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10

Scientific Methodologies in Collision

The History of the Study of the Extinction of the Dinosaurs

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INTRODUCTION

The extinction of the dinosaurs is a major topic in modern paleontology, and indeed in a variety of disciplines that touch on the history of the earth and the history of life. It has also become a major theme in popular accounts, in newspaper and TV reports of science, and in museums. However, this has not always been the case.

About 70 years ago, the extinction of the dinosaurs was regarded as a minor hiccup in the progression of life, no more significant than, say, the extinction of the labyrinthodont amphibians, or the origin of the mammal-like reptiles. It acquired a certain notoriety in the 1950s and 1960s because of its popular appeal, and a vast array of hypotheses was presented, many of them rather bizarre in retrospect. The methods of research and the criteria of hypothesis testing during these years were often very loose.

Finally, in the 1970s and 1980s, major advances in paleobiological methodology and in geochemical and astrophysical research focused strong attention on the question, both from scientists and from the press. The three phases of study of dinosaurian extinction this century may be designated very broadly as follows: (1) the nonquestion phase (up to 1920); (2) the dilettante phase (1920–1970); (3) the professional phase (1970 onward).

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These three phases are not temporally exclusive, but are based on the majority of publications on the subject each year. General opinions and approaches to the question of the extinction of the dinosaurs have changed in a progressive way from phase 1 to phase 2 to phase 3, and clearly the majority of scientists have followed the broad trends. However, a number of individuals approached this subject in new ways long before the majority of researchers did. For example, Nopcsa (1911, 1917) was considering reasons for dinosaurian extinction in a "dilettante" way long before this became the common approach, in the 1930s and 1940s. At the other end of the spectrum are those individuals who persisted in the old way long after the main body of their science had moved on. So, for example, several paleontologists in the 1950s and 1960s regarded the extinction of the dinosaurs as a nonquestion, while even today many regard this as a subject not capable, not worthy, of serious scientific analysis. On the other hand, several highly significant serious studies were carried out in the 1960s. Hence, the dates given above are only very approximate indications.

The aims of this chapter are to review these stages in the study of the extinction of the dinosaurs and to illustrate the key aspects of each with published examples. Most attention is given to the present, professional phase, the roles of biology and physics in the debate, and the role of the press.

THE NONQUESTION PHASE (1825–1920)

Early Nineteenth Century Views of Extinction

The extinction of the dinosaurs was not regarded as a major event by most 19th century scientists for two reasons. Before 1840, very few dinosaurs had been described, and their uniqueness had not been recognized, so that the early 19th century catastrophists did not focus their attention on them. After 1840, and the naming of the Dinosauria, catastrophism was replaced by uniformitarianism in geology, and Darwinian natural selection emphasized the gradual and continuous nature of extinction. It was assumed then that the dinosaurs had dwindled in a progressive fashion during the Cretaceous. Thus, most 19th century and early 20th century paleontologists did not regard the extinction of the dinosaurs as a particular problem.

The first dinosaurs were described in 1824 and 1825, but they were initially interpreted simply as curious giant lizards. The idea of extinction at the species or the genus level was generally accepted by 1825, and there seemed to be little unusual in finding a few such curious extinct reptiles. The theological arguments of the 18th century, that to admit the possibility of extinction was to accuse God of having made a mistake in Creation, were no longer made (Mayr, 1982; Bowler, 1984; Buffetaut, 1987), since pragmatic arguments against extinction had been effectively rebuffed. Discoveries of mammoths and mastodons from 1750 onward convinced many that there were extinct species. Nevertheless, as late as 1771, Thomas Pennant could write about these fossil elephants, "as yet the living animal has evaded our search; it is more than possible that it yet exists in some of those remote parts of the vast new continent, unpenetrated as yet by Europeans" (Pennant, 1771). New discoveries of the remains of large fossil animals that had never been found alive—the giant ground sloth, the giant Irish deer, giant cattle, and the much older plesiosaurs and ichthyosaurs—allowed Cuvier and others to demonstrate the reality of extinction to the satisfaction of most savants by 1825.

Cuvier's work on fossil vertebrates from 1799 onward convinced him that many large mammals had become extinct in the not too distant past. He was also able to demonstrate successive earlier faunas of vertebrates and invertebrates in the Tertiary sediments of the Paris Basin. Cuvier invoked a catastrophic explanation for the extinction of these earlier faunas:

> Life in those times was often disturbed by these frightful events. Numberless living things were victims of such catastrophes: some, inhabitants of the dry land, were engulfed in deluges; others, living in the heart of the sea, were left stranded when the ocean floor was suddenly raised up again; and whole races were destroyed forever, leaving only a few relics which the naturalist can scarcely recognise. (Cuvier, 1825, Vol. 1, p. 9.)

Cuvier did not, however, extrapolate from his theory of localized catastrophic extinctions to the global scale. He imagined that physical catastrophes acted within basinal areas only, since life must have survived elsewhere in order to provide the continuity of the fossil record.

Cuvier also expressed views on the vertebrates of the Mesozoic and Cenozoic. At that time (Cuvier, 1825), the dinosaurs were barely known, and the only Mesozoic reptiles were aquatic forms—Jurassic crocodilians, ichthyosaurs, and plesiosaurs, Cretaceous turtles, and older Permian lizardlike animals. Cuvier, then, argued that, until the end of the Mesozoic, vertebrates were essentially marine, or at most swamp-dwellers. He regarded the Tertiary mammals as the first fully dry-land forms. Cuvier recognized a major faunal change, then, at the Cretaceous–Tertiary (K–T) boundary, and he related it to a supposed major phase of regression when the great Mesozoic seas retreated.

The idea of a major shift in vertebrate evolution at the K–T boundary from the sea to the land was rejected by 1830 because of increasing evidence of terrestrial reptiles and mammals in the Mesozoic. Mantell (1831) heralded this in a popular paper entitled, "The geological age of reptiles," and this transition from an Age of Reptiles to an Age of Mammals has held sway ever since.

Buckland (1823) and others more explicitly extrapolated Cuvier's ideas to develop the fully catastrophist geology in which truly global calamities had occurred. Buckland developed his catastrophist hypotheses from his studies of mammal bones in Pleistocene caves. He argued that these "relics of the Flood" had been wiped out by a universal deluge, and extrapolated this back to cover earlier major faunal replacements. Critics of catastrophism, such as Fleming (1826), pointed out that most of the mammals in the Pleistocene caves could have been hunted to death by early humans, and he also indicated that earlier extinctions might also have been caused by predators. Increasing knowledge of the fossil record led to the view by 1849 that at least 29 catastrophes were needed (Bourdier, 1969), each corresponding to a major stratigraphic boundary.

The causes of these catastrophes were not clear, but Buckland wrote, in reference to the sudden change in climate after the last catastrophe (the Flood), "What this cause was, whether a change in the inclination of the earth's axis, or the near approach of a comet, or any other cause or combination of causes purely astronomical, is a question the discussion of which is foreign to the object of the present memoir" (Buckland, 1823, pp. 47–48). These remarkably modern-sounding speculations gave way later to the proposal that the cooling earth had induced the major catastrophes (Buckland, 1836).

The noncatastrophist view was presented by Lyell (1832). He also regarded extinction as important, but more at the species level than necessarily globally. His view was that the species present at any time depended on the environmental conditions, and when such conditions became hostile, extinction inevitably followed.

In the 1820s and 1830s, extinction was viewed broadly in five ways. One view was that extinctions had occurred catastrophically a number of times when most species were wiped out (Buckland). Agassiz took this view one step further, and considered that all species were killed off at times of extinction, to be replaced by a fresh divine Creation. The third view was that extinctions occurred essentially at the local level owing to catastrophic physical effects (Cuvier). The fourth and fifth views were that extinctions occurred at the species level: because conditions became unsuitable (Lyell), or because the species had outlived its natural span.

The Dinosauria

By 1842, several genera of dinosaurs had been described, including *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus*, and in that year, Richard Owen recognized them as a distinctive order for which he introduced the term Dinosauria (Owen, 1842). Desmond (1979) has argued that Owen "invented" the Dinosauria for a very specific purpose that had little to do with descriptive paleontology, but a great deal to do with then-current views of the history of life. Between 1830 and 1855, there was an active debate about the idea of progression

in the history of life (Bowler, 1976). One view was that life had progressed from simple to more and more complex forms through time, as argued by Robert E. Grant and others, a view emanating from Buffon and Lamarck in the 18th century. Richard Owen opposed this simple notion, and sought to argue that the fossil record showed that degeneration was really the order of the day. Owen's new Dinosauria were described by him (Owen, 1842) as animals "which in structure most nearly approach Mammalia," and which "from their superior adaptation to terrestrial life, [may be concluded] to have enjoyed the function of such a highly organised centre of circulation in a degree more nearly approaching that which now characterizes the warm-blooded Vertebrata." Owen then used these "mammal-like" dinosaurs as direct evidence against the progressionist doctrines of Lamarck, Grant, and others, arguing that these earliest reptiles were the most advanced of all, and that the stock had degenerated to leave only the poor crocodiles, lizards, snakes, and turtles of today.

Owen (1842) argued that the Creator had chosen the Mesozoic Era as suitable for the dinosaurs because of its different atmospheric conditions. He believed that the air then was deficient in oxygen, and that this suited the dinosaurs. As reptiles, they had lower metabolic rates than the birds and mammals and could survive on less energy. He argued that oxygen levels rose during the Mesozoic and that the atmosphere became more "invigorating." The world then became uninhabitable for the huge saurians, and they died out, together with the giant marine reptiles and the flying pterosaurs. This argument was essentially circular, since Owen's evidence for low oxygen levels in the Mesozoic was simply the presence of dinosaurs and other prehistoric reptiles and the virtual absence of mammals and birds. He was explaining the presence of these early reptiles in Mesozoic rocks, very different from the dominant mammals and birds of today, in terms of precise matching by a benevolent Creator of living things and physical environments. He was not primarily trying to explain why the dinosaurs died out when they did—for him, that would have been a preordained event in the Creator's plan.

