Giant Meteor Impacts and Great Eruptions: Dinosaur Killers?

Previously overlooked evidence challenges the impact and volcanic scenarios of dinosaur extinction

by Gregory S. Paul

The idea that the impact of a giant asteroid or comet can wipe out a large portion of the Earth's fauna and flora and clear the way for new, different organisms has generated both great enthusiasm and controversy (Alvarez et al. 1980, 1988, Alvarez 1983, 1986, 1987, Silver and Schultz 1982). An extension of this concept proposes that comet showers are the force behind pulses of extinction and renewal every 26–50 million years (Davis et al. 1984, Hut et al. 1987, Rampino and Stothers 1984, Raup and Sepkoski 1984, Whitmire and Jackson 1984). An alternative scenario offers giant periodic volcanic eruptions as the cause of extinction (Courtillot et al. 1988, Cox 1988, Duncan and Pyle 1988, McLean 1988, Officer et al. 1987). It has even been suggested that giant impacts or comet showers may combine with or trigger periods of intense volcanism to create global catastrophes (Alvarez 1986, Cox 1988, Officer et al. 1987, Rampino and Stothers 1988).

The various hypotheses of impact and volcanic events have been used to explain the extinction of dinosaurs and their flying pterosaur relatives approximately 65 million years ago. In the geologic record this corresponds to the boundary between the Cretaceous and Tertiary periods (the K-T boundary), at the end of the Mesozoic era. However, the evidence provided by a series of natural tests challenges both the impact and volcanic scenarios for dinosaur extinction. Multiple giant impacts and periods of supervolcanism earlier in the Mesozoic appear to have had no discernible effect on the dinosaurs and pterosaurs of the time. This evidence, part of which is based on old data, has been virtually ignored. This article is a brief examination of the problem; only dinosaurs and pterosaurs are considered in detail.

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The impact hypothesis

The premise that a giant meteorite, or a cluster of them, hit the earth at the K-T boundary rests on the worldwide layer of sediment containing anomalously high concentrations of iridium and other noble metals, usually found at low concentrations on Earth, along with grains of split quartz and other associated microscopic particle debris. No giant crater has yet been found to correspond with the layer, although some smaller craters dating from about that time may represent a simultaneous cluster hit (Alvarez et al. 1988). Hut et al. (1987), Kerr (1987), and Sharpton and Burke (1987) also cite the existence of craters as evidence for a comet shower at that time, but the noble metal record does not yet confirm this interpretation. Alvarez et al. (1988) hint at sedimentary evidence for two closely timed impacts at the K-T boundary. Evidence for a very large tsunami at the K-T boundary has also been used to support the impact hypothesis (Bourgeois 1988), although such waves may have arisen from volcanic or seismic activity.

Those arguing for intense volcanism as the cause of extinction also cite the anomalous layer at the K-T boundary (Officer et al. 1987), especially its high iridium concentration. But many scientists dispute whether the layer's distinctive particle debris could have been formed by a terrestrial explosion. Increasing evidence indicates that the vast basalt flows of India, known as the Deccan traps, formed at the end of the Cretaceous (Courtillot 1988, Cox 1988, Duncan and Pyle 1988, Rampino and Stothers 1988).

Just what the environmental effects of such impacts and volcanism would be is a complex, often contradictory matter. Climatic models of the nuclear winter expected to result from a modern mass nuclear war have been used.

In general, scientists have proposed meteorite impact to cause a global false winter perhaps three to six months long. The tremendous explosion of the impact would have projected a massive cloud of microscopic debris into suborbital trajectories. Within an hour the earth would have been enshrouded, blocking any sunlight or warmth from reaching the surface (Silver and Schultz 1982). The fairly consistent density of the cloud and further atmospheric mixing would have made the effect globally uniform, so the site of the impact would not be critically important.

