY
with the generous support and cooperation of THE AMERICAN
ASSOCIATION OF PETROLEUM GEOLOGISTS*

VOLUME 44

MAY 1970

NUMBER 3

ANIMAL EXTINCTIONS, OXYGEN CONSUMPTION, AND ATMOSPHERIC HISTORY

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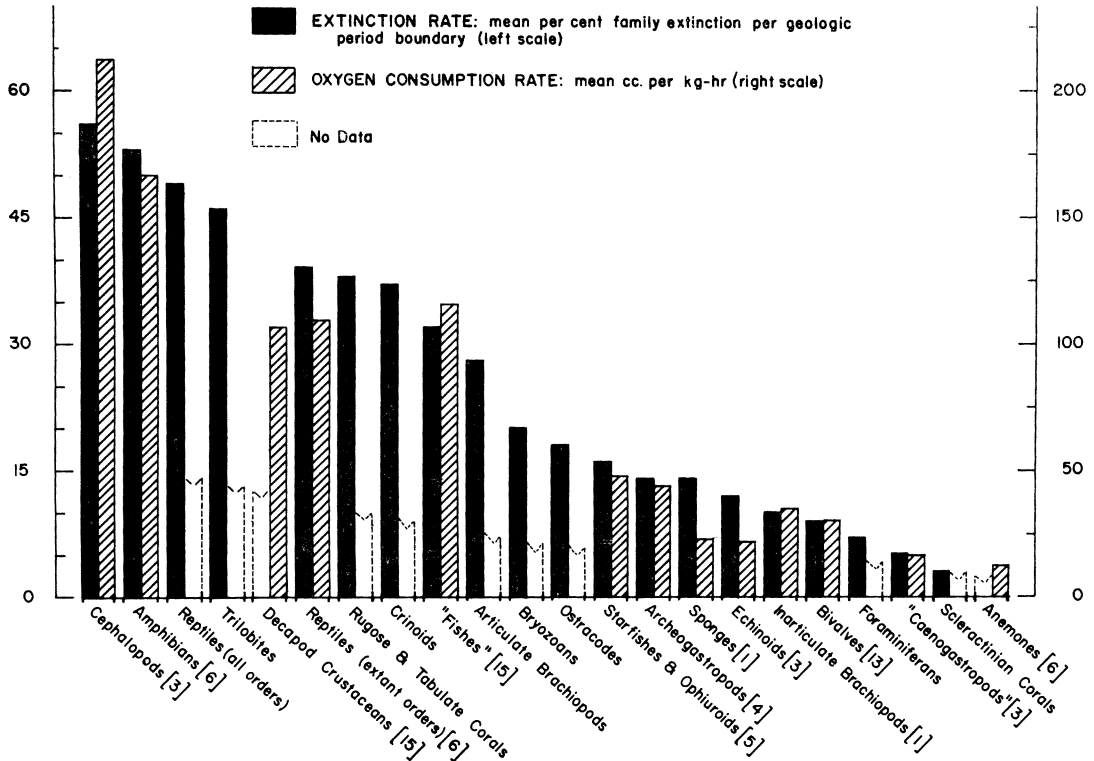
ABSTRACT—Past susceptibility to family-level extinctions within major taxa of fossil animals shows a close positive correlation ($r = .905$) with oxygen uptake in Recent representatives of the same taxa. Taxa that have had high extinction rates have high present-day rates of oxygen consumption; taxa that have had unusually stable histories have very low rates. This correlation shows that periodic episodes of animal extinction were caused by environmental stresses that selectively eliminated animals having high rates of energy utilization. Past variation in the concentration of atmospheric oxygen appears to be among the most probable environmental changes that could be expected to produce such an effect.

PERIODIC episodes of animal extinction have long been among the most problematic aspects of the history of life. Recent summaries by Harland and others (1967) and Newell (1967) have provided modern documentation of the puzzling effect of such “crisis intervals” on the principal taxa of fossil animals. Certain groups of both terrestrial and aquatic habit show severe and simultaneous reductions, while others do not. Some carnivores, herbivores, suspension feeders, and deposit feeders are greatly affected, while other groups with similar diets persist with little change. Even closely related subgroups within one phylum or class commonly show radically different histories. In short, there is no obvious taxonomic or adaptive pattern in the effect of extinction intervals on different animal taxa.

