4 August 1978, Volume 201, Number 4354 SCIENCE

A Terminal Mesozoic "Greenhouse": Lessons from the Past

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Summary. The late Mesozoic rock and life records implicate short-term (up to 10^5 to 10^6 years) global warming resulting from carbon dioxide–induced "greenhouse" conditions in the late Maestrichtian extinctions that terminated the Mesozoic Era. Oxygen isotope data from marine microfossils suggest late Mesozoic climatic cooling into middle Maestrichtian, and warming thereafter into the Cenozoic. Animals adapting to climatic cooling could not adapt to sudden warming. Small calcareous marine organisms would have suffered solution effects of carbon dioxide–enriched waters; animals dependent upon them for food would also have been affected. The widespread terrestrial tropical floras would likely not have reflected effects of a slight climatic warming. In late Mesozoic, the deep oceanic waters may have been triggered into releasing vast amounts of carbon dioxide into the atmosphere in a chain reaction of climatic warming and carbon dioxide expulsion. These conditions may be duplicated by human combustion of the fossil fuels and by forest clearing.

Human combustion of the fossil fuels coal, oil, and gas and of forest clearing is measurably increasing the carbon dioxide content of the atmosphere. Modern theoreticians have expressed vaguely defined fears about the potential effects of a warming of the earth's surface brought about by the infrared trapping capacity of atmospheric CO_2. An examination of the rock and life records at the Mesozoic-Cenozoic time interface, which was a time of worldwide faunal extinctions, spells out the potential effects of a global temperature elevation on living organisms, and suggests that human alteration of the carbon cycle could trigger conditions resembling those of the so-called "Time of Great Dying" that terminated the Mesozoic Era.

Many hypotheses have been formulated to account for the late Mesozoic wave of animal extinctions. Whereas extinctions occurred continuously throughout a long span of late Mesozoic time and may have been caused in part by a decreasing equability of the climate, as suggested by Axelrod and Bailey (*1*), the Mesozoic-Cenozoic boundary itself was marked by a "brief crisis characterized by an abnormally high rate of extinction" (*2*, p. 796). During the final extinction interval of 10^5 to 10^6 years (*3*), or possibly as few as 1 to 100 years (*4*), many diverse types of marine and terrestrial organisms disappeared or were reduced in importance; at that time the dinosaurs and many of their relatives vanished. Such a selective pattern seems to indicate an environmental stress that some organisms were adapted to meet and others were not.

Recently derived information on the carbon cycle and on the marine paleontological and sedimentological records and my reappraisal of selected physiological aspects of the vertebrate survivors of the late Mesozoic (late Maestrichtian) extinctions implicate geologically short term (10^5 to 10^6, or fewer, years) climatic warming as a causative factor in the extinctions. Research on the carbon cycle has revealed a mechanism that might account for a natural increase in the atmospheric CO_2 content and a consequential climatic warming. Temperatures lower than those required to damage somatic (body) cells can severely damage male reproductive (germinal) cells (*5*), and thus may have been a factor in the extinction of the dinosaurs. A temperature elevation of only a few degrees, and easily within the 6°C increase in global temperatures over the next century or two that is predicted by the Energy and Climate Panel of the National Academy of Sciences (*6*) as a result of human-generated alteration of the carbon cycle, could trigger worldwide extinctions.

Late Maestrichtian Extinctions

Russell (*4*) estimated that about 75 percent of the species living in terminal Mesozoic time vanished at the beginning of the Cenozoic. His estimate of the maximum duration of the extinction interval is about 2×10^6 years; however, the minimum could have been as short as 1 to 100 years. Worsley (*3*) has suggested that the terminal Mesozoic extinction interval spanned about 10^5 to 10^6 years.