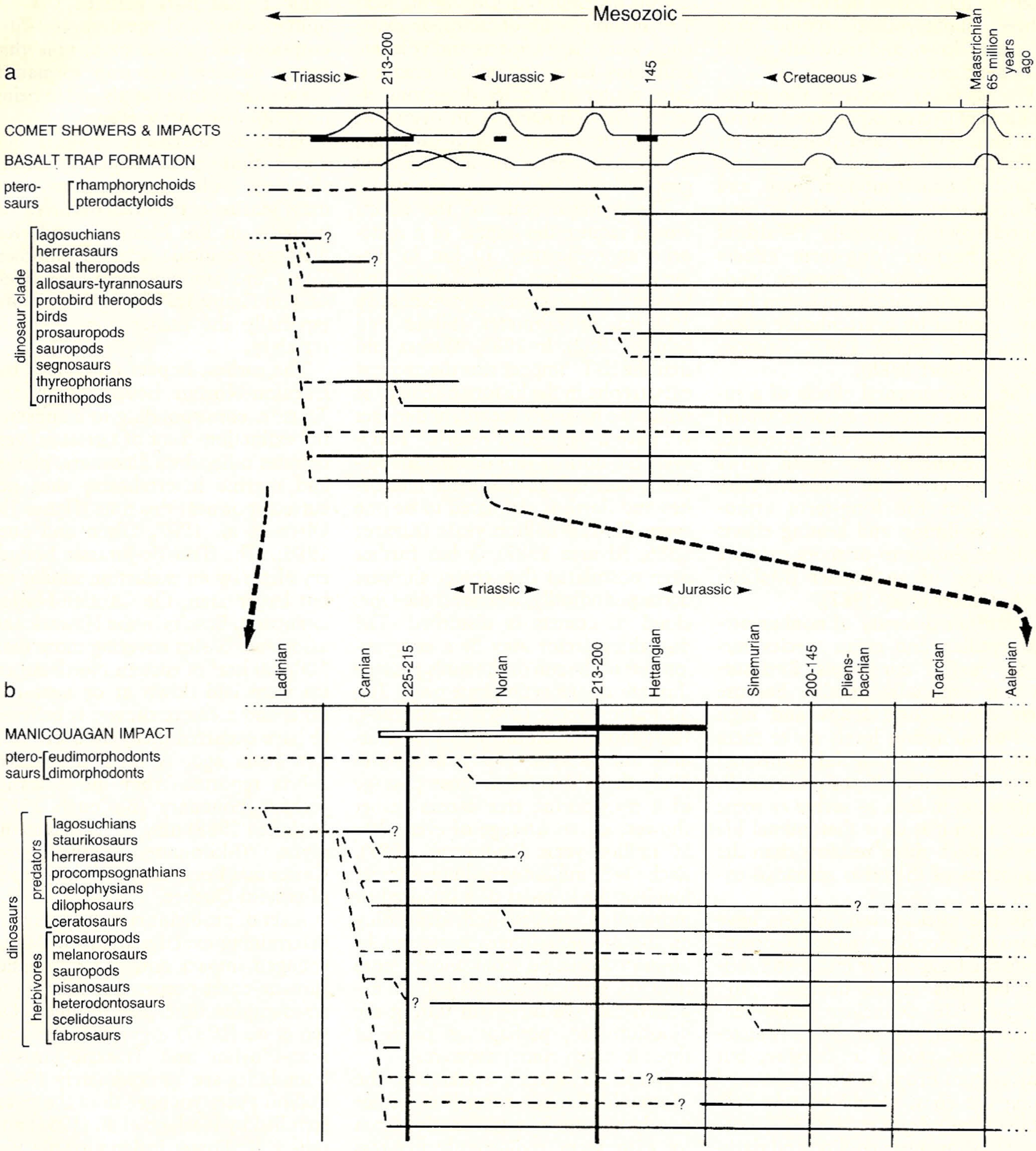

Figure 1. a. A simplified chart of meteoritic impacts, possible showers, super eruptions, and the major pterosaur, dinosaur, and bird groups during the Mesozoic; ages in millions of years ago. Possible formation times of three known craters 70–80 km in diameter are indicated by solid bars below the oscillating line charting comet showers. Note that the times for the showers and eruptions cover dating uncertainties; each event lasts 0.3–3.0 million years. **b.** A closer look at the radiation of pterosaurs and dinosaur groups and the Manicouagan impact in the mid-Triassic to early Jurassic. The heavy bar indicates the radiometric date-range for the impact relative to Olsen et al. (1987) stratigraphic dates; the open bar indicates the same range relative to Harland et al. (1982) figures. Times of two apparent mass extinctions of nondinosaurian life are indicated by heavy lines. For both charts, the dates of group origins and extinctions are approximate. Question marks indicate especially questionable first and final appearances, dashed lines indicate supposed presence based on phylogenetic and temporal evidence, solid lines are documented in the fossil record, dotted lines indicate extent of a group beyond the chart's time limits. Distribution and phylogenetics in part after Paul (1984a,b, 1988b), Olsen and Sues (1986, except that lagosuchians are Ladinian, not Carnian), and Galton (1987). Data for extinction events are in part from Alvarez and Muller (1984) and Hut et al. (1987); comet shower data are from Alvarez and Muller (1984) and Hut et al. (1987); eruption data are from Cox (1988), MacDougall (in press), and Rampino and Stothers (1988).

Until the dust settled out of the atmosphere, photosynthesis would have been shut down, and snowfalls would have been extensive.