The progressionists and the supporters of degeneration models for the history of life did not regard the extinction of the dinosaurs as a particular issue, since there were so few of them known, and since they had far more pressing controversial issues to consider: the role of the Creator, the possibility of progression, transmutation (evolution), and so on. The progressionists would probably have interpreted the disappearance of the dinosaurs in terms of the isolated death and replacement of each of the three species then known. The nonprogressionists would have had a number of attitudes. Owen's view, that living reptiles are degenerate forms compared to the dinosaurs and other extinct reptiles, is an example of a theory of "discontinuous progression" (Bowler, 1976), in which a group is created and subsequently remains constant or declines. Another nonprogressionist view, espoused by Charles Lyell, was that living things matched the available habitats and they changed in response to physical changes. Thus, if conditions were right at some time in the future, the dinosaurs would return to inhabit the earth. In none of these views did suprageneric extinction really come into question.

Post-Darwinian Interpretations

The advent of the Darwinian theory of evolution by natural selection in 1859 and subsequent studies of phylogeny based on the fossil record by Haeckel, Huxley, Cope, Marsh, and others did not lead to any real discussion of mass extinctions, nor of the extinction of the dinosaurs in particular, as issues worthy of explanation. Indeed, Darwin (1859) saw the rapid disappearance of the ammonites at the end of the Cretaceous as probably as much to do with gaps in the fossil record as with any real phenomenon. In his paper "On the classification of the Dinosauria . . . ," Huxley (1870) noted the 16 genera of dinosaurs that were known at that date, spanning most of the Mesozoic Era, and based on discoveries in Europe, North America, Africa, and Asia. However, neither here nor elsewhere did he have any statements to make regarding their extinction. Marsh (1882) listed 46 dinosaur genera, and simply noted that they "continued in diminishing numbers to the end of the Cretaceous period, when they became extinct." In a later work, Marsh (1895) listed 68 genera of Dinosauria, but made no mention of their extinction at all.

In the late 19th and early 20th centuries, many paleontologists and biologists moved to non-Darwinian viewpoints, such as orthogenesis and finalism (Bowler, 1983). These models assumed that evolution was directed in some way and that there are regular patterns laid out along which evolution proceeds. The dinosaurs could be viewed as primitive lumbering beasts that *had* to give way to the more advanced mammals.

This then led to views of *racial senility*—the belief that certain long-lived groups of animals became old and their store of evolutionary novelty dried up. There was a parallel here between the life-span of an individual plant or animal and that of an evolutionary stock. Youth and early racial vigor were equated and seen to be just as inevitable as the old age and death of an individual and the racial senescence and eventual extinction of a major phylogenetic group. According to this view, the dinosaurs had been around for a long time, and they simply ran out of the genetic variability that was necessary to survive. The remarkable horns, frills, and spines of some late Cretaceous dinosaurs were occasionally cited as evidence for this racial senility, but in general the extinction of the dinosaurs remained a nonquestion.

Standard textbooks of general paleontology and vertebrate paleontology of the latter half of the 19th century and the first decades of the 20th, like the technical

papers, barely mention the extinction of the dinosaurs. Woodward (1898, p. 213) notes that "toward the close of the Mesozoic period [sic], . . . the Dinosaurs gradually became extinct," and later (p. 418), he states that the dinosaurs of the Cretaceous "became more specialised and almost fantastic just before they disappear." Von Zittel (1902, 1932), Hutchinson (1910), Jaekel (1911), Williston (1925), and Kuhn (1937) barely refer to this topic at all. Even into the 1950s and 1960s, several authors on vertebrate palaeontology continued virtually to ignore the extinction of the dinosaurs as a topic (e.g., von Huene, 1956; Orlov, 1964; A. H. Müller, 1968).

THE RISE OF INTEREST IN DINOSAURIAN EXTINCTION

I hope to show below that the study of the extinction of dinosaurs went through several phases in the 20th century. There was a long time, from about 1920 to 1970, when it was seen generally as a moderately interesting (and moderately amusing) topic, attracting only a few pages of scientific commentary each year. Then, after 1970, the level of interest increased, as did the rates of publication.

An attempt has been made to survey everything that has been published on the extinction of the dinosaurs in order to provide a basis for this survey of attitudes to this topic. I searched through my reprint collection, noting all technical papers, books, and popular works that dealt solely with the extinction of the dinosaurs, or that covered the Cretaceous–Tertiary (K–T) boundary event, or that devoted at least a few pages to the question. I supplemented these figures with references given in the various *Bibliographies of Vertebrate Palaeontology* (indexed 1928–1973). The total number of publications is 597. When these are plotted according to the year of publication (Fig. 1), it is clear that the rate of publication has been erratic, but has risen in the 1960s and again, dramatically, in the late 1970s and 1980s.

The total number of publications per annum range from 0 to 7 (mean 1.8) for 1910–1959, from 3 to 11 (mean 7.8) for 1960–1969, from 8 to 36 (mean 15.2) for 1970–1979, and from 21 to 85 (mean 50.1) for 1980–1986. Until 1960, most of the papers on the subject of the extinction of the dinosaurs were isolated publications that did not give rise to any real debate, but some, such as the work of Cowles and Bogert in the 1940s on reptilian thermoregulation (e.g., Cowles, 1945, 1949; Colbert *et al.*, 1946), gave rise to brief flurries of papers. In the 1960s and 1970s, more sustained work on dinosaurian biology and on paleoclimates led to a steady number of four or five papers every year.

The main boosts in rates of publication seem to have come from nondinosaurian quarters. Indeed, the annual number of papers devoted to the extinc-

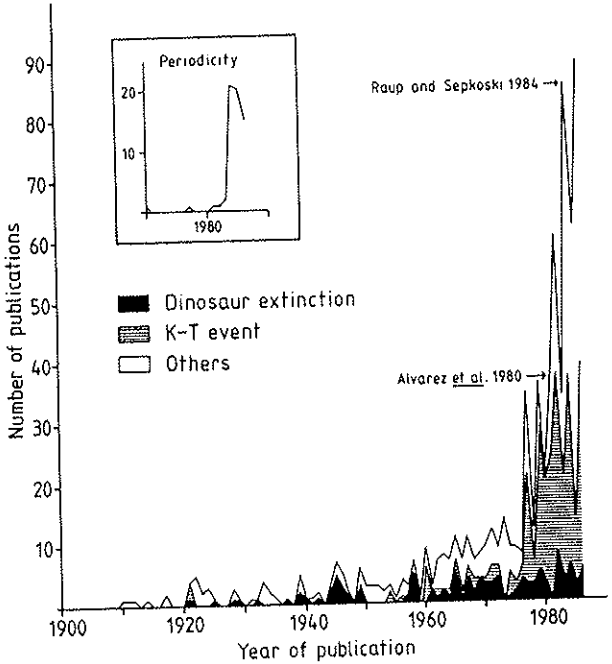

FIG. 1 The increasing rate of publication on dinosaur extinction, and the K-T event, from 1900 to 1986. Figures are plotted year by year, based on a compilation of publications that are concerned solely or mainly with dinosaur extinction, with the K-T event (including stratigraphic accounts), and with broad questions of extinction that relate to the K-T event (shown as "others"). Since 1980, most of the publications that fall in the last category concern the periodicity debate, and these are also plotted separately in the inset. Two seminal papers, in 1980 and 1984, are noted in the diagram.

tion of the dinosaurs alone has remained fairly constant (Fig. 1) at a figure between 0 and 8 per annum (mean 2.0 per annum in the 1960s; 2.8 per annum in the 1970s; 3.7 per annum in the 1980s). The total number of papers has been boosted by general interest in the K–T boundary events, by the rise of catastrophic extraterrestrial theories [particularly in the 1970s, and after the Alvarez *et al.* (1980) paper], and by the more recent interest in the periodicity of mass extinctions following the publication of Raup and Sepkoski (1984). Papers devoted essentially to the K–T event, but mentioning dinosaurian extinction, and papers about periodicity of mass extinctions are indicated separately in Fig. 1. It can be seen that these two categories constitute most of the overall increase in number of publications over the past few years. Overlaid on the general rising pattern are considerable annual fluctuations in number of papers; the peaks generally correspond to the publication of symposium volumes on the K–T event

(1960, 1979), on catastrophic models for mass extinction (1977, 1982 [two]), and on general aspects of mass extinction and diversity in the fossil record (1977, 1981, 1984 [three], 1985 [two], 1986 [three]).

The pattern of publication about the extinction of the dinosaurs may be divided, rather artificially, as has already been noted, into two main phases, the first running from about 1920 to 1970, and the second from 1970 to the present day.

THE DILETTANTE PHASE (1920–1970)

Racial Senility

During the early part of the 20th century, a small number of authors began to treat the extinction of the dinosaurs as an event, and as an event that was worth explaining. A typical early account was given by Arthur Smith Woodward (1910) in his address to the British Association for the Advancement of Science. He argued that the end of the dinosaurs was largely the result of racial senility. He pointed to the great spinescence, excess growth, and loss of teeth of the later dinosaurs as evidence. Loomis (1905, p. 842) wrote about the dorsal bony plates of the stegosaurs: "with such an excessive load of bony weight entailing a drain on vitality, it is little wonder that the family was short-lived." Racial senility as a theory of extinction held sway in some quarters for a long time. Schuchert (1924, p. 12) wrote: "when races are senile, or overspecialized, or are giants of their stocks, they are apt to disappear with the great physiographic and climatic changes that periodically appear in the history of the earth." These kinds of views were also expressed by Beurlen (1933) and Swinton (1939), for example, although they had been earlier rejected by Stromer von Reichenbach (1912), Hennig (1922), and Audova (1929).