This paper reports the results of an attempt to relate the differing extinction histories of the major taxa of fossil animals to certain physiological parameters in present-day representatives of the same taxa. The study was prompted by recent suggestions that fluctuations in the abundance of atmospheric oxygen have played a fundamental role in the history of life (Berkner and Marshall, 1964, 1965, 1967; Cloud, 1968; Fischer, 1965; Tappan, 1968). If this were the case, then a clue to a pattern in

animal extinctions is suggested, for groups with high overall susceptibility to extinction should be those having a high sensitivity to changes in oxygen abundance whereas groups with comparatively stable histories should have a low sensitivity to such changes. This hypothesis can be tested with two sets of data, one showing the relative susceptibility to extinction of fossil animal taxa, and the other indicating the potential sensitivity of these same taxa to fluctuations in available oxygen.

Data concerning the extinction patterns of the major taxa of fossil animals, based in large part on compilations by Newell, are summarized by the dark bars of Text-figure 1, which show the mean per cent of family-level extinction taking place per geologic period boundary in all major animal taxa (other than mammals) with reasonably long and abundant fossil records. The percentages reflect that proportion of the families occurring in the *last* epoch of each geologic period that are unknown from younger epochs, averaged over the geologic range of the taxon. Geologic period boundaries were emphasized in the compilation because they generally reflect intervals of unusually severe extinction. The percentages, which range from a high of 56 per cent per period boundary in cephalopods, to a low of 3 per cent per period boundary in scler-



TEXT-FIG. 1.—Comparison of extinction rates (dark bars) in the principal taxa of fossil animals with oxygen consumption rates (light bars) in Recent representatives of the same taxa. Oxygen consumption rates in Recent decapod crustaceans and anemones are included for comparison with extinction rates of trilobites and scleractinian corals, respectively. Numbers in brackets indicate number of Recent species for which oxygen consumption measurements are available. Extinction rates from Newell (1967, figs. 4 and 5) with additions for brachiopods, cephalopods, starfishes, and ophiuroids from data in relevant volumes of Moore (1953–1967), and for extant reptiles from data in Romer (1966). All extinction percentages based on total occurrence of less than 10 families per period boundary omitted except for inarticulate brachiopods. Oxygen consumption rates from: Altman *et al* (1958, p. 278–282), Belcik (1968, p. 179), Davies (1966), Farmanfarmaian (1966, p. 254), Ghiretti (1966, p. 195), Hammen *et al* (1962, p. 188), Hyman (1967, p. 390), Nicol (1967, p. 150–151), and Wolvekamp & Waterman (1960, p. 45). All values reported in these sources have been included except those for aquatic species with “emergency” adaptations for aerial respiration (principally gastropods and fresh water fishes). Such species show anomalously high values when breathing air and, for this reason, intertidal gastropods with such adaptations have been omitted, and the value shown for fishes is the mean of 15 marine species reported in Nicol (1967).

actinian corals, provide an overall measure of the susceptibility to extinction within the major taxa of fossil animals.

Data concerning the probable sensitivity of these same taxa to fluctuations in the abundance of atmospheric oxygen are less readily available. Perhaps the most relevant evidence would be long-term experiments on the effects of abnormally high or low oxygen partial pressures on living representatives of the many groups which exist today. Some suggestive studies of this kind have been made (Belkin, 1963; Fox and Taylor, 1955; Siegel and others, 1965; Zeuthen, 1955) but, as yet, these have been too few for broad historical comparison. There is, however, a

larger body of physiological data of another sort that bears on the question—measurements of the normal rate of oxygen consumption, per unit of body weight, in various recent animal species. Such oxygen consumption measurements provide an indirect measure of the total energy utilization, or metabolic rate, of the animal, and are a standard tool of comparative physiology. If atmospheric oxygen fluctuations have been an important cause of animal extinctions, then it seems reasonable to predict that taxa with high overall oxygen requirements should have been more susceptible to such extinction than those with low oxygen requirements.