For years or centuries the entire globe might have experienced corrosive rain, severe water pollution, air pollution a thousand times worse than the harshest modern smog, and airborne toxic metals lethal to any nonburrowing animals (Waldorf 1988). Further long-term effects might have included massive wildfires, droughts, and a long-term heat wave created by a greenhouse effect (Prinn and Fegley 1987, Crutzen 1987, Waldorf 1988).

The environmental effects of a superexplosive volcanic eruption would grossly parallel those of a meteorite impact. Nonexplosive basalt flows would not create an extensive false winter, but the long-term atmospheric pollution and heating effects could be similar to or more extreme than those of an impact (McLean 1988, Officer et al. 1987).

Yet a fair diversity of nonburrowing reptilian and avian species survived the K-T conditions. Bird survival is especially notable because their rapid-action lungs and high food-consumption levels make them sensitive to environmental toxins and low food supplies. If postcrisis conditions were, in fact, as severe as some think, then it is clear that animal life can be much more resilient than the supporters of the crisis scenarios expect.

As the nuclear war models have improved, they have tended to downgrade the false winter into a still serious but less severe nuclear "fall" (Berger 1986, Schneider 1987, Schneider and Thompson 1988). A meteoric winter would be harsher, but temperature drops in the winter and along the coast would be relatively moderate. O'Keefe et al. (1988) note that the short-term cooling and darkening effects of an impact may also have been overestimated.

Evidence of Mesozoic impacts and volcanism

Skeletal remains of the first protodinosaurs appear approximately 235–230 million years ago in the Ladinian stage of the late Triassic (see Figure 1b for Triassic-Jurassic stages and dinosaur distribution). During the next 170 million years of dinosaur existence, were there impacts and volcanic eruptions large enough to create a false winter and other disastrous effects? The following is an overview, rather than a comprehensive analysis, of the often uncertain and complex geophysical information available.

The massive scale of the effects would require the impact of a meteorite approximately 10 km in diameter, expending 10^{29-30} ergs and blasting out a crater approximately 100 km in diameter (Silver and Schultz 1982). In 1983, Alvarez said that the K-T "impact was the greatest catastrophe in the history of Earth, of which we have any record, and in fact we have a very good record." However, the normal rate of random collisons between 10-kilometer meteorites and Earth is estimated to be one every 50–100 million years (Alvarez 1986, Alvarez 1987). It has further been postulated that comet showers occur periodically, whenever the Oort cloud of comets is disturbed. The disturbing factor may be a companion star of the sun or the sun's passage through the galactic plane every 26–30 million years (Davis et al. 1984, Rampino and Stothers 1984, Whitmire and Jackson 1984); it is more likely that the random close passage of a neighboring star causes comet showers on an average of every 30–50 million years (Hut et al. 1987). Each 1–3 million-year-long shower involves the impacts of a hundred or more minor objects and, depending on the shower's intensity, several 1–10-km objects. So from one to more than six giant meteorites can be expected to have hit Earth during the dinosaur era, perhaps as parts of three to seven comet showers.

Despite Alvarez's statement, the Mesozoic impact record is rather poorly known. The systematic search for craters and sedimentary markers of impacts is less than a decade old and is hampered by the many geological processes that destroy or hide the markers. Because basalt flows are larger, they are more readily preserved and located. Courtillot et al. (1988), McLean (1988), and Officer et al. (1987) have claimed that the Deccan traps, covering more than 500,000 km^2, may be the largest of these from the Mesozoic. Each volcanic period lasts perhaps 0.3–3.0 million years and involves 100–500 eruptions of various sizes; note that comet showers and trap formation are similar both in length and in being made up of multiple events.

There is increasing physical evidence that giant impacts, comet showers, volcanic eruptions, and mass marine extinctions occurred repeatedly in the Mesozoic and that they may coincide with one another. These are summarized chronologically in Figure 1a. The ages of events, especially the earlier ones, vary in certainty.

The earliest impact may mark the Carnian-Norian boundary in the Triassic, corresponding to a substantial extinction event of terrestrial vertebrates other than dinosaurs, plants, and marine invertebrates that occurred at or near this time (Figure 1b; Olsen et al. 1987, Olsen and Sues 1986). The Triassic-Jurassic boundary also saw an extinction similar to, but larger than, the Carnian-Norian extinction. Basalts in the Newark and associated basins covering more than 100,000 km^2 of eastern North America were laid down at or near this time, and a comet shower is believed to have occurred then, circa 210 million years ago. A layer of particle debris reported from the Triassic-Jurassic boundary (Boslough 1987, McLaren 1988) may be related to the giant, 70-kilometer Manicouagan Crater that lies in the hard shield rock of eastern Quebec.