Ideas of orthogenesis and racial senility of the dinosaurs were effectively demolished by the advent of the modern synthesis or neo-Darwinian model of evolution in the 1930s and 1940s. There was no longer any place for preordained patterns in this view of evolution. However, the notions of racial senility and of dinosaurs as inferior, lumbering monsters still live on, even if rather subconsciously, in the minds of scientists and the public alike. There seem to be two aspects of this lingering "crypto-orthogenesis": (1) we would like to believe in some form of progress as an optimistic view of the meaning and aim of life; and (2) we would like to believe that *Homo sapiens*, and mammals in general, are at the top of the tree, and that they somehow proved it by overwhelming the dinosaurs. Many evolutionists have wrestled with the idea of progress in neo-Darwinism (e.g., Julian Huxley, George Gaylord Simpson, Francisco Ayala, Theodosius Dobzhansky), or in punctuated macroevolution (e.g., Steven Stanley), but they have met with difficulties (Gould, 1985; Benton, 1987). It has proved virtually impossible to define "progress" in a modern view of evolution in anything other than a Whig manner [i.e., we can only see it from our present standpoint, and judge it with present values (Schopf, 1979)]. The lumbering dinosaur doomed to extinction is an insistent metaphor that refuses to die.

Biotic and Physical Factors

A number of authors, however, eschewed racial senility, and concentrated on biotic and physical factors that might have caused the extinction of the dinosaurs. Baron Franz Nopcsa was one of the first. He noted, for example (Nopcsa, 1911, p. 148), that the great amount of cartilage that he believed was necessary for growth to huge size "perhaps . . . was one of the causes for the rapid extinction of the Sauropoda." Later Nopcsa (1917, p. 345) summarized a number of views on the extinction of the dinosaurs: their "low power of resistance," their huge size, a shortage of food, or "a reduction in their sexual functions." He hints that a key factor may be the supposed "increase in function of the hypophysis" (pituitary gland) which was related to their very large body size. Secretions from the pituitary caused giantism, partly by the production of large masses of cartilage as precursors of bone, and partly by a form of acromegaly, or pathological excess thickening and overgrowth of limb bones and facial bones. He notes that "the increase in weight of the limbs in the dinosaurs recalls the eunuch condition."

William Diller Matthew (1921) presented early evidence for a model of dinosaurian extinction that involved gradual topographic change and progressive replacement by mammals. His study of the late Cretaceous and Paleocene in North America suggested that there was extensive mountain building and continental uplift. The dinosaur faunas, which were adapted to lowland and marsh situations, were displaced, and the placental mammals, which were adapted to upland zones, moved in. The new mammal faunas apparently had their origins in Asia. Nopcsa (1922, pp. 110–113) presented a modified version of this model, although he laid more stress on floral changes and the loss of marsh-type vegetation.

Other suggestions of these times were that climatic cooling was the cause (Jakovlev, 1922), that disease levels had risen markedly in the late Cretaceous dinosaurs (Moodie, 1923), that early mammals ate all of the dinosaur eggs (Wieland, 1925), or that volcanic eruptions were responsible (L. Müller, 1928).

Audova (1929) reviewed the whole question of the extinction of the dinosaurs in some detail in a remarkable 61-page paper in the short-lived German journal *Palaeobiologica*. He rejected racial senility and simple natural selection

as explanations, and focused on environmental change. His favored view, after surveying geological evidence on paleotemperatures and physiological evidence on the thermoregulation of modern reptiles, was that temperature had declined gradually, and that this acted directly on the dinosaurs and other Mesozoic reptiles by preventing proper embryonic development.

This approach typified much of the literature on dinosaurian extinction from the 1930s to the 1960s. Only a small number of papers was published on this topic, ranging from detailed investigations of dinosaurian physiology (e.g., Colbert *et al.*, 1946) and of patterns of diversity and extinction (e.g., Newell, 1952; Simpson, 1952), to brief suggestions and musings on the subject [e.g., de Laubenfels (1956): "Dinosaur extinction: One more hypothesis"].

A Survey of Theories for the Death of the Dinosaurs

It is not possible to discuss all of the hypotheses for dinosaurian extinction that were proposed during the dilettante phase. Jepsen (1964) listed 40 separate hypotheses, and there are doubtless many more than that. I summarize these hypotheses, together with key references where possible, and add numerous others that I have tracked down. In order to bring some semblance of order into this list, I have tried to classify the hypotheses under major headings. The list is probably more comprehensive than any survey yet published, but it is probably still far from complete.

In addition, I have attempted to distinguish the theories that were presented as deliberate jokes (marked with an asterisk) from those that were intended seriously (no asterisk), and those that, in retrospect at least, would appear to be testable at least in part (T) from those that seem to offer no hope of refutation (no T). Hypotheses marked (T?) were presented as speculative ideas which would require some assumptions and extensive testing, while those marked (T) were supported by some evidence and had been tested to some extent.

I. *Biotic causes*

A. "Medical problems"

1. Metabolic disorders
   - a. Slipped vertebral discs
   - b. Malfunction or imbalance of hormone systems
     - i. Overactivity of pituitary gland and excessive (acromegalous?) growth of bones and cartilage (Nopcsa, 1917)
     - ii. Malfunction of pituitary gland leads to excess growth of unnecessary and debilitating horns, spines, and frills
     - iii. Imbalances of vasotocin and estrogen levels leading to pathological thinning of egg shells (Erben *et al.*, 1979)

c. Diminution of sexual activity (Nopcsa, 1917)
d. Cataract blindness (Croft, 1982)
e. Disease: caries, arthritis, fractures, and infections reached a maximum in late Cretaceous reptiles (Moodie, 1923) (T?)
f. Epidemics
g. Parasites
h. AIDS caused by increasing promiscuity (F. Hoyle and N. C. Wickramasinghe, press reports, 1986–1987) (*)
i. Change in ratio of DNA to cell nucleus

2. Mental disorders
a. Dwindling brain and consequent stupidity (Raymond, 1939, pp. 148–150)
b. Absence of consciousness, and absence of the ability to modify behavior (Fremlin, 1979)
c. Development of psychotic suicidal factors (*)
d. *Paleoweltschmerz* (*)

3. Genetic disorders: excessive mutation rate induced by high levels of cosmic rays and/or ultraviolet light, leading to small population size burdened by a high genetic load, and consequent vulnerability to environmental shock (Tsakas and David, 1987)

B. Racial senility ("phylogeronty")
1. Evolutionary drift into senescent overspecialization, as evinced in gigantism, spinescence (e.g., loss of teeth, and "degenerate form") (e.g., Woodward, 1910; Schuchert, 1924; Beurlen, 1933; Swinton, 1939)
2. Racial old age [Will Cuppy (1964): "the Age of Reptiles ended because it had gone on long enough and it was all a mistake in the first place"] (*)
3. Increasing levels of hormone imbalance leading to ever-increasing growth of unnecessary horns and frills (see above)

C. Biotic interactions
1. Competition with other animals
a. Competition with the mammals—invasion of North America by Asian mammals (Nopcsa, 1922) (T?)
b. Competition with caterpillars, which ate all of the plants (Flanders, 1962)

2. Predation
a. Overkill capacity by predators (the carnosaurs ate themselves out of existence)
b. Egg-eating by mammals, which reduced hatching success of the young, and drained gene pools (Wieland, 1925; Thaler, 1965)

3. Floral changes
a. Spread of angiosperms and reduction in availability of gymnosperms, ferns, etc. This led to a reduction of fern oils in dinosaur diets, and to lingering death by terminal constipation (Baldwin, 1964) (*)
b. Floral change and loss of marsh vegetation (Nopcsa, 1922) (T?)
c. Floral change and increase in forestation, leading to a loss of habitat (Krassilov, 1981) (T?)
d. Reduction in availability of plant food as a whole
e. Presence of poisonous tannins and alkaloids in the angiosperms (Swain, 1976) (T?)
f. Presence of other poisons in plants (T?)
g. Lack of calcium and other necessary minerals in plants (T?)
h. Rise of angiosperms, and of their pollen, led to extinction of dinosaurs by terminal hay fever (Dott, 1983) (*)

II. *Abiotic (physical) causes*

A. Terrestrial explanations
1. Climatic change
a. Climate became too hot as a result of high levels of carbon dioxide in the atmosphere, and the "greenhouse effect" (McLean, 1978); extinction was caused by the high temperature and increased aridity (Colbert *et al.*, 1946), which either inhibited spermatogenesis (Cowles, 1945), unbalanced the male: female ratio of hatchlings (Ferguson and Joanen, 1982), killed off juveniles (Cowles, 1949), or led to overheating in summer, especially if the dinosaurs were endothermic (Cloudsley-Thompson, 1978) (T?)
b. Climate became too cold (Jakovlev, 1922; Nopcsa, 1922), and this led to extinction because it was too cold for embryonic development (Audova, 1929), because the endothermic dinosaurs lacked insulation and could not maintain a constant body temperature (L. S. Russell, 1965; Bakker, 1972, 1975), and they were also too large to hibernate (Cys, 1967), or, even if they were inertial homeotherms (i.e., not endotherms), the cold winter temperatures finished them off (Spotila *et al.*, 1973) (T?)
c. Climate became too dry (Colbert *et al.*, 1946) (T?)
d. Climate became too wet (T?)
e. Reduction in climatic equability and increase in seasonality (Axelrod and Bailey, 1968) (T)

2. Atmospheric change
a. Changes in the pressure or composition of the atmosphere [e.g., excessive amounts of oxygen from photosynthesis (Schatz, 1957)] (T?)
b. High levels of atmospheric oxygen, leading to fires following an impact (Anderson, 1987) (T)

c. Low levels of carbon dioxide removed the "breathing stimulus" of endothermic dinosaurs (Wieland, 1942) (T?)
d. Excessively high levels of carbon dioxide in the atmosphere and asphyxiation of dinosaur embryos in the eggs (Oelofson, 1978) (T?)
e. Extensive vulcanism and the production of volcanic dust (T?)
f. Poisoning by selenium from volcanic lava and dust (Koch, 1967) (T?)
g. Toxic substances in the air, possibly produced from volcanoes, which caused thinning of dinosaur egg shells (Erben, 1972) (T?)