Colbert (*7*) has noted that reptiles were abundant in late Mesozoic and that the last of the dinosaurs lived at the very end of the era but not beyond. At that time they, and possibly some marine reptiles, seem to have vanished "rather suddenly and simultaneously" all over the world (*7*, p. 198). Whereas some authors have suggested that dinosaurs declined in diversity during latter Late Cretaceous to the point that few taxa were left by terminal Cretaceous time, Russell (*8*) has shown that a rich fauna existed until the end of the period, when it suddenly disappeared. (I avoid the controversy over whether the dinosaurs were or were not

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warm blooded; it is not important to the extinction model presented herein.)

Russell (*8*) has pointed out that the reptilian extinctions "coincided with marine extinctions which were of global extent and relatively brief geochronological duration." In addition to the reptilian extinctions, many genera of the larger benthic forms of the foraminifera became extinct; the marine planktonic family, Globigerinacea, was nearly wiped out. In addition, the echinoids declined markedly at the Mesozoic-Cenozoic boundary. The rudistids and the clam *Inoceramus* also do not occur above the Maestrichtian (*9*). The coccolithophorids (Chrysophyta), the marine algae which had produced the vast Mesozoic chalk deposits, underwent catastrophic reduction in diversity and abundance in late Maestrichtian.

Evidences of Late Maestrichtian Warming

Colbert, Cowles, and Bogert (*10*), in their work on the temperature tolerances of the alligator, a modern archosaurian relative of the dinosaurs, suggested the possibility that a rise in the average temperature was instrumental directly or indirectly in the extinction of the dinosaurs. Colbert (*7*) noted that the "principal consideration in favor of the theory of reptilian extinctions by rising temperatures is based upon the known temperature tolerance of modern reptiles." Cowles' (*11*) experiments with the thermal tolerance of modern reptiles led him to conclude that elevation of temperatures triggered extinction of the dinosaurs. These researchers lacked evidence from the rock and other paleontological records that would support a terminal Mesozoic temperature elevation.

Evidences from recent marine sedimentological and paleontological investigations may indicate late Maestrichtian warming. The work of Worsley (*3*, p. 94) indicates that all Deep Sea Drilling Project (DSDP) cores penetrating pelagic sediments at the Cretaceous-Tertiary boundary display a major unconformity between the Cretaceous and Tertiary. According to Tappan (*12*), faunal evidence of paraconformities indicates widespread submarine solution of carbonates at the end of the Mesozoic. Worsley (*3*) has suggested that the carbonate solution event coincides with the terminal Mesozoic extinctions and estimated the time involved to be about 10^5 to 10^6 years. Plants remove carbon dioxide from the atmosphere during photosynthesis. Shackleton (*13*) has suggested that expansion of forests would pump carbon dioxide out of the oceans via the atmosphere, thus allowing preservation and accumulation of carbonates in the oceans. Conversely, the destruction of terrestrial vegetation would inject carbon dioxide into the oceans, thus causing carbonate dissolution. The late Maestrichtian extinctions of the formerly vast coccolithophorid floras should have produced the same effect as reduction of terrestrial vegetation, thereby triggering the late Maestrichtian carbonate solution event.

Isotope studies of Late Cretaceous and early Cenozoic benthic and planktonic foraminifera and calcareous nannofossils (marine algae) by Kroopnick *et al.* (*14*) suggest a general Late Cretaceous cooling trend followed by late Maestrichtian warming. From Campanian time upward into middle Maestrichtian, carbonate tests of benthic foraminifera show a trend toward decreasingly heavy ($\delta^{13}C$) carbon istopes, but increasingly heavy ($\delta^{18}O$) oxygen isotopes. This suggests cooling of oceanic bottom waters, with maximum cooling in middle Maestrichtian. In late Maestrichtian, and extending into the Cenozoic, is a trend toward increase in heavier carbon isotopes and lighter oxygen isotopes, thus suggesting warming of bottom waters. Isotope trends of planktonic foraminifera and calcareous nannofossils generally parallel the trends of the benthic foraminifera.