A set of problems currently impairs determining exactly when the Manicouagan impact and other Triassic-Jurassic crises occurred in relation to stratigraphic time. For instance, Olsen et al. (1987) argue that the Carnian-Norian and Triassic-Jurassic boundaries are approximately 10–13 million years younger than the dates supplied by Harland et al. (1982) and others. Radiometric dates for the Manicouagan Crater cover a 19-million-year spread that straddles the two boundaries (Figure 1). That the Carnian-Norian extinction may have been gradual, with plants apparently failing 2 million years before animals, lessens the probability that it was caused by the Manicouagan event (Olsen and Sues 1986). The more sudden extinction and the anomalous debris layer at the Triassic-Jurassic boundary make it more likely that the Manicouagan meteorite fell then, in agreement with Olsen and Sues (1986) and Olsen et al. (1987), who first associated this impact with the extinction event.

The approximately 180-million-year-old Puchezh-Katunki crater in the middle Jurassic strata near Gorki, USSR, may be the result of a comet shower. With an 80-kilometer diameter, it is the biggest crater yet known from the Mesozoic (Silver and Schultz 1982). A particle debris layer and an iridium anomaly have been reported that are similar in age to the crater (Boslough 1987, McLaren 1988), and a modest marine extinction is attributed to this time. The South African Karoo basalts date from about 195–180 million years ago. Covering over 1,500,000 km^2, they appear to be much larger than the Deccan traps, and thicker too. At the middle to late Jurassic, extensive Antarctic and Tasmanian flows date from some 170–160 million years ago. The next comet shower may date from 160 million years ago. It also is contemporary with an iridium anomaly (McLaren 1988) and a modest depletion of marine life.

The 70-km Duolun Crater of Inner Mongolia, China, appears to date from the late Jurassic to early Cretaceous (Hsu 1987, McLaren 1988). In the Cretaceous, craters indicate that a shower was possible at circa 130 million years ago in the early half of the period. South America's approximately 130-million-year-old Parana traps, covering 1,200,000 km^2, are more extensive than the Deccan traps, and the 50,000-square-kilometer traps of southwest Africa are approximately the same age. A modest marine extinction occurred about this time as well. In the mid-Cretaceous, the 200,000-square-kilometer Indian Rajmahal basalts are some 110 million years in age. A seawater strontium spike indicates that a great impact occurred 100 million years ago (MacDougall 1988), whereas craters imply a comet shower. A major marine extinction occurred fairly close to this time.

Because all five Mesozoic comet showers are believed to be associated with worldwide extinctions of marine life and other organisms, they appear to include impacts approaching the K-T event in scale. The 70–80-kilometer Puchezh-Katunki and Manicouagan craters seem to have been formed during such showers, and they are in the same size and energy class as the supposed K-T collision (Schmidt and Holsapple 1982, and McLaren 1988). Indeed, the Triassic-Jurassic debris layer that may have been laid down by the Manicouagan impact has been claimed to be heavier than that at the K-T boundary (Boslough 1987). Because much of the world's land surface is unexplored for craters, it is unlikely that the three known giant Mesozoic continental craters are all that exist, or that they are the largest. Furthermore, the ocean basins are virtually unexplored for Mesozoic craters. Statistically they should have captured approximately three times more giant meteorites than the continents, although this assertion cannot be verified because of ocean plate subduction.

Therefore, the Mesozoic saw at least three impacts in the same class as the K-T impact, and it is plausible that there were many more. At least some of these giant impacts may have been part of five possible comet showers. Five volcanic periods approaching or exceeding the K-T eruptions are known from the Mesozoic, and they either coincide with or are close in time to the showers. Although tentative, the available data warrant investigation of the observed biological consequences of extraterrestrial encounters and terrestrial eruptions.

Figure 2. Jackal-sized *Coelophysis bauri* is the earliest well-known dinosaur, shown here in the petrified forest of late Triassic Arizona. It lived not long before a period of impacts and volcanism. Drawings: G. Paul

Effects of Mesozoic impacts and eruptions on dinosaurs

Meteorite and comet impacts and volcanic eruptions might adversely affect certain kinds of life, especially marine forms. But the extinction of the dinosaurs might have been separate and coincidental. We do not yet know if the dinosaurs' disappearance was because of a long-term depression in the rate of species formation rather than because of excessive rates of extinction. Some evidence suggests that dinosaurs had already disappeared when the K-T noble metal anomaly was laid down (Archibald 1987, Bohor et al. 1987). Others argue they were present afterward (Sloan et al. 1986), and Carpenter (1988) points to the lack of fossil evidence of a mass K-T dinosaur die-off.