3. Oceanic and topographic change
   a. Marine regression (Ginsburg, 1964; Newell, 1967; Hallam, 1984) (T)
   b. Lowering of global sea level leading to dinosaur extinction, on the assumption that they were underwater organisms (Wilfarth, 1949) (T?)
   c. Floods (T?)
   d. Mountain building, for example, the Laramide Revolution (Matthew, 1921) (T?)
   e. Drainage of swamp and lake habitats (Swinton, 1939) (T?)
   f. Stagnant oceans caused by high levels of carbon dioxide (Keith, 1983) (T)
   g. Bottom-water anoxia at start of transgression (Hallam, 1984) (T)
   h. Spillover of Arctic water (fresh) from its formerly enclosed condition into the oceans, which led to reduced temperatures worldwide, reduced precipitation, and a 10-year drought (Gartner and Keany, 1978; Gartner and McGuirk, 1979) (T?)
   i. Reduced topographic relief, and reduction in terrestrial habitats (Tappan, 1968; Bakker, 1977) (T?)
4. Other terrestrial catastrophes
   a. Sudden vulcanism (L. Müller, 1928; Vogt, 1972; McLean, 1982) (T?)
   b. Fluctuation of gravitational constants (T?)
   c. Shift of the earth's rotational poles (T?)
   d. Extraction of the moon from the Pacific Basin (T?)
   e. Poisoning by uranium sucked up from the soil (Neruchev, 1984) (T?)

B. Extraterrestrial explanations
1. Entropy; increasing chaos in the Universe and hence loss of large organized life forms
2. Sunspots
3. Cosmic radiation and high levels of ultraviolet radiation (Marshall, 1928; Schindewolf, 1958) (T?)
4. Destruction by solar flares of the ozone layer, and letting in ultraviolet radiation (Stechow, 1954; Reid *et al.*, 1976) (T?)

5. Ionizing radiation (Terry and Tucker, 1968; Ruderman, 1974; Yayanos, 1983) (T?)
6. Electromagnetic radiation and cosmic rays from the explosion of a near-by supernova (D. A. Russell and Tucker, 1971; D. A. Russell, 1971; Tucker, 1977) (T?)
7. Interstellar dust cloud (Renard and Rocchia, 1984) (T?)
8. Flash heating of atmosphere by entry of meteorite (de Laubenfels, 1956) (T?)
9. Oscillations about the galactic plane (Hatfield and Camp, 1970) (T?)
10. Impact of an asteroid (Alvarez *et al.*, 1980), a comet (Hsü, 1980), or comet showers (Hut *et al.*, 1987), which caused extinction by a number of postulated mechanisms (see below) (T)

Problems with the "Dilettante" Approach

Certain of these suggestions are perfectly reasonable ideas on the basis of present knowledge, but the obviously ludicrous nature of many has had two consequences. First, many paleontologists were led to believe that this approach was the only one to a study of mass extinction, and therefore that mass extinctions were of little importance to a serious paleontologist. Second, the whole approach was apparently so easy and such fun that everyone felt that they had the opportunity, if not the duty, to solve the question of why the dinosaurs died out. Many of the ideas listed above were presented by nonpaleontologists, and certainly most of the authors had little first-hand knowledge of the late Cretaceous fossil record of dinosaurs—hence the "dilettante" soubriquet. A large number of the theories, most of which were published in standard scientific journals by scientists who were no doubt expert in their own fields, show a remarkable relaxation of scientific standards. It was as if, at the mere mention of "dinosaur extinction," scientists breathed a sigh of relief and felt freed from the straitjacket of normal scientific hypothesis-testing.

I believe that there are four main arguments in support of this view.

1. Many of the authors demonstrated an ignorance of the basic paleontological data. For example, the hypotheses were often restricted to explaining why the dinosaurs alone died out, and no mention was made of the marine plankton, invertebrates, and other vertebrates that also disappeared. The question of the survivors of the K–T event was often not tackled: some scenarios were so extreme or catastrophic that it is hard to understand how the land plants, insects, frogs, lizards, snakes, crocodiles, turtles, birds, placental mammals, and so on were not detectably affected. Assumptions have also been made about the suddenness and synchroneity of the K–T event, facts that are not yet established in detail. In other cases, the timing of evolutionary events is wrong: for example, the flowering plants appeared 40–50 million years before the K–T event, the

mammals 150 million years before. Neither group could have caused the demise of the dinosaurs unless some other major evolutionary innovation in one or the other is called in.

2. A number of the theories apparently ignored basic biological principles. Could caterpillars really compete with herbivorous dinosaurs and eat all of the plants (Flanders, 1962)? Could dinosaurs really have been like automata, and unable to modify their behavior (Fremlin, 1979)? Is it possible to model a terrestrial biosphere in which a single biotic factor—epidemics, parasites, glandular malfunction, competition, predation—would lead to a complete ecological breakdown?

3. The mode of argumentation in many papers was by strong advocacy. "If it is assumed that dinosaurs were endothermic/that UV radiation was increasing during the Cretaceous/that caterpillars competed for food with plant-eating dinosaurs, then it follows that . . . . If it is further assumed that climates were becoming warmer, or colder, or drier, or wetter, then it follows that . . . ." It is rare to find careful weighing of evidence both for and against particular hypotheses.

4. There is the overall assumption by some authors that the whole subject is really just a parlor game, and not terribly serious. If a vertebrate paleontologist were to write an account of his or her theory of the origin of the universe or of a cure for cancer or of why caterpillars turn into butterflies, he or she would probably fail to get into print in a reputable scientific journal. However, most of the dilettante theories of the extinction of the dinosaurs were published in very reputable journals: *Science, Nature, American Naturalist, Journal of Paleontology, Evolution,* and so on.

Fortunately, scientific approaches to the question of the extinction of the dinosaurs, the K–T event, and extinctions in general have improved markedly over the past 20 years or so.

THE PROFESSIONAL PHASE (1970 ONWARD)

Background

The professional phase, in which investigators attempted to study the *pattern* of events at the K–T boundary in detail and to present testable hypotheses for the extinction of the dinosaurs, began in the mid 1960s. Sloan and Van Valen (Sloan, 1964, 1970; Van Valen and Sloan, 1972, 1977) attempted to analyze in detail the changes in vertebrate faunas across the K–T boundary in Montana. L. S. Russell (1965), Ostrom (1970), and Bakker (1971, 1972) began detailed studies of dinosaurian physiology and its relation to extinction, while

Axelrod and Bailey (1968) and others surveyed paleobotanical evidence of climatic change. Newell (1962, 1967), Valentine (1969, 1974), and Raup (1972) began general studies of the fossil record and the identification of mass extinctions. Catastrophic terrestrial and extraterrestrial scenarios for extinction were explored by Terry and Tucker (1968), Hatfield and Camp (1970), Crain (1967), Hays (1971), D. A. Russell and Tucker (1971), and Urey (1973), while explanations involving sea-level change were presented by Ginsburg (1964), Newell (1967), and others. Studies in the 1970s and 1980s have generalized from tackling the question of dinosaur extinction alone to the problem of the whole K–T event.

None of the proposed scenarios for K–T extinction, or the extinction of dinosaurs alone, is conducive to a single test. However, each entails a number of hypotheses, some of which are testable. For example, tests can be made of the pattern of a particular event [what was its duration, synchroneity worldwide, synchroneity for all taxa, what did and did not go extinct (any size, habitat, geographic correlations?), absolute and relative taxic effects] as well as many particular predictions made by the different scenarios (e.g., synchroneity of geochemical anomalies worldwide and with the extinction events, terrestrial and extraterrestrial sources of geochemical spikes, matching of timing of extinction events with other physical changes—topography, sea level, climate, chemical composition of seawater, temperature, atmospheric composition).

The Current Scenarios

The two main current scenarios to explain the K–T event (including the extinction of the dinosaurs) are the "gradualist" ecological succession model of Van Valen and others and the "catastrophist" extraterrestrial impact model of Luis Alvarez and others. Recent reviews include Van Valen (1984), Officer *et al.* (1987), and Hallam (1987) on the one side, and L. Alvarez (1983, 1987) and W. Alvarez (1986) on the other side of the issue. There is a considerable amount of evidence of different kinds for both scenarios: mainly paleontological and stratigraphic for the ecological succession model, and mainly geochemical and astrophysical for the extraterrestrial impact model. A "catastrophist" would envisage that the main extinction event lasted less than, say, 1 year, while a gradualist would regard the time span as somewhat more than, say, 1000 years (Van Valen, 1984). At these levels of distinction, the stratigraphy is not good enough to distinguish these time spans: although very different on a biological time scale, they are both geologically "instantaneous." Gradualists typically view the events as very long term; Sloan *et al.* (1986) suggests 7 million years for the extinction of the dinosaurs, with an acceleration in the rate in the last 0.3 million years. On the other hand, catastrophists have offered a range of timings.

Alvarez *et al.* (1980, p. 1099) showed durations of 1–5000 years for the whole event, with the main extinctions occurring in 1–10 years. However, Hsü (1984) has indicated that the knock-on effects of an impact could have lasted for more than 1000 years. Other analyses of the geochemical evidence have given durations of 0.1–0.25 million years (Rocchia *et al.*, 1984; Officer and Drake, 1985), figures that overlap the timings of many gradualist models.

The recent proposal of "stepwise extinction" patterns (Kauffman, 1986; Hut *et al.*, 1987) expands the time scale for extraterrestrially induced mass extinction to 3.5 million years or more. The proposal is that showers of comets arrive on the surface of the earth over intervals of typically 1–3 million years and that pulses of cometary impact cause a major global extinction event in three or four steps. This notion could be seen as a compromise between the instant catastrophe models and the gradualist models (Raup, 1986), a kind of additive long-term catastrophe. However, the stepwise extinction model derives from the extraterrestrial catastrophe models, and it explains mass extinctions by bolide impact, even if by several impacts spaced over 1–3 million years. This may be a necessary modification to the single-impact scenario, as a result of more detailed paleontological evidence, but it is in no way concordant with the earthbound gradualist models as regards the ultimate causation of extinction.