Broecker (*15*) noted that "everywhere we look, there is evidence of more dissolution of [carbonate] sediments during warm periods that during cold periods. For any place in the oceans for which we have data, apparently the sedimentary carbonate was more severely attacked by the waters at that spot during warm periods than during cold periods."

Other paleontological data also indicate Maestrichtian warming. Voight (*16*) demonstrated that during the late Mesozoic, warmwater larger foraminifera, reef corals, and rudistids were most widespread outside the Tethys region during Maestrichtian; his distribution diagrams indicate a cool early Maestrichtian with subsequent warming in late Maestrichtian. Wicher (*17*) concluded from work on the stratigraphic range and areal distribution of the foraminifer *Pseudotextularia elegans* that a warmwater phase of the earlier part of late Maestrichtian continued through late Maestrichtian. Jeletzky (*18*) noted that the reappearance of *Belemnitella* in previously abandoned northern seas and its subsequent displacement by *Belemnella* required Maestrichtian warming (although he suggested cooling toward the close of the Maestrichtian).

Evidence from the vertebrate survivors of the terminal Mesozoic extinctions suggests warming as a causative factor in the extinctions. Mesozoic vertebrate faunas prior to the late Maestrichtian extinctions included birds, small mammals (the size of cats or smaller), and reptiles of all sizes, some of which weighed many tons. The birds and mammals then, as now, were endothermal (able to maintain a constant body temperature during environmental temperature changes). The reptiles, on the other hand, included both ectothermal (unable to maintain a constant body temperature during environmental temperature changes) and, as suggested by various workers, possibly endothermal types as well. After the extinctions, only the birds, mammals, and relatively small ectothermal reptiles remained. Russell (*4*, p. 16) notes that no land vertebrate more massive than 25 kilograms survived the late Mesozoic extinctions; selection favored relatively small size. An inquiry into body size as affected by environmental temperatures can perhaps illuminate environmental conditions which prevailed at the close of Mesozoic time. A modest elevation of temperature is probably more damaging physiologically than is a comparable drop. In addition, small animals would be more likely to survive an abnormal prolonged temperature elevation than would large ones. The fact that only relatively small vertebrates survived the late Mesozoic extinctions is, in itself, excellent evidence favoring late Maestrichtian climatic warming.

Endothermy is based on heat production and conservation and not on cooling and heat loss. It involves maintenance of body temperatures that are higher than average environmental temperatures. Whereas some mammals function routinely at temperatures far lower than their body temperatures (for example, sea lions in polar waters), few can withstand environmental temperatures more than a few degrees above the body temperature for extended periods. External heat elevates the metabolic rate which increases regularly with increasing temperatures. Animals have various methods of combating external heat; some physically escape the heat by seeking shade or by assuming nocturnal habits; others utilize physiological methods, such as the evaporative techniques of sweating or panting, to dissipate body heat. The physiological methods are effective only at temperatures below, around, or slightly above body temperature and cannot counteract high temperatures for protracted periods.

Ectothermal animals lack effective surface insulation and hypodermal adipose tissue and lose most of the little body heat that they generate to the environment, but they too are heat sensitive. The reptiles adapted to rigorous desert conditions crowd the thermal ceiling of physiological tolerance (*11*). Cowles and Mitchell (*19*) showed that desert reptiles are not notably resistant to the heat of the desert and that only a few minutes exposure to spring or summer solar radiation can prove fatal. Cowles' (*11*) experiments with desert lizards indicated that serious discomfort and damage can result from thermal exposures of only 3°C above optimum. Colbert, Cowles, and Bogert's (*10*) study of the alligator showed that temperatures only a few degrees above its optimum were also potentially fatal for that reptile.