The lighter bars of Text-figure 1, compiled

from many sources, summarize the available oxygen consumption data for Recent representatives of the principal taxa of fossil animals. Mammals are not included because, as homeotherms, they have unusually high oxygen consumption values that are not directly comparable with those of poikilothermic animals, which include all other taxa with good fossil records. Text-figure 1 shows that there is a close positive correlation ($r = .905$; $N = 11$) between the susceptibility to family-level extinctions in a fossil animal taxon and the mean oxygen consumption of Recent representatives of the same taxon. Taxa with high rates of oxygen consumption have had high rates of extinction, and vice-versa. This correlation provides a new insight into the previously enigmatic patterns of animal extinctions for, regardless of habitat, feeding type, or taxonomic position, the taxa most affected during episodes of extinction are those with high oxygen requirements and high metabolic rates. In general, the highest rates of both extinction and oxygen consumption occur in complex, active groups, but note that the detailed pattern of Text-figure 1 could never be predicted from simple considerations of organizational complexity or overt activity. For example, cephalopods show far higher oxygen consumption and extinction rates than do equally active "fishes," while active "caenogastropods" show much lower rates than either sedentary bivalves or less complex inarticulate brachiopods.

This extinction-oxygen consumption correlation is clearly consistent with the suggestion that atmospheric oxygen fluctuations have been a primary cause of Phanerozoic animal extinctions because intervals of abnormally low, or toxically high, concentrations of atmospheric oxygen would most probably cause selective extinction of those animals with high oxygen requirements. This conclusion cannot be accepted without reservation, however, because other environmental variations might have the same effect. Oxygen consumption is an indirect measure of metabolic rate, that is, it reflects the animal's total rates of energy consumption and expenditure. These rates, in turn, might be expected to be sensitive to variations in certain other environmental parameters. Temperature, in particular, has a profound influence on animal metabolism; large-scale historical changes in the Earth's temperature regime might, therefore, also selectively favor extinction of animals with high metabolic rates and lead to the observed correlation between oxygen consumption and extinction.

There can be little doubt that large-scale cli-

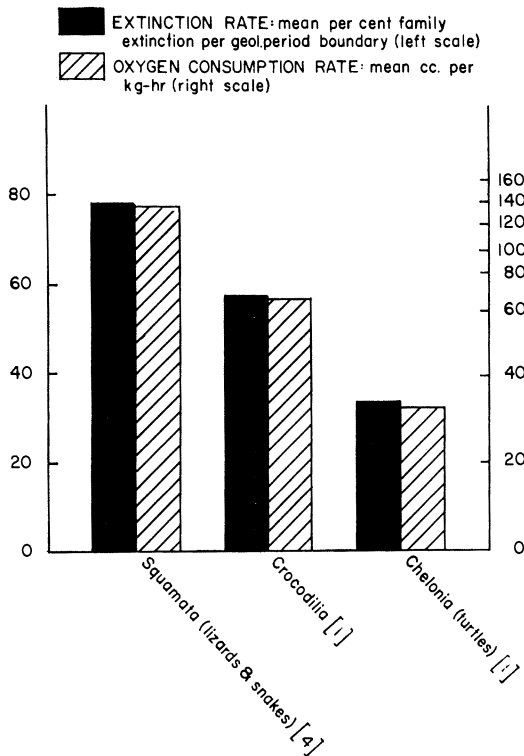
matic changes have altered the Earth's temperature regime many times during Phanerozoic time but, at present, such changes do not appear to be a promising explanation for periodic episodes of animal extinction. The most compelling reason is that the unusually large climatic fluctuations of Pleistocene time have not been accompanied by such large-scale extinctions. Indeed, there are reasonable theoretical arguments suggesting that such intervals of climatic stress tend, in general, to favor animal diversification, rather than extinction (Valentine, 1968).

On the other hand, the hypothesis that atmospheric oxygen fluctuations have been a primary (but certainly not the *only*) cause of periodic animal extinctions has much to recommend it. The hypothesis would explain the many coincident extinctions of aquatic and terrestrial animals because the amount of dissolved oxygen in the waters of the Earth is primarily controlled by, and directly proportional to, the partial pressure of atmospheric oxygen (Gilbert, 1964; Richards, 1965). Furthermore, changes in atmospheric oxygen concentration, whatever their cause, are unlikely to have been catastrophically sudden, but would more probably have taken place gradually over millions of years. Animal extinctions, although concentrated at certain times in geologic history, are known to be similarly spread over millions of years.