The "Gradualist" Models

The gradual ecosystem evolution model has been largely based on the progressive appearance of a mammal community (the *Protungulatum* Community) of distinctive Paleocene aspect in the last 300,000 years of the Cretaceous in Montana. As the mammals increase in abundance, the dinosaurs apparently decline until they disappear altogether (Van Valen and Sloan, 1977; Sloan *et al.*, 1986). This gradual replacement is explained in terms of diffuse competition between dinosaurs and mammals set against a major change in habitats. The lush subtropical dinosaur habitats were apparently giving way to cooler temperate forests which favored the mammals. It has been argued, however (Fastovsky and Dott, 1986), that the occurrence of dinosaurs and mammals in these particular cases are in channel sediments that cannot be dated as either Cretaceous or Paleocene.

The gradualist scenario has been extended to cover all aspects of the K–T events. Thus, Perch-Neilsen *et al.* (1982) note that the planktonic extinctions took 10,000 years, and various groups were already declining well before the boundary (Signor and Lipps, 1982). A variety of sea-bottom livers and filter-feeders died out, but sea-bottom predators and detritus-feeders were little affected. Extinction patterns of many marine groups show gradual declines throughout the late Cretaceous (Kauffman, 1984). Many gradualists also link the extinctions to marine regressions, as well as to declining temperatures (e.g., Ginsburg, 1964; Hallam, 1984, 1987). Gradualists also argue that the fact that many groups did not go extinct at the K–T boundary is hard to understand in the face of some of the devastating catastrophist scenarios (Buffetaut, 1984). On land, placental mammals, birds, lizards, snakes, crocodiles, champsosaurs, and tortoises and other freshwater organisms were little affected, and the plant record shows only modest and gradual changes (Hickey, 1981).

The "Catastrophist" Models

There is a huge literature now on the catastrophist extraterrestrial scenarios [for review see L. Alvarez (1983, 1987), Hsü (1984), W. Alvarez (1986)]. Basically, these postulate the impact of an asteroid or a comet on the earth. The impact caused mass extinctions either by throwing up a vast dust cloud which blocked out the sun and prevented photosynthesis (Alvarez *et al.*, 1980), by releasing cyanide (Hsü, 1980), by flash heating of the atmosphere on entry (Hsü, 1980), by excessive cooling of the atmosphere (Turco *et al.*, 1983), by releasing poisonous arsenic and osmium (Hsü *et al.*, 1982), by global wildfires (Wolbach *et al.*, 1985), or by a combination of darkness, extreme cold, and acid rain (Prinn and Fegley, 1987). These chemical and darkness models are postulated to explain most of the extinctions, while the extinction of the dinosaurs is often ascribed to thermal stress (Hsü, 1984).

The best evidence for the impact hypothesis is said by some to be the iridium (Ir) enhancement at the boundary, now recorded from nearly 60 locations worldwide (Alvarez, 1983), while others emphasize the importance of shocked quartz (Bohor *et al.*, 1987). Further evidence includes the occurrence of spherules in a few sections (Smit and Kyte, 1984), the similarity of the ratios of elements in boundary clays to those of chondrites, isotopic changes in O and C, and the actual presence of clays at the boundary in so many sections. A catastrophic extinction is also indicated by abrupt shifts in pollen ratios at some K–T boundaries (Tschudy *et al.*, 1984; Wolfe and Upchurch, 1986), as well as abrupt plankton and other extinctions in certain sections (Alvarez *et al.*, 1984*a;* Surlyk and Johansen, 1984).

In opposition to the catastrophist explanations, Van Valen (1984) and Hallam (1987) note the following criticisms: supposed extraterrestrial material below the K–T boundary, absence of the effects of elimination of stratospheric ozone, and problems with the darkness, cooling, acid rain, and other predicted results of impact. Officer and Drake (1985) and Hallam (1987) have further argued that the Ir could be of terrestrial volcanic origin, and that the Ir spikes lasted from 10,000 to 100,000 years. This idea of a relatively long Ir spike and the evidence for long-term decline of dinosaurs and certain marine groups could suggest a combination of the gradualist and catastrophist views in which certain groups were already declining when a bolide impact, or intense vulcanism, finished them off—a kind of "last-strawist" view point (cf. Buffetaut, 1984).

A CONFLICT OF STYLES

Physics versus Paleontology

The two main models for dinosaurian extinction are based on rather different kinds of data, as mentioned above: essentially paleontological and stratigraphic for the gradualist models, and mainly geochemical and astrophysical for the catastrophic models. This has inevitably meant that it has been hard for the proponents of one view to assess the evidence that supposedly favors the other view, as noted by Van Valen (1984). There is, however, apparently a more fundamental source of potential conflict between certain biologists and physicists, or "soft" scientists and "hard" scientists, as Raup (1986, p. 212) describes the pecking order.

The initial publications by Alvarez *et al.* (1980) were greeted skeptically by many paleontologists and geologists with long-term expertise on aspects of the K–T boundary. No doubt, they resented the intrusion into their subject by a group of physicists, and Luis Alvarez's (1983, p. 632) lengthy catalogue of his team's credentials (a physicist, two nuclear chemists, and a geologist) may not seem so unusual in view of this resentment: "suddenly I realised that we combined in one group a wide range of scientific capabilities, and that we could use these to shed some light on what was really one of the greatest mysteries in science—the sudden extinction of the dinosaurs." Walter Alvarez (1986) characterizes the two main geological prejudices that the impacters faced: a deeply-held belief in uniformitarianism and gradualism among many geologists, and detailed objections from paleontologists who saw no general large-scale instant catastrophe in the fossil record.

The crux of the dispute was outlined by Jastrow (1983, p. 152): "Professor Alvarez was pulling rank on the palaeontologists. Physicists sometimes do that; they feel they have a monopoly on clear thinking. There is a power in their use of math and the precision of their measurements that transcends the power of the softer sciences." The very titles of their papers could be seen to exemplify this: Alvarez *et al.* (1980) is "Extraterrestrial cause for the Cretaceous–Tertiary extinction—Experimental results and theoretical implications," while Alvarez (1983) is "Experimental evidence that an asteroid impact led to the extinction of many species 65 million years ago." Van Valen (1984, p. 122) commented that "to call [the Alvarez] evidence "experimental" is misleading propaganda; it refers merely to the fact that some observations were made in the laboratory rather than in the field, not to an active experimental test."

Luis Alvarez is surprisingly revealing throughout his 1983 paper. He is dismissive of his critics:

> I think the first two points—that the asteroid hit, and that the impact triggered the extinction of much of the life in the sea—are no longer debatable points. Nearly everybody now believes them. But there are always dissenters. I understand that there is even one famous American geologist who does not yet believe in plate tectonics. . . . People have telephoned with facts and figures to throw the theory into disarray, and written articles with the same intent, but in every case the theory has withstood these challenges. (Alvarez, 1983, p. 67.)

He later outlines the advantages of physics in comparison with paleontology: "The field of data analysis is one in which I have had a lot of experience" (Alvarez, 1983, p. 638), and "In physics, we do not treat seriously theories with such low *a priori* probabilities" (p. 640). He writes, "That is something that made me very proud to be a physicist, because a physicist can react instantaneously when you give him some evidence that destroys a theory that he previously had believed. . . . But that is not true in all branches of science, as I am finding out" (p. 629). Public utterances from Luis Alvarez about his "opponents" have frequently been more critical than these examples to the point of being libellous (e.g., Browne, 1988). Van Valen (1984, pp. 136–137) complains about how Alvarez "makes fun" of paleontologists, while Halstead (1986) and Archibald (1987) argue that it is wrong to argue that physics is necessarily better than paleontology—it is only different.

On the other hand, much of the distrust of the physicists by certain paleontologists has surely been unfounded, as Raup (1986, pp. 104–105) notes. He quotes at length a statement by Robert Bakker, a dinosaur paleobiologist, originally published in the *New York Times:*

> The arrogance of those people is simply unbelievable. They know next to nothing about how real animals evolve, live and become extinct. But despite their ignorance, the geochemists feel that all you have to do is crank up some fancy machine and you've revolutionized science. The real reasons for the dinosaur extinctions have to do with temperature and sea level changes, the spread of diseases by migration and other complex events. But the catastrophe people don't seem to think such things matter. In effect, they're saying this: "We high-tech people have all the answers, and you paleontologists are just primitive rock hounds."

The impact hypothesis, being a new idea, was initially at a disadvantage, as Raup (1986, pp. 195–197) argues. In order to displace the established wisdom, the impacters would have to present overwhelmingly strong evidence which would be much more critically scrutinized than the gradualists' evidence. Indeed, the catastrophist hypothesis was on trial in a way that the gradualist hypothesis was not. As Clemens *et al.* (1981) wrote of the proposed asteroid impact, "analyses of the paleobiological data suggest that such an event is not required to explain the biotic changes during the Cretaceous–Tertiary transition."

Styles of Argumentation

Elsabeth Clemens (1986) has analyzed the nature of the debate about "asteroids and dinosaurs," and she argues that there are many nonscientific undercurrents, such as styles of argumentation and the role of professional and popular publication.

First, the broadly-based research enterprise that has developed around the question of the extinction of the dinosaurs—geologists, paleontologists, chemists, physicists, astronomers—is not a single community. It is a body consisting of several factions, each going in different directions, and with very little communication, a point noted also by Van Valen (1984, p. 121). Clemens goes on to suggest that the Alvarez theory gained rapid notice and acceptance in many quarters because catastrophism in geology was becoming intellectually fashionable. Catastrophic theories for mass extinction had been made for years (e.g., de Laubenfels, 1956; Terry and Tucker, 1968; McLaren, 1970; D. A. Russell and Tucker, 1971; Urey, 1973; Reid *et al.*, 1976), but they contradicted the strictly gradualistic "geological dogma" of the day. However, the supernova theories (Terry and Tucker, 1968; D. A. Russell and Tucker, 1971; Béland *et al.*, 1977) probably did prepare the way for the asteroid theory.