Whereas even modest temperature elevations can be damaging to reptiles, many can tolerate temperatures far below their optimum without suffering apparent damage, at least for short periods. Cowles (*11*) demonstrated that some desert lizards submitted freely to a lowering of the temperature by as much as 9°C below their optimum; some snakes and lizards were refrigerated to body temperatures of 1° to 2°C without suffering apparent harm. Colbert, Cowles, and Bogert (*10*), noted that alligators could withstand temperature drops of 20°C below their optimum without suffering damage. Of course, they could not maintain normal life processes at abnormally low temperatures. Cowles (*20*) suggested that adaptation to desert conditions favored small size because small reptiles as compared to large ones can warm themselves more rapidly in sunshine. Cole (*21*) placed greater emphasis on the fact that small size permits more rapid cooling than does large size. Most interestingly, Colbert, Cowles, and Bogert (*10*) demonstrated that small alligators are able to attain temperatures higher than the average critical maximum for larger specimens and to survive provided that the temperatures are not maintained for more than a few minutes. Body size is an important factor in body temperature regulation and probably played an important role in the late Maestrichtian extinctions. Because only relatively small vertebrates survived the extinctions, climatic warming is indicated.

Body Size and Heat Dissipation

The ability to dissipate body heat into the environment is dependent on the ratio of body surface to volume. Colbert, Cowles, and Bogert (*10*) demonstrated that in alligators the rate of heat loss is inversely proportional to the mass of the animal, being most rapid in small animals and slowest in large ones. They suggested that in reptiles of large size, body-heat loss would be retarded and more stable levels of body temperature could be maintained; in short, the physiological advantages of large size may have been the cause of the evolution of the large Mesozoic reptiles. Cowles (*22*) suggested that the large reptiles could have conserved the relatively little internally generated heat they produced because of their relatively small ratios of surface area to volume and have become functionally "endotherm-like" but not truly warm-blooded animals. If this is so, and if the Bergmann principle (warm-blooded organisms increase their size with declining temperatures) is applicable, the retention of large body size by various dinosaurian lineages would accord well with declining temperatures of about 5°C over the final 20 million years of the Mesozoic Era (from Santonian to Maestrichtian) (*23*).

Whereas large size could offer advantages to organisms that were adapting to generally cooling conditions, it would be disadvantageous during an abrupt climatic reversal from cooling to abnormally rising temperatures. The amount of heat generated during exertion depends on body volume and is greater in large animals. Because large animals have relatively small surface-to-volume ratios, they cannot dissipate body heat as efficiently as can small animals. Colbert, Cowles, and Bogert (*10*) noted that if body temperatures of adult dinosaurs were maintained at about optimal levels, it would have been disadvantageous for them to be exposed to the sun for considerable periods because it would result in their body temperatures rising faster than the heat could be dissipated. Cowles (*11*) maintains that, if the Mesozoic reptiles had the dark pigmentation of the modern archosaurians (the crocodiles) but lacked the faculty for color change, there would be "little doubt that exposure to temperatures even a few degrees above those to which they were adapted would have led to their rapid disappearance or would have necessitated habit and habitat adjustment." Small body size, which allows relatively rapid loss of body heat, plus the ability to more readily escape direct sunlight by physical means would offer the greatest selective advantage during a relatively sudden change from cooling to warming conditions. Why the ability to stay cool during a time of environmental temperature increase would offer evolutionary advantage is discussed below.

Temperature and Extinction: Cowles Revisited

Far more significant than temperature levels that damage somatic cells are the temperatures that damage reproductive germinal cells. Temperatures below those that will physically damage somatic cells can reduce the viability or number of the male germinal (sperm) cells. Temperatures only a few degrees above normal, and even below those that cause discomfort to an organism, can induce sterility (*24*). Cowles (*5*) suggested that the susceptibility of male sperm, at least during active spermatogenesis, to temperatures above normal for the testes may have played a significant role in vertebrate evolution. For the Mesozoic reptilian extinctions Cowles (*22*) noted that it mattered little whether or not maximum temperatures reached a level that would damage somatic cells; the critical thermal threshold of the male sperm may have been reached. Thus, late Maestrichtian extinctions of reptiles and other vertebrates may have been generated by a temperature increase of such modest magnitude that evidence for it has been subtly hidden in the rock record.