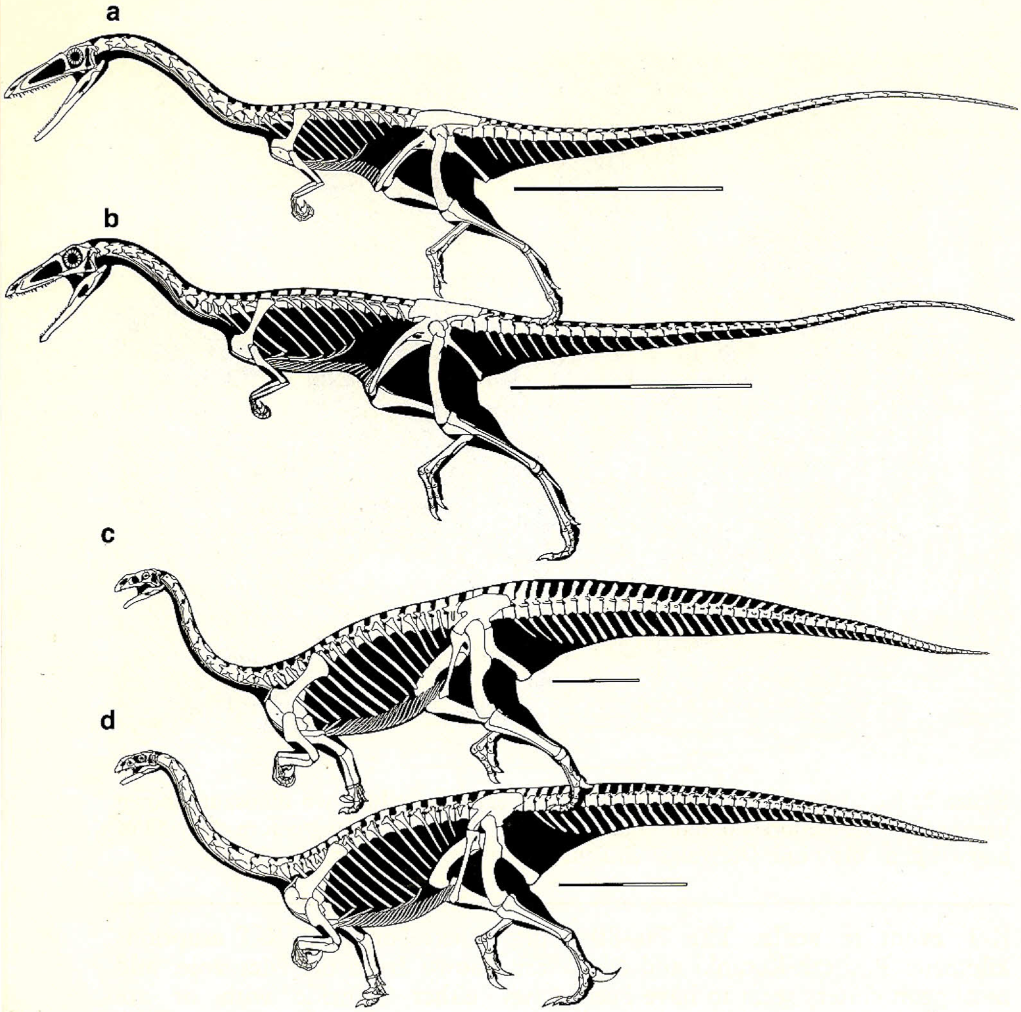

Figure 3. Two dinosaur genera that survived the late Triassic. The predaceous theropods *Coelophysis bauri* (a) of the North American late Carnian and *Coelophysis* (also *Syntarsus*) *rhodesiensis* (b) of the African Hettangian had been classified as two separate genera (Raath 1977), but the characteristics used to distinguish *Syntarsus* from *Coelophysis* have since been shown not to exist (Paul 1988b). A new taxon that can be assigned to *Coelophysis* has been found in Pliensbachian deposits (T. Rowe, 1986, personal communication, Balcones Research Center, Austin, Texas). The herbivorous prosauropods *Plateosaurus engelhardti* (c) from mid-Norian Europe and Hettangian-Pliensbachian *Massospondylus carinatus* (d) show no more variation in form than do some modern herbivore genera and may be one genus. *M. carinatus* comes from the same sediments as *C. rhodesiensis*. Scale bars equal 0.5 m.