Clemens (1986) argues that it was the mode of presentation of the Alvarez hypothesis that won it such wide attention and acceptance: "In a sense, the problem of the K–T boundary was framed so as to be amenable to the methods of particle physics." The bulk of the long 1980 paper (14 pages in all) was confined to the geological and physical evidence for an impact, and the physical results of the impact. The discussion of the biological results of the impact occupies only half a page. The paper was restricted then to a rather simple astrophysical hypothesis which could be tested in many ways, and the more complex aspects of stratigraphic imprecision and complexity of the evolution of biological communities were largely omitted. These issues had to be taken on board later, however. Alvarez *et al.* (1984*b*) allowed from 10^4 to 10^5 years for the overall length of time involved in the extinctions, while Alvarez *et al.* (1984*a*, p. 1135) note that "the paleontological record thus bears witness to terminal-Cretaceous extinctions on two time scales: a slow decline unrelated to the impact and a sharp truncation synchronous with and probably caused by the impact." The recent proposal of a stepwise extinction model involving comet showers (Kauffman, 1986; Hut *et al.*, 1987) extends the catastrophists' time scale to 3.5 million years or more. However, by 1984, the simplicity of the "instant-extinction" model of 1980 had ensured its general acceptance by many scientists. The later modifications noted here are seen by Clemens (1986, pp. 434, 441) as rather *ad hoc* qualifiers that tend to protect the impact theory from refutation by stratigraphic or paleontological evidence. The extension of the impact scenario to "nuclear winter" models in 1981, to theories of extraterrestrially induced periodic mass extinctions in 1983, and to the comet shower model of 1987 further helped to cement its professional and popular appeal.

The Role of the Professional and Popular Press

Clemens (1986) then goes on to argue that the nature of the professional and popular press has largely shaped the development of models of dinosaurian extinction since 1980. She points out that the 1980 *Science* article (Alvarez *et al.*, 1980) was twice as long as such articles usually are, and it was published in a prominent position, at the start of the issue. This one article gained a very wide readership, particularly in the United States, whereas articles that presented similar theories at the same time (Smit and Hertogen, 1980; Hsü, 1980; Ganapathy, 1980) were much less widely read (Hoffman and Nitecki, 1985). Since 1980, it has been alleged, pro-impact papers have been much favored by the editorial board of *Science*, and the argument has spilled over into the commentary and review sections of leading journals and into the newspapers (e.g., Lewin, 1983, 1985*a,b;* Maddox, 1985; Hoffman, 1985; Browne, 1985, 1988). Clemens (1986) suggests that the very format of publication has had a restrictive effect, since most of the debate has been carried on so far in the pages of *Science* and *Nature*, both of which normally publish only very short papers of three or four pages in length, and both of which require papers to be readily understandable to a wide audience. It is easier to present a simple hard view, such as the impact, she argues, than to argue about the imprecision of present methods for dating rocks, or the complexity of biological communities.

CONCLUSION

There are clearly a number of layers to the "catastrophists versus gradualists" controversy, ranging from purely scientific aspects, to matters of style, modes of argumentation, and the nature of publication. These all add spice to the controversy, but do not necessarily lead to progress toward its resolution. At present, it is hard to see how the two viewpoints will be fused, since there can only be one correct explanation for the extinction of the dinosaurs, whether "gradualistic," "catastrophic," or a bit of both. From its rather modest image only 20 or so years ago, the extinction of the dinosaurs has now become one of the most studied unique events in the history of life. Indeed, there is now a sort of "bandwagon" effect, as new topics are spawned—nuclear winter, periodicity, comet showers—which keep public interest alive, and which keep levels of funding for research at record levels. In general, the controversy has been good for the historical sciences (geology, paleontology), and it can only be hoped that the uncomfortable grating between physicists and paleontologists will eventually lead to a more satisfactory and fully cooperative research effort.

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REFERENCES

Alvarez, L. W., 1983, Experimental evidence that an asteroid impact led to the extinction of many species 65 million years ago, *Proc. Natl. Acad. Sci. USA* **80**:627–642.
Alvarez, L. W., 1987, Mass extinctions caused by large bolide impacts, *Phys. Today* **1987**(7):24–33.
Alvarez, L. W., Alvarez, W., Asaro, F., and Michel, H. V., 1980, Extraterrestrial cause for the Cretaceous–Tertiary extinction—Experimental results and theoretical implications, *Science* **208**:1095–1108.
Alvarez, W., 1986, Toward a theory of impact crises, *Eos* **67**(35):649, 653–655, 658.
Alvarez, W., Kauffman, E. G., Surlyk, F., Alvarez, L. W., Asaro, F., and Michel, H. V., 1984*a*, Impact theory of mass extinctions and the invertebrate fossil record, *Science* **223**:1135–1141.
Alvarez, W., Alvarez, L. W., Asaro, F., and Michel, H. V., 1984*b*, The end of the Cretaceous: Sharp boundary or gradual transition?, *Science* **223**:1183–1186.
Anderson, I., 1987, Dinosaurs breathed air rich in oxygen, *New Sci.* **116**(1585):25.
Archibald, J. D., 1987, Stepwise and non-catastrophic late Cretaceous terrestrial extinctions in the Western Interior of North America: Testing observations in the context of an historical science, *Mém. Soc. Géol. Fr.* **150**:45–52.
Audova, A., 1929, Aussterben der Mesozoischen Reptilien, *Palaeobiologica* **2**:222–245, 365–401.
Axelrod, D. I., and Bailey, H. P., 1968, Cretaceous dinosaur extinction, *Evolution* **22**:595–611.
Bakker, R. T., 1971, Dinosaur physiology and the origin of mammals, *Evolution* **25**:636–658.
Bakker, R. T., 1972, Anatomical and physiological evidence of endothermy in dinosaurs, *Nature* **238**:81–85.
Bakker, R. T., 1975, Dinosaur renaissance, *Sci. Am.* **232**(4):58–78.
Bakker, R. T., 1977, Tetrapod mass extinctions—A model of the regulation of speciation rates and immigration by cycles of topographic diversity, in: *Patterns of Evolution as Illustrated by the Fossil Record* (A. Hallam, ed.), pp. 439–468, Elsevier, Amsterdam.
Baldwin, E., 1964, *An Introduction to Comparative Biochemistry*, 4th ed., Cambridge University Press, Cambridge.

Béland, P., Feldman, P., Foster, J., Jarzen, D., Norris, G., Pirozynski, K., Reid, G., Roy, J. R., Russell, D., and Tucker, W., 1977, Cretaceous–Tertiary extinctions and possible terrestrial and extraterrestrial causes, *Syllogeus* **1977**(12):1–162.
Benton, M. J., 1987, Progress and competition in macroevolution, *Biol. Rev.* **62**:305–338.
Beurlen, K., 1933, Vom Aussterben der Tiere, *Nat. Mus.* **63**:1–8, 55–63, 102–106.
Bohor, B. F., Modreski, P. J., and Foord, E. E., 1987, Shocked quartz in the Cretaceous–Tertiary boundary clays: Evidence for a global distribution, *Science* **236**:705–709.
Bourdier, F., 1969, Geoffroy Saint-Hilaire versus Cuvier: The campaign for paleontological evolution (1825–1838), in: *Toward a History of Geology* (C. J. Schneer, ed.), pp. 36–63, Harvard University Press, Cambridge, Massachusetts.
Bowler, P. J., 1976, *Fossils and Progress: Paleontology and the Idea of Progressive Evolution in the Nineteenth Century*, Science History Publications, New York.
Bowler, P. J., 1983, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades around 1900*, Johns Hopkins University Press, Baltimore, Maryland.
Bowler, P. J., 1984, *Evolution: The History of an Idea*, University of California Press, Berkeley, California.
Browne, M. W., 1985, Dinosaur experts resist meteor extinction idea: Paleontologists say dissenters risk harm to their careers, *N. Y. Times* **1985**(29 October):21–22.
Browne, M. W., 1988, Debate over dinosaur extinction takes an unusually rancorous turn, *N. Y. Times* **1988**(19 January):19, 23.
Buckland, W., 1823, *Reliquiae Diluvianae*, Murray, London.
Buckland, W., 1836, *Geology and Mineralogy Considered with Reference to Natural Theology*, Murray, London.
Buffetaut, E., 1984, Selective extinctions and terminal Cretaceous events, *Nature* **310**:276.
Buffetaut, E., 1987, *A Short History of Vertebrate Palaeontology*, Croom Helm, London.
Clemens, E. S., 1986, Of asteroids and dinosaurs: The role of the press in the shaping of scientific debate, *Soc. Stud. Sci.* **16**:421–456.
Clemens, W. A., Archibald, J. D., and Hickey, L. J., 1981, Out with a whimper not a bang, *Paleobiology* **7**:293–298.
Cloudsley-Thompson, J. L., 1978, *Why the Dinosaurs Became Extinct*, Meadowfield, Shildon, England.
Colbert, E. H., Cowles, R. B., and Bogert, C. M., 1946, Temperature tolerances in the American alligator and their bearing on the habits, evolution and extinction of the dinosaurs, *Bull. Am. Mus. Nat. Hist.* **86**:327–274.
Cowles, R. B., 1945, Heat-induced sterility and its possible bearing on evolution, *Am. Nat.* **79**:160–175.
Cowles, R. B., 1949, Additional speculations on the role of heat in evolutionary processes, *J. Entomol. Zool.* **41**:3–22.
Crain, I. K., 1967, Possible direct causal relation between geomagnetic reversals and biological extinctions, *Bull. Geol. Soc. Am.* **82**:2603–2606.
Croft, L. R., 1982, *The Last Dinosaurs*, Elmwood Books, Chorley, Lancashire, England.
Cuppy, W., 1964, *How to Become Extinct*, Dover, New York.
Cuvier, G., 1825, *Discours sur les Revolutions de la Surface de la Globe, et sur les Changements qu'elles ont Produites dans la Regne Animal*, Dufour et d'Ocagne, Paris.
Cys, J. M., 1967, On the inability of the dinosaurs to hibernate as a possible key factor in their extinction, *J. Paleontol.* **41**:226.
Darwin, C. R., 1859, *On the Origin of Species by Means of Natural Selection*, Murray, London.
De Laubenfels, M. W., 1956, Dinosaur extinction: One more hypothesis, *J. Paleontol.* **30**:207–218.
Desmond, A. J., 1979, Designing the dinosaur: Richard Owen's response to Robert Edmond Grant, *Isis* **70**:224–234.
Dott, R. H., Jr., 1983, Itching eyes and dinosaur demise, *Geology* **11**:126.