Because large reptiles would dissipate body heat relatively slowly during a prolonged temperature increase, their internal body temperatures may have become elevated to the point that the male sperm was damaged. Even short-term elevation of gonadal temperatures can induce temporary sterility. A prolonged temperature increase extending throughout the breeding season (many animals breed in the spring when temperatures are relatively low) could, if it extended over the life-span of many generations, cause extinctions. Cowles (*5*) noted that normal low temperatures probably did not play a major part in reproductive processes because most, if not all, ectotherms operate most efficiently at temperatures only slightly below the threshold where thermal damage is inevitable.

The geologic record provides direct evidence that an environmental stress factor affected dinosaurian reproduction immediately prior to their relatively abrupt terminal Maestrichtian extinction phase. This evidence, from dinosaur eggs, when examined in light of modern birds which also lay hard, calcareous eggs, strongly implicates environmental warming as a causative factor in the extinctions. Eggs of Crocodilia (relatives of the dinosaurs) are virtually identical to those of birds (*25*). Erben (*26*) studied dinosaur eggs from late Maestrichtian strata stratigraphically upward to the extinction event. In the older strata investigated by Erben, dinosaur egg shells were relatively thick (up to 2.5 millimeters); upward in the section, however, they became progressively thinner-shelled (about 1.0 millimeter) and fragile. In other instances, many eggs were whole; for some reason they had not hatched. The possibility of infertility is thus raised. An alternative is that the shells may have been so thin as to disrupt calcium metabolism and skeletal development of the embryo. Embryos of crocodilians and birds recover large amounts of calcium from the eggshell for ossification of the bones (*27*). Most significantly, elevated temperatures disrupt calcium metabolism in some modern birds, including chickens, causing them to lay thin-shelled eggs; even normal hot summer temperatures cause some birds to produce thin-shelled eggs (*28*). Siegel (*29*) notes that chickens exposed to 5 percent levels of CO_2 in the breathing air for several hours lay thin-shelled eggs because of lowering of the pH of the chicken blood. Desmond (*30*) notes that "Dinosaurs were reacting to a brief but protracted period of stress in the same way as birds today, by laying eggs with ever-thinning shells." This stress was probably due to elevated environmental temperatures.

Mammals are similarly affected by higher than normal temperatures. Heating of mammalian testes to temperatures above normal will induce sterility. Among the scrotal animals, even normal body temperatures applied to the testes can cause degeneration and sterility. Cowles and Burleson (*24*) note that the continued existence of many mammals seems ensured by scrotal and other testicular cooling methods. Thus, even though the Mesozoic mammals were small, those that lacked efficient testicular cooling methods would, during a time of increasing environmental temperatures, have suffered reduced fertility or, at worst, sterility. In fact, any organisms, whether large or small, endothermal or ectothermal, which had low thresholds for thermal damage of the male reproductive organs could have suffered reproductive impairment, and possibly extinction, during abruptly warming conditions.

Summary of Paleontological Information

In late Mesozoic, animals that had adapted to the slowly cooling climatic conditions during the 20-million-year interval from Santonian to Maestrichtian were suddenly (in a geologic sense) faced with warming conditions to which many taxa could not adapt. At that time, animals that could not dissipate body heat efficiently would have suffered from the effects of increased temperatures on the male germinal cells; some reptiles may have suffered from thermally induced disruption of calcium metabolism. The animals most affected would have been those greater than 25 kilograms (*4*) because of their body-heat–retaining capacities, regardless of whether they were endothermal or ectothermal, and those with low thermal-sensitivity thresholds to the male germinal cells. Thus, many small vertebrates could have been eliminated along with the large ones. Animals with heat-dissipating systems efficient enough to protect the male germinal cells from thermal damage were the probable survivors of the terminal Mesozoic extinctions.

During an environmental warming, many types of marine reptiles would also have been adversely affected, and perhaps more so than some of their terrestrial contemporaries. During warming of the oceanic waters, marine reptiles would not have been able to utilize evaporative techniques to reduce body temperatures, or to easily physically escape elevated temperatures by assuming nocturnal habits or by seeking shade.