Alvarez (1983) incorrectly used statistics to argue that articulated dinosaur bones should not show up immediately under the level of their extinction. This is because extensive lateral surveys of any level of sediments containing a reasonable number of fossils will periodically turn up dinosaur skeletons if they were present. Whether the chemistry of the sediments just below the heavy metal layer was suitable for preserving dinosaur bones is a matter of question (Leahy 1987, Retallack and Leahy 1986). Assertions that dinosaurs were alive after the K-T boundary will remain unconfirmed unless articulated fossils are found. If the dinosaurs' demise was not coincident with the heavy metal layer, then the extinction of the dinosaurs may not be a part of the general extinction of species at that time, contrary to long-standing assertions that it must be.

If the impact of a 10-kilometer meteorite or great volcanic eruptions extinguished all the dinosaurs at the K-T boundary, then at least some of the similar events earlier in the dinosaur era should have strongly affected populations of these animals. At the least, dinosaur populations should have suffered sudden and substantial depletions—in particular, extreme diversity and size bottlenecks reducing species to a handful of small-bodied examples, which then rebounded to form a new and radically different radiation.

The Triassic Manicouagan impact and the extinctions at the Carnian-Norian or Triassic-Jurassic boundary are the best documented at this time; hence, they will be examined in the most detail, along with the possible comet shower and Newark volcanism at that time. The key point is that dinosaurs and pterosaurs were definitely present before and after the Manicouagan and other impacts and also the laying of the Newark basalts.

Dinosaurs within range of the immediate blast, heat, and other direct results of the Manicouagan impact were undoubtedly destroyed, and resulting wildfires in any dry, well-vegetated areas within a 1500-kilometer radius may have incinerated more dinosaurs (Wolbach et al. 1985). Yet the dinosaur fossils preserved in the Newark Supergroup of sedimentary formations, sited 750–2000 km south of the impact point and directly among the basalt flows, show no significant disruption at about 220–190 million years ago (Olsen and Sues 1986).

Even more important, dinosaurs worldwide show no signs of having been affected during this time. Late Triassic and Early Jurassic dinosaur faunas are fairly well known from their skeletal remains and footprints so that general patterns of evolution can be mapped (Figure 1). By the mid-to-late Carnian—and before the earliest possible dates for the Manicouagan impact, the comet shower, or the Newark volcanism—small and big predatory species were already diverse (Figure 2). By the time of the Carnian-Norian boundary, herbivorous dinosaurs were also present, and although some dinosaur groups may have evolved at the beginning of the Norian, no notable extinctions took place at this time. The classic "coelophysian-prosauropod" communities, of the type illustrated in Figure 2, were in full swing before the middle of the Norian. Except for the apparent extinction of the staurikosaurs and herrerasaurs during the Norian, the afore-mentioned dinosaur groups continued throughout the Norian stage.

The coelophysian-prosauropod communities were once thought to have become extinct at the end of the Triassic, but more recently the upper formations bearing these faunas have been considered to be early Jurassic (Olsen and Galton 1977, Olsen and Sues 1986; Colbert [1986] still defends a Triassic age for these formations, but it is a minority view). So dinosaurs continued into the Hettangian stage of the Jurassic with remarkably little change in form, no known extinctions of any major groups, and an increase in diversity (Figures 1, 3, and 4). Essentially the same coelophysian-prosauropod community persisted into the Pliensbachian stage, after the latest possible dates for the Manicouagan impact and the shower and volcanism. Indeed, some of the early Jurassic dinosaurs are extremely similar to their late Triassic predecessors, and at least one or two genera definitely survived the age's extraterrestrial and terrestrial pyrotechnics (Figure 3). As the timing of the crises and the nature of the Triassic-Jurassic dinosaur fauna become better known, it is likely that more genera will be shown to have survived the Triassic.

Figure 4. *Coelophysis rhodesiensis* and its prey *Plateosaurus carinatus* in the dunes of early Jurassic Zimbabwe. These dinosaurs were components of the coelophysid-prosauropod community that dominated the latest Triassic and early Jurassic. Such a fauna very likely survived the crises at the boundary of the two periods.

The current data show that dinosaur and pterosaur speciation and extinction rates in the late Triassic and early Jurassic were roughly similar to other periods of their existence, although such comparison requires statistical confirmation beyond the scope of this paper. In the long run, the Triassic-Jurassic meteorites and eruptions at most moderately altered the faunas of that time.