Erben, H. K., 1972, Ultrastrukturen und Dicke der Wand pathologischer Eischalen, *Akad. Wiss. Lit. Mainz, Abh. Math.-Naturwiss, Kl.* **6**:193–216.
Erben, H. K., Hoefs, J., and Wedepohl, K. H., 1979, Paleobiological and isotope studies of eggshells from a declining dinosaur species, *Paleobiology* **5**:380–414.
Fastovsky, D. E., and Dott, R. H., Jr., 1986, Sedimentology, stratigraphy, and extinctions during the Cretaceous–Paleogene Tertiary transition at Bug Creek, Montana, *Geology* **14**:279–282.
Ferguson, M. W. J., and Joanen, T., 1982, Temperature of egg incubation determines sex in *Alligator mississippiensis, Nature* **296**:850–853.
Flanders, S. E., 1962, Did the caterpillar exterminate the giant reptile?, *J. Res. Lepidopt.* **1**:85–88.
Fleming, J., 1826, The geological Deluge, as interpreted by Baron Cuvier and Professor Buckland, inconsistent with the testimony of Moses and the phenomena of nature, *Edinb. Philos. J.* **14**: 205–239.
Fremlin, J., 1979, Dinosaur death: The unconscious factor, *New Sci.* **81**:250–251.
Ganapathy, R., 1980, A major meteorite impact on the earth 65 million years ago: Evidence from the Cretaceous–Tertiary boundary clay, *Science* **209**:921–923.
Gartner, S., and Keany, J., 1978, The terminal Cretaceous event: A geologic problem with an oceanographic solution, *Geology* **6**:708–712.
Gartner, S., and McGuirk, J. P., 1979, Terminal Cretaceous extinction: Scenario for a catastrophe, *Science* **206**:1272–1276.
Ginsburg, L., 1964, Les regressions marines et le problème de renouvellement des faunes au cours des temps géologiques, *Bull. Soc. Géol. Fr.* **6**:13–22.
Gould, S. J., 1985, The paradox of the first tier: An agenda for paleobiology, *Paleobiology* **11**:2–12.
Hallam, A., 1984, Pre-Quaternary sea-level changes, *Annu. Rev. Earth Planet. Sci.* **12**:205–243.
Hallam, A., 1987, End-Cretaceous extinction event: Argument for terrestrial causation, *Science* **238**: 1237–1242.
Halstead, L. B., 1986, The physicists and the palaeontologists in the battle of the giants, *Guardian* **1986**(5 September):11.
Hatfield, C. B., and Camp, M. J., 1970, Mass extinctions correlated with periodic galactic events, *Bull. Geol. Soc. Am.* **81**:911–914.
Hays, J. D., 1971, Faunal extinctions and reversals of the earth's magnetic field, *Bull. Geol. Soc. Am.* **82**:2433–2447.
Hennig, E., 1922, Paläontologische Beiträge zur Entwicklungslehre, *Tübinger Naturwiss. Abh.* **4**: 27–35.
Hickey, L. J., 1981, Land plant evidence compatible with gradual, not catastrophic, change at the end of the Cretaceous, *Nature* **282**:529–531.
Hoffman, A., 1985, [untitled letter], *Science* **230**:8.
Hoffman, A., and Nitecki, M. H., 1985, Reception of the asteroid hypothesis of terminal Cretaceous extinctions, *Geology* **13**:884–887.
Hsü, K. T., 1980, Terrestrial catastrophe caused by a cometary impact at the end of the Cretaceous, *Nature* **285**:201–203.
Hsü, K. T., 1984, A scenario for the terminal Cretaceous event, *Init. Rep. DSDP* **73**:755–764.
Hsü, K. T., He, Q., McKenzie, J. A., Weissert, H., Perch-Nielsen, K., Oberhänsli, H., Kelts, K., LaBrecque, J., Tauxe, L., Krähenbühl, U., Percival, S. F., Jr., Wright, R., Karpoff, A. M., Petersen, N., Tucker, P., Poore, R. Z., Gombos, A. M., Pisciotto, K., Carman, M. F., Jr., and Schreiber, E., 1982, Mass mortality and its environmental and evolutionary consequences, *Science* **216**:249–256.
Hut, P., Alvarez, W., Elder, W. P., Hansen, T., Kauffman, E. G., Keller, G., Shoemaker, E. M., and Weissman, P. R., 1987, Comet showers as a cause of mass extinctions, *Nature* **329**:118–126.
Hutchinson, H. N., 1910, *Extinct Monsters and Creatures of Other Days*, Chapman and Hall, London.

Huxley, T. H., 1870, On the classification of the Dinosauria, with observations on the dinosaurs of the Trias, *Q. J. Geol. Soc. Lond.* **26**:32–51.
Jaekel, O., 1911, *Die Wirbeltiere; Eine übersicht über die fossilen und lebenden Formen*, Borntraeger, Berlin.
Jakovlev, N. N., 1922, Vymiranye i Evo Prichiny kak Osnovnoy Vopros Biológii, *Mysl* **2**:1–36.
Jastrow, R., 1983, The dinosaur massacre: A double-barrelled mystery, *Sci. Digest* **1983**(September):151–153.
Jepsen, G. L., 1964, Riddles of the terrible lizards, *Am. Sci.* **52**:227–246.
Kauffman, E. G., 1984, The fabric of Cretaceous marine extinctions, in: *Catastrophes and Earth History*, (W. A. Berggren and J. A. van Couvering, eds.), pp. 151–246, Princeton University Press, Princeton, New Jersey.
Kauffman, E. G., 1986, High-resolution event stratigraphy: Regional and global bio-events, in: *Global Bio-events* (O. Wallisser, ed.), pp. 279–335, Springer-Verlag, Heidelberg.
Keith, M. L., 1983, Violent volcanism, stagnant oceans and some inferences regarding petroleum, stata-bound ores and mass extinctions, *Geochem. Cosmochim. Acta* **47**:2621–2637.
Koch, N. C., 1967, Disappearance of the dinosaurs, *J. Paleontol.* **41**:970–972.
Krassilov, V. A., 1981, Changes of Mesozoic vegetation and the extinction of dinosaurs, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **34**:207–224.
Kuhn, O., 1937, *Die fossilen Reptilien*, Borntraeger, Berlin.
Lewin, R., 1983, Extinctions and the history of life, *Science* **221**:935–937.
Lewin, R., 1985*a*, Catastrophism not yet dead, *Science* **229**:640.
Lewin, R., 1985*b*, Catastrophism not yet dead, *Science* **230**:8.
Loomis, F. B., 1905, Momentum in variation, *Am. Nat.* **39**:839–843.
Lyell, C., 1832, *Principles of Geology*, Murray, London.
Maddox, J., 1985, Periodic extinctions undermined, *Nature* **315**:627.
Mantell, G. A., 1831, The geological age of reptiles, *Edinb. New Philos. J.* **11**:181–185.
Marsh, O. C., 1882, Classification of the Dinosauria, *Am. J. Sci. (3)* **23**:81–86.
Marsh, O. C., 1895, On the affinities and classification of the dinosaurian reptiles, *Am. J. Sci. (3)* **1**: 483–498.
Marshall, H. T., 1928, Ultra-violet and extinction, *Am. Nat.* **62**:165–187.
Matthew, W. D., 1921, Fossil vertebrates and the Cretaceous–Tertiary problem, *Am. J. Sci. (5)* **2**: 209–227.
Mayr, E., 1982, *The Growth of Biological Thought: Diversity, Evolution and Inheritance*, Harvard University Press, Cambridge, Massachusetts.
McLaren, D. J., 1970, Time, life and boundaries, *J. Paleontol.* **44**:801–815.
McLean, D. M., 1978, A terminal Mesozoic "greenhouse": Lessons from the past, *Science* **201**: 401–406.
McLean, D. M., 1982, Deccan volcanism and the Cretaceous–Tertiary extinction scenario: A unifying causal mechanism, *Syllogeus* **39**:143–144.
Moodie, R. L., 1923, *Paleopathology*, University of Illinois, Urbana, Illinois.
Müller, A. H., 1968, *Lehrbuch der Paläozoologie*, Vol. III, Part 2, *Reptilien und Vögel*, Gustav Fischer, Jena.
Müller, L., 1928, Sind die Dinosaurier durch Vulkanausbrüche ausgeratet worden? *Unsere Welt* **20**: 144–146.
Neruchev, S. G., 1984, *Uranium and Life in the History of the Earth*.
Newell, N. D., 1952, Periodicity in invertebrate evolution, *J. Paleontol.* **26**:371–385.
Newell, N. D., 1962, Paleontological gaps and geochronology, *J. Paleontol.* **36**:592–610.
Newell, N. D., 1967, Revolutions in the history of life, *Spec. Pap. Geol. Soc. Am.* **89**:63–91.
Nopcsa, F., 1911, Notes on British dinosaurs. Part IV: *Stegosaurus priscus*, sp. nov., *Geol. Mag. (5)* **8**:143–153.