Even marine microscopic protozoans and algae which utilize calcium carbonate, but which have relatively large ratios of surface area to volume, would have been adversely affected by a temperature increase. Their shells would have undergone solution along with other carbonate sediments during the late Maestrichtian carbonate solution event, thereby terminating the geologic ranges of many taxa. Marine invertebrates which utilized the vast crops of coccolithophorids (marine algae) as a food source would also have undergone reductions in late Mesozoic.

The primary argument against a terminal Mesozoic temperature increase has been that terrestrial floras existing then underwent neither great geographic shifts nor the vast extinctions experienced by the contemporary faunas. A counter to this argument lies in the nature of the Late Cretaceous floras themselves. Hughes (*31*) notes that the width of the Cretaceous equatorial belt may have been at least 80° (latitude); thus, floras acclimated to warmth were widespread. Such floras would not have responded as dramatically to a short-term warming of only a few degrees as would have typical temperate floras. In fact, short-term experiments in a greenhouse have shown that, within reasonable limits, elevation of temperatures and of atmospheric CO_2 can enhance plant growth; a 10 percent increase of atmospheric CO_2 increases plant growth by 5 to 8 percent (*32*). Conversely, the magnitude, degreewise, of a temperature decrease which would have caused abrupt extinctions of terrestrial and marine faunas would have been greater than that of a temporary increase and would probably have been reflected by striking changes in the Late Cretaceous tropical floras.

A Natural "Greenhouse" Mechanism: Triggers and Chain Reactions

In late Mesozoic, two worldwide interrelated factors were affecting life on the earth: shallow epeiric seas that had flooded the continents earlier in the Mesozoic were regressing to the ocean basins, and the climate was undergoing a 20-million-year cooling trend (Santonian to Maestrichtian). As the epeiric seas disappeared, widespread ecological niches were eliminated. At the close of the Mesozoic, during late Maestrichtian time, the coccolithophorids, which had been vastly abundant in the Mesozoic seas, underwent catastrophic reductions in abundance and in the number of taxa. Bramlette (*33*) has suggested that the overturn of the coccolithophorids was caused by nutrient depletion below a critical level. Whatever the cause of the extinctions of the coccolithophorids, their reduction would have radically affected the natural carbon cycle and, ultimately, the amount of free carbon dioxide in the atmosphere, and could have triggered the initial stages of climatic warming.

Plants consume CO_2 from their environment and produce food, plant tissue, and oxygen through the photosynthesis reaction; large-scale variations in productivity would affect the carbon cycle. Modern plants, including both terrestrial and marine floras, consume and fix about 73 billion tons of carbon in the form of CO_2 annually. Marine phytoplankton alone consume about 25 billion tons (*34*). These figures may not be significantly different from late Mesozoic figures prior to the late Maestrichtian extinctions. Sharp reduction of the vast coccolithophorid floras in late Maestrichtian would have reduced total productivity. Thus, CO_2 that had previously been utilized by the coccolithophorids would have accumulated in the atmosphere.

Because CO_2 is transparent to incoming solar radiation but absorbs part of the infrared radiated from the earth, increasing quantities of CO_2 in the atmosphere should cause warming of the lower atmosphere and of the surface of the earth. Theoretically, a 10 percent increase in atmospheric CO_2 concentration results in a temperature increase of 0.32°C; and a doubling of CO_2 results in an increase of 2.4°C (*35*). Warming of the earth's surface would warm the oceans. As the water warms, the solubility of CO_2 decreases and it is driven from the oceans into the atmosphere. Theoretically, an increase of 1.0°C of the upper oceans will generate a 6 percent increase in atmospheric CO_2 (*36*); this will cause additional heating of the upper oceans and additional expulsion of CO_2 into the atmosphere. Maximum attainable "greenhouse" conditions would result if the deep oceanic waters warmed sufficiently to generate release of their excess CO_2. The probable structure of the late Mesozoic oceans makes the likelihood of this event plausible.