Another advantage relates to the often-noted evolutionary trend toward increasing body size in many animal taxa (Newell, 1949). It is a well-established principle of respiratory physiology that the rate of oxygen consumption, per unit of body weight, is not constant within and between animal species, but decreases sharply with increasing body size. In other words, large animals require considerably less oxygen to support a gram of body tissue than do small animals. This suggests that the "phyletic size increase" seen in many animal groups may have had its origin in repeated adaptations to atmospheric oxygen fluctuations, an idea that has been previously suggested in a different context by the physiologist Zeuthen (1953).

Perhaps the most attractive aspect of the oxygen-extinction hypothesis is its high predictive value and potential for further testing, both from the fossil record, and from observations on present-day animals. If oxygen fluctuations have played a major role in animal extinctions, then more detailed studies should reveal additional correlations between respiratory physiology and evolutionary history.

As a preliminary attempt at further analysis, extinction-oxygen consumption values have been calculated separately for three of the four sur-



TEXT-FIG. 2—Comparison of extinction rates (dark bars) in fossil representatives of the three principal orders of surviving reptiles with oxygen consumption rates (light bars: note logarithmic scale) in Recent species of the same orders. Numbers in brackets indicate the number of Recent species for which oxygen consumption measurements are available. Extinction rates from Romer (1966); oxygen consumption rates from Altman *et al* (1958). Measurements reported by Altman *et al* from Benedict (1932) have been omitted because they are an order of magnitude lower than those reported from all other sources and have been repudiated by their original author (Benedict, 1932, p. 150-152).

viving orders of reptiles (unfortunately, no oxygen consumption values are available for the fourth order, the relict Rhynchocephalia). Although based on a relatively spotty fossil record, and on only single oxygen consumption values for two of the orders, the results, shown in Text-figure 2, are encouraging. They show a close correlation when the oxygen consumption values are plotted on a logarithmic scale rather than on the arithmetic scale of Text-figure 1. This suggests that extinctions of air breathing poikilotherms may vary as a logarithmic function of oxygen consumption, rather than arithmetically as do the aquatic groups, which dominate Text-figure 1.

Still other kinds of testing of the oxygen-ex-

tingtion hypothesis are possible. Detailed analysis should show a correlation between inferred respiratory physiology and the sequence in which various taxa diminish or become extinct during episodes of extinction. A strong confirmation would be the discovery, predicted by the pattern of Text-figure 1, that present-day crinoids, articulate brachiopods, bryozoans, and ostracodes, groups for which no oxygen consumption measurements are available, have relatively high oxygen consumption rates.

Finally, the oxygen-extinction hypothesis is suggested by independent geochemical considerations because the composition of the Earth's tenuous shell of atmospheric gases is directly controlled, on a geologically short time scale, by the metabolic activities of the living world. In particular, all but an insignificant fraction of the free oxygen present in the atmosphere appears to have been produced by photosynthetic plants. In spite of the seemingly limitless volume of atmospheric oxygen available today, it has been calculated that all of the molecules in this reservoir pass through living organisms once every 7000 years (Gilbert, 1964). With this rate of turnover it is probable that small changes in either the rate of oxygen production by green plants, or the rate of oxygen loss by such processes as organic decay and oxidation of inorganic materials, could substantially change the composition of the atmosphere over relatively short spans of geologic time. The probabilities are high that such changes have taken place in Phanerozoic time and their more exact specification, through detailed consideration of both the fossil record and the geochemical cycling of oxygen, carbon, and other biologically important elements, shows promise for new insight into the complex and interrelated histories of the biosphere, atmosphere, and lithosphere.

ACKNOWLEDGMENTS

The author thanks the following colleagues for discussion and advice: Z. P. Bowen, P. E. Cloud, Jr., J. T. Gregory, W. D. Hartman, C. MacClintock, N. D. Newell, J. H. Ostrom, G. Pannella, D. C. Rhoads, K. S. Thomson, K. K. Turekian, J. W. Valentine, K. M. Waage, and J. C. G. Walker.

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MANUSCRIPT RECEIVED JUNE 16, 1969