Nopcsa, F., 1917, Über Dinosaurier, *Centralbl. Mineral. Geol. Paläontol.* **1917**:332–351.

Nopcsa, F., 1922, On the geological importance of the primitive reptilian fauna in the uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallikobotion*), *Q. J. Geol. Soc. Lond.* **79**:100–116.

Oelofson, B. W., 1978, Atmospheric carbon dioxide/oxygen imbalance in the late Cretaceous, hatching of eggs and the extinction of biota, *Palaeontol. Afr.* **21**:45–51.

Officer, C. B., and Drake, C. L., 1985, Terminal Cretaceous environmental events, *Science* **227**: 1161–1187.

Officer, C. B. Hallam, A., Drake, C. L., and Devine, J. D., 1987, Late Cretaceous and paroxysmal Cretaceous–Tertiary extinctions, *Nature* **326**:143–149.

Orlov, J. A., 1964, *Osnovi Paleontologii (Amphibians, Reptiles, and Birds)*, Izdatelistvo, Moscow.

Ostrom, J. H., 1970, Terrestrial vertebrates as indicators of Mesozoic climates, *Proc. N. Am. Paleontol. Conv. D* **1970**:347–376.

Owen, R., 1842, Report on the British fossil reptiles, *Rep. Br. Assoc. Advan. Sci.* **1841**:60–204.

Pennant, T., 1771, *Synopsis of Quadrupeds*, Chester.

Perch-Nielsen, K., McKenzie, J., and He, Q., 1982, Biostratigraphy and isotope stratigraphy and the "catastrophic" extinction of calcareous nannoplankton at the Cretaceous/Tertiary boundary, *Spec. Pap. Geol. Soc. Am.* **190**:353–371.

Prinn, R. G., and Fegley, B., Jr., 1987, Bolide impacts, acid rain, and biospheric traumas at the Cretaceous–Tertiary boundary, *Earth Planet. Sci. Lett.* **83**:1–15

Raup, D. M., 1972, Taxonomic diversity during the Phanerozoic, *Science* **177**:1065–1071

Raup, D. M., 1986, *The Nemesis Affair*, Norton, New York

Raup, D. M., and Sepkoski, J. J., Jr., 1984, Periodicities of extinctions in the geologic past, *Proc. Natl. Acad. Sci. USA* **81**:801–805.

Raymond, P. E., 1939, *Prehistoric Life*, Harvard University Press, Cambridge, Massachusetts.

Reid, G. C., Isaksen, I. S. A., Holzer, T. E., and Crutzen, P. J., 1976, Influence of ancient solar-proton events on the evolution of life, *Nature* **250**:177–179.

Renard, M., and Rocchia, R., 1984, Extinction des espèces au Secondaire: La terre dans un nuage interstellaire?, *Recherche* **15**:393–395.

Rocchia, R., Renard, M., Boclet, D., and Bonte, P., 1984, Essai d'evaluation de la durée de la transition Crétacé/Tertiaire par l'evolution de l'anomalie en iridium; implications dans la recherche de la cause de la crise biologique, *Bull. Soc. Géol. Fr. (7)* **26**:1193–1202.

Ruderman, D. A., 1974, Possible consequences of nearby supernova explosions for atmospheric ozone and terrestrial life, *Science* **184**:1079–1081.

Russell, D. A., 1971, The disappearance of the dinosaurs, *Can. Geogr. J.* **83**:204–215.

Russell, D. A., and Tucker, W., 1971, Supernovae and the extinction of the dinosaurs, *Nature* **229**: 553–554.

Russell, L. S., 1965, Body temperature of dinosaurs and its relationships to their extinction, *J. Paleontol.* **39**:497–501.

Schatz, A., 1957, Some biochemical and physiological considerations regarding the extinction of the dinosaurs, *Proc. Penn. Acad. Sci.* **31**:26–36.

Schindewolf, O. H., 1958, Über die möglichen Ursachen der grossen erdgeschichtlichen Faunenschnitte, *Neues Jb. Geol. Paläontol. Monatsh.* **1958**:457–465.

Schopf, T. J. M., 1979, Evolving paleontological views on deterministic and stochastic approaches, *Paleobiology* **5**:337–352.

Schuchert, C., 1924, *Historical Geology*, Wiley, New York.

Signor, P. W., III, and Lipps, J. H., 1982, Sampling bias, gradual extinction patterns, and catastrophes in the fossil record, *Spec. Pap. Geol. Soc. Am.* **190**:291–296.

Simpson, G. G., 1952, Periodicity in vertebrate evolution, *J. Paleontol.* **26**:359–370.

Sloan, R. E., 1964, Paleoecology of the Cretaceous–Tertiary transition in Montana, *Science* **146**: 430.

Sloan, R. E., 1970, Cretaceous and Paleocene terrestrial communities of western North America, *Proc. N. Am. Paleontol. Conv. D* **1970**:427–453.

Sloan, R. E., Rigby, J. K., Jr., Van Valen, L. M., and Gabriel, D., 1986, Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation, *Science* **232**:629–632.

Smit, J., and Hertogen, J., 1980, An extraterrestrial event at the Cretaceous–Tertiary boundary, *Nature* **285**:198–200.

Smit, J., and Kyte, F. T., 1984, Siderophile-rich magnetic spheroids from the Cretaceous–Tertiary boundary in Umbria, Italy, *Nature* **310**:403–405.

Spotila, J. R., Lommen, P. W., Bakken, G. S., and Gates, D. M., 1973, A mathematical model for body temperatures of large reptiles: Implications for dinosaur ecology, *Am. Nat.* **107**:391–404.

Stechow, E., 1954, Zur Frage der Ursache des grossen Sterbens am Ende der Kreidezeit, *Neues Jb. Geol. Paläontol. Monatsh.* **1954**:183–186.

Stromer von Reichenbach, E., 1912, *Lehrbuch der Paläozoologie, Part 2*, B. G. Teubner, Leipzig.

Surlyk, F., and Johansen, M. B., 1984, End-Cretaceous brachiopod extinctions in the Chalk of Denmark, *Science* **223**:1174–1177.

Swain, T., 1976, Angiosperm–reptile coevolution, *Linn. Soc. Symp. Ser.* **3**:107–122.

Swinton, W. E., 1939, Observations on the extinction of vertebrates, *Proc. Geol. Assoc.* **50**:135–146.

Tappan, H., 1968, Primary production, isotopes, extinctions and the atmosphere, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **4**:187–210.

Terry, K. D., and Tucker, W. H., 1968, Biological effects of supernova, *Science* **159**:421–423.

Thaler, L. S., 1965, Les oefs des dinosaures du Midi de la France livrent le secret de leur extinction, *Sci. Prog. Nat.* **1965**(2):41–48.

Tsakas, S. C., and David, J. R., 1987, Population genetics and the Cretaceous extinction, *Génét. Sélect. Evol.* **19**:487–496.

Tschudy, R. H., Pillmore, C. L., Orth, C. J., Gilmore, J. S., and Knight, J. D., 1984, Disruption of the terrestrial plant ecosystem at the Cretaceous–Tertiary boundary, Western Interior, *Science* **225**:1030–1032.

Tucker, W. H., 1977, The effect of a nearby supernova explosion on the Cretaceous–Tertiary environment, *Syllogeus* **12**:111–124.

Turco, R. P., Toon, O. B., Ackerman, T. P., Pollack, J. B., and Sagan, C., 1983, Nuclear winter: Global consequences of multiple nuclear explosions, *Science* **222**:1283–1292.

Urey, H. C., 1973, Cometary collisions and geological periods, *Nature* **242**:32–33.

Valentine, J. W., 1969, Patterns of taxonomic and ecological structure of the shelf benthos during Phanerozoic time, *Palaeontology* **12**:684–709.

Valentine, J. W., 1974, Temporal bias in extinctions among taxonomic categories, *J. Paleontol.* **48**: 549–552.

Van Valen, L. M., 1984, Catastrophes, expectations, and the evidence, *Paleobiology* **10**:121–137.

Van Valen, L. M., and Sloan, R. E., 1972, Ecology and the extinction of the dinosaurs, *Proc. 24th Int. Geol. Congr.* **7**:214.

Van Valen, L. M., and Sloan, R. E., 1977, Ecology and the extinction of the dinosaurs, *Evol. Theory* **2**:37–64.

Vogt, P. R., 1972, Evidence for global synchronism in mantle plume convection, and possible significance for geology, *Nature* **240**:338–342.

Von Huene, F., 1956, *Paläontologie und Phylogenie der niederen Tetrapoden*, G. Fischer, Jena.

Von Zittel, K. A., 1902, *Text-book of Paleontology*, Vol. 2, Macmillan, London.

Von Zittel, K. A., 1932, *Text-book of Paleontology*, Vol. 2, 2nd ed., Macmillan, London.

Wieland, G. R., 1925, Dinosaur extinction, *Am. Nat.* **59**:557–565.

Wieland, G. R., 1942, Too hot for the dinosaur!, *Science* **96**:359.

Wilfarth, M., 1949, *Die Lebensweise der Dinosaurier*, E. Schweizerbart, Stuttgart.

Williston, S. W., 1925, *The Osteology of the Reptiles*, Harvard University Press, Cambridge, Massachusetts.

Wolbach, W. S., Lewis, R. R., and Anders, E., 1985, Cretaceous extinctions: Evidence for wildfires and search for meteoritic material, *Science* **230**:167–170.

Wolfe, J. A., and Upchurch, G. R., 1986, Vegetation, climatic and floral changes at the Cretaceous–Tertiary boundary, *Nature* **324**:148–152.

Woodward, A. S., 1898, *Outlines of Vertebrate Palaeontology for Students of Zoology*, Cambridge University Press, Cambridge.

Woodward, A. S., 1910, Presidential Address to Section C, *Rep. Br. Assoc. Advan. Sci.* **1909**:462–471.

Yayanos, A. A., 1983, Thermal neutrons could be a cause of biological extinctions 65 Myr ago, *Nature* **303**:797–800.