The diversity patterns of dinosaurs and pterosaurs at times of other possible Mesozoic impacts and eruptions are less clear than at the Triassic-Jurassic boundary, but are still informative. The fossil record of middle Jurassic dinosaurs has been too poor to closely examine dinosaur diversity, but new Asian discoveries are improving the record. A number of dinosaur groups, including the giant sauropods, were present before, during, and after this time, and they seem to have remained similar in general makeup. About the time of the Duolun impact, a fauna of predatory dinosaurs, sauropods, stegosaurs, bipedal ornithopods, and other dinosaurs were in the midst of a spectacular, high-diversity radiation. The North American Morrison formation holds half a dozen or more genera of sauropods alone from just before, and probably immediately after, the end of the Jurassic. The fossil record deteriorates at the end of the Jurassic, and it becomes difficult to tell whether any mass extinctions occurred. But a diversity squeeze was unlikely in the early Cretaceous because, although more advanced bipedal ornithopods had become dominant and stegosaurs were rare by the latter part of the early Cretaceous, the larger predatory dinosaurs at this time were similar to late Jurassic forms (Paul 1988b), and sauropods were still an important component of the world fauna. It cannot be shown whether the number of dinosaur species suddenly declined approximately 100 million years ago, but most if not all dinosaur groups, and at least some genera (Figure 5a,b), continued through this time and to the end of the Cretaceous.

Overall, dinosaur group and species diversity was high throughout the Mesozoic, and remarkably few major dinosaur groups went extinct before the K-T boundary. Most of those that did were archaic groups that left descendents, and their loss cannot be conclusively tied to the various Mesozoic impacts and eruptions. Many groups survived for extremely long periods of time. For example, the middle or late Cretaceous coelophysian-clade theropods, segnosaurs, and basal ornithopods are little different from their Triassic–early Jurassic ancestors. Many more groups extend from the late Jurassic through the Cretaceous (megalosaurs, allosaurs, nodosaurs, the camptosaur-iguanodont-hadrosaur clade, and sauropods).

The uniquely large sauropods are especially informative. Although such giants are thought to be easily disrupted by ecological crises, sauropods were present from the early Jurassic to the final extinction and were always diverse. Even in the Maastrich-

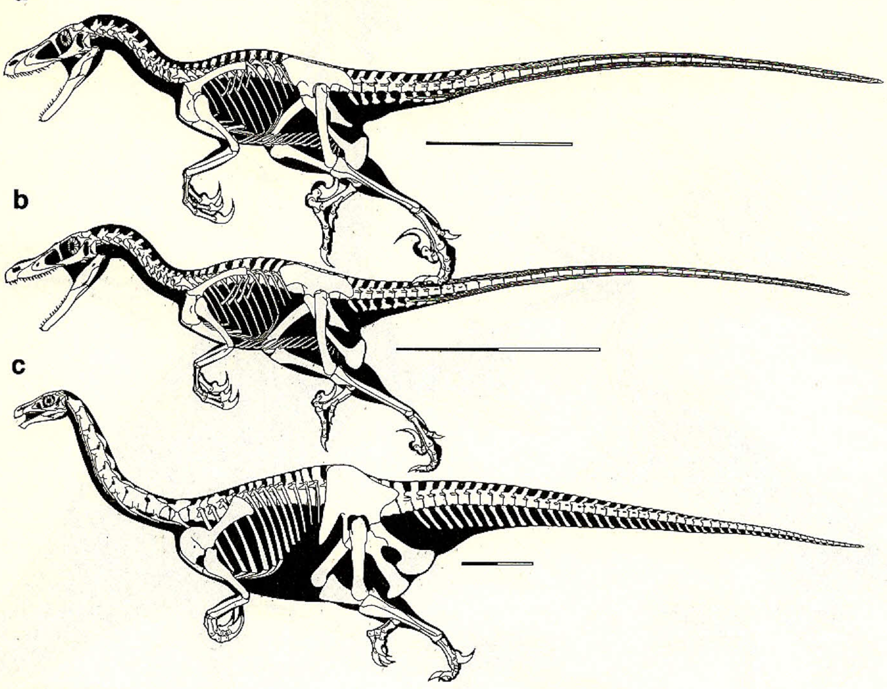

Figure 5. Two Cretaceous dinosaur genera that were similar to forms that survived the Triassic-Jurassic impacts and volcanics: **a.** The small, birdlike, theropod *Velociraptor antirrhopus* lived about 110 million years ago in North America, before a supposed comet shower and super eruption. **b.** Late Cretaceous, Asian *Velociraptor mongoliensis* lived well after these crises; however, species of *Velociraptor* were present in the North American Maastrichtian and did not survive the K-T event (Paul 1988b). (Compare with Figure 3**a**, **b**.) **c.** The Asian segnosaur *Nanshiungosaurus brevispinus,* restored with parts from other segnosaurs (compare with Figure 3**c**, **d**). Scale bars equal 0.5 m.

tian, the final stage of the Mesozoic, there were titanosaur, diplodocid, and perhaps camarasaur sauropods, groups that first appear in the late Jurassic.