During late Mesozoic, the polar regions, as far as we know, were relatively warm and free of ice. The Mesozoic oceans were thus warmer and probably better mixed vertically than the modern oceans which, largely because of the cold polar regions, show sharp vertical density stratification into several layers; these are a deep cold layer, a pycnocline, and a relatively warm surface layer. Vertical mixing among the layers occurs today by upwelling, diffusion, and the like (*37*) and would probably have been more prevalent in the warmer late Mesozoic oceans. Interestingly, Worsley (*3*, p. 111) indicates that there is little evidence of a Mesozoic carbonate compensation depth (CCD) and that the oceans offer no evidence that a CCD existed in the Late Jurassic or Early Cretaceous; he suggests that the CCD first appeared in the Late Cretaceous in the Pacific Ocean and at the end of the Cretaceous in the Atlantic Ocean.

In the late Mesozoic, while the epeiric seas were regressing to the ocean basins, declining world temperatures would have allowed the oceans to store increasing quantities of CO_2. Conversely, a climatic reversal from cooling to warming conditions would have warmed the surface waters thereby triggering them into expelling some of their CO_2 and thus enhancing the warming effect. Because of the probable extensive vertical mixing of the Mesozoic oceans, the deep waters could have readily warmed, thereby expelling excess CO_2. Ultimately, the deep ocean waters could have overturned, liberating vast quantities of CO_2 into the atmosphere. Extinction of the vast coccolithophorid floras in late Maestrichtian could have triggered an initial warming of the climate and of the oceans. A consequential chain reaction of alternating CO_2 expulsion and enhanced warming would have resulted in a late Mesozoic "greenhouse" effect.

Human-Generated Carbon Dioxide: A Modern Trigger?

For several hundred million years, plant materials generated by photosynthesis have accumulated in the earth as the fossil fuels coal, oil, and gas. In photosynthesis, plants consume and store CO_2 and produce oxygen. Today, by burning fossil fuels, we are, in effect, reversing the photosynthesis reaction: we are consuming oxygen and liberating CO_2. Some of the human-generated CO_2 is taken up by plants of the biosphere and some by the oceans; the remainder accumulates in the atmosphere.

Since the beginning of the Industrial Revolution and with increased utilization of the fossil fuels as energy sources, CO_2 has steadily accumulated in the atmosphere, from about 290 parts per million (ppm) (by volume) in the middle 1880's (*38*) to about 330 ppm today. By the year 2000 it will theoretically rise to an estimated 385 ppm (*38*). Since the middle to late 1800's the temperature has increased about 0.5°C, and at least part of this increase is attributed to CO_2 (*39*). By the year 2000 it could theoretically increase by another estimated 0.5°C.

Damon and Kuenen (*40*) provide new information on the question of whether the climate will warm or cool in the immediate future. They indicate that the effects of atmospheric CO_2 would appear first in the Southern Hemisphere where human activity and human-generated particulate pollution is lowest. Their measurements show increases in temperature in the Southern Hemisphere and potential early stages of "greenhouse" conditions. Koerner's work (*41*) on the Devon ice sheet in the Canadian Arctic does not support the contention of a recent cooling trend for that area. Mitchell (*39*) indicates that, barring the emergence of unsuspected factors, the effects of CO_2 will ultimately prevail over those of particulate matter. If so, consumption of the total fossil fuel reserves alone could increase the mean earth temperature by several degrees Celsius.

Manabe and Wetherald (*42*) suggest that the effects of warming in the polar regions is significantly greater than for the typical atmosphere of lower latitudes. The polar amplification of warming can potentially affect the density stratification of the oceans. The vertical density stratification of the modern oceans into a deep cold layer, a pycnocline, and a surficial warm layer, is caused by the cold polar regions where ice-age conditions yet remain. In the polar regions, cold dense waters descend and migrate equatorially along the ocean bottom; these waters constitute the cold bottom layer. Turekian (*43*) has noted that the structure of the oceans can be maintained only if there is a continuous supply of each type of water to give continuing definition to the water masses; the structure would otherwise be lost by the process of random mixing. Warming of the polar regions, and ultimately of the waters which now descend to form the cold bottom layer, would alter the density stratification of the oceans. Eriksson (*44*) noted that a 1°C increase in surface temperature in regions of deep water would increase the atmospheric CO_2 content by about 4.2 percent. The modern oceans contain about 60 times the amount of CO_2 in the atmosphere and, if only 5 percent of the deep oceanic waters were to release their excess CO_2, the atmospheric content would increase by 25 percent, an amount larger than that estimated to result from combustion of the fossil fuels for the next 30 years (*36*). Thus, it is obvious that warming of the polar regions could have great impact on the climate. The combination of human-generated CO_2 and that liberated from the oceans could trigger "greenhouse" conditions of major porportions and potentially within a relatively short time span. Broecker (*45*) suggests that, by the first decade of the next century, global temperatures may be warmer than any in the last 1000 years. He maintains that the natural cooling trend of the past few years will reach a minimum in the next decade or so and that then the onset of CO_2-induced warming may present us with a "climatic surprise" in the form of dramatic climatic warming.

Climatic warming, in addition to thermal damage to animal reproductive systems, can have a potentially great impact on life by inducing accelerated melting of the polar ice caps. Emiliani (*46*) suggested "About 11,600 years ago, the North American ice sheet underwent a sudden collapse followed by rapid melting." He estimates that the period of flooding associated with the melting occurred about 12,000 to 10,000 years ago, peaking about 11,600 years ago. He noted (*47*) that the accelerated rise in sea level was on the order of decimeters per year. Present day surging or collapse of polar ice masses (or both) and the consequent rapid rise in sea level could be beyond the capacity of humans to easily adjust to it. Thus, the combined negative thermal effects on animal life and the flooding associated with melting of the ice caps signal potential catastrophy ahead if the increasing atmospheric content of human-generated CO_2 is not brought under control.

A critical problem for humans is to avoid arriving inadvertently at a critical threshold that might trigger an abrupt accelerated warming of the climate beyond their capacity to control, or to adapt to, it. The duration of such a "greenhouse" would, in human terms, last an interminable period, and its impact on life would be incalculable. Animals today are generally adapted to relatively cool conditions, as were faunas prior to the terminal Mesozoic extinctions. A sudden climatic warming could potentially impose on us conditions comparable to those that terminated a geologic era.

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Higher Order Structure of Simian Virus 40 Chromatin

Histone H1 is responsible for the condensation of intranuclear viral DNA-protein complexes.

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The DNA in the nuclei of all eukaryotic cells is packaged by association with histone proteins into chromatin fibers consisting of a linear array of particles termed ν-bodies (*1*), nucleosomes (*2*), or platysomes (*3*). Each nucleosome contains about 140 base pairs of DNA complexed with a pair of each of the four histone types H2A, H2B, H3, and H4 (*4*, *5*). The nucleosomes are connected by DNA linkers varying in length between about 30 and 70 base pairs, depending on the source of the tissue investigated (*4*). The fifth type of histone, H1, is not part of the nucleosome proper and is probably bound to the linker regions between adjacent particles (*6*, *7*). The DNA helix is coiled around the outside of the nucleosomes, giving rise to a flexibly jointed chain of repeating units (*5*, *8*). Chromatin fibers vary in appearance in the electron microscope, depending on the conditions employed during preparation. When nuclei are lysed on the specimen grid at very low ionic strength, the nucleosomes are well separated and alternate with segments of uncoiled DNA (*1*, *2*, *9*); this structure is referred to as the "beads-on-a-string" conformation. Frequently, however, chromatin fibers prepared by gentle methods and spread at low ionic strength are in a less extended state and

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