After achieving high diversity, the rhamphorynchoid pterosaurs briefly overlapped at the late Jurassic with a diverse radiation of pterodactyloid pterosaurs before going extinct. Because the latter had a more dynamic, tailless design, the long-tailed rhamphorynchoids may have suffered from the competition. Pterodactyloid diversity sharply declined in the late Cretaceous (Unwin 1987).

Dinosaurs and pterosaurs not only avoided wholesale extinctions, there is good evidence that during evolution these animals never went through a catastrophic diversity and body-size bottleneck. Their continuing evolutionary health throughout the Mesozoic after repeated impacts and eruptions implies that dinosaurs and pterosaurs were more resilient to the kind of adverse climatic conditions brought on by the catastrophes, or that the severity of such events has been overstated, or both.

Dinosaurs as impact and eruption survivors

What might have helped dinosaurs to live through great meteoritic and volcanic experiences before the K-T impact? They maintained a high diversity in the face of 170 million years of often turbulent Earth history. Dinosaurs have often been portrayed as exceptionally vulnerable to sudden climatic changes, and this is a tacit assumption of the scenarios of Alvarez (1983, 1986), McLean (1988), and Officer et al. (1987) because other tetrapods survived the end of the Cretaceous. Many dinosaur species were big, so they had relatively small populations and low birthrates that might be easily upset. But large animals can go without food for longer periods than can small animals of similar physiology, and they can range further in search of food.

Impact scenario advocates often neglect to note that even deciduous plants would retain their leaves for an extended period during a long artificial night, that the evergreens common in the Mesozoic would have never dropped their leaves, and that twigs and bark are additional food sources. (Note that, whatever the time of an impact, some of the world's forests would happen to be in their growing seasons and, as Argyle [1986] notes, be too wet to burn immediately after an impact.) Even without new growth the digestible plant biomass available at the beginning of a meteoritic night would act as an energy reserve for many months, one superior to the less leafy flora available to large herbivores at the beginning of modern temperate winters. Large herbivores often feed in the dark. So it is possible that the food available at the beginning of a false winter, combined with the larger dinosaurs' ability to go without food for extended periods, could have allowed them to survive.

The great bulk of big dinosaurs also provided a degree of insulation against temperature fluctuations. The probability that dinosaurs had higher metabolic rates than is typical for reptiles (Morell 1987, Paul 1988a, b) implies further resistance to temperature fluctuations. McLean's (1988) assertion that high greenhouse temperatures hindered dinosaur reproduction neglects that dinosaurs probably regulated their nest temperatures at least as well as contemporary reptiles do. Indeed, the survival of both reptiles and mammals through the K-T and other crises suggest that the influence of physiology on the extinction problem is a subtle one.

Among the small dinosaurs, the predatory theropods were big-brained, agile, well-armed, certainly endothermic, and perhaps insulated (Paul 1988b). With their relatively large populations, they should have been able to survive post-explosion winters by feeding off the carcasses of dinosaurs that died in the blast, then preying on the other small vertebrates that survived the event. The good hearing and big eyes of small theropods would have allowed them to function in the dark of a false night. The importance of this point is enhanced by the modern consensus that birds are the direct descendents of theropods like *Velociraptor* (Paul 1988b), and birds survived the darkness of the K-T crisis. Rapidly reproducing small dinosaur species could have repopulated the world.

Perhaps the dinosaurs' greatest asset, conferred by their status as the dominant land animals, was their diversity in species and numbers of individuals. Alvarez (1983) argues that dinosaur populations were too resilient to be destroyed by almost any environmental trauma except a giant impact. But this argument can be turned around. If dinosaur populations at the time were reasonably healthy, it is difficult to see how even a series of impacts or eruptions could wipe out every population of every dinosaur species. Indeed, McKinney (1987) shows how the first in a series of impacts may eliminate those species vulnerable to such events, but leave a core of resistant species that will survive subsequent landings. The resilience of large modern tetrapods can be demonstrated by the east African rinderpest epidemic, which started in the 1890s. Masai, their cattle, cape buffalo, and wildebeest were in some cases nearly wiped out. They have all since recovered their abundant populations in protected areas (Sinclair and Norton-Griffiths 1979).

A critical source of dinosaur survivors may be found in the polar regions. Cretaceous sediments approximately 10° in latitude away from the north and south poles (at the time) have produced substantial remains of adult and juvenile dinosaurs, including extensive layers of bones (Brouwers et al. 1987, Douglas and Williams 1982, Russell 1973, 1984a). (Triassic-Jurassic polar dinosaurs have not been extensively sought.) Dinosaurs probably weathered dark, cold polar winter conditions, which parallel false winters in many regards (Paul 1988a). It is unlikely that dinosaurs migrated away from polar winters because the distances and energy expenditures involved were too great even for endothermic dinosaurs.

Although the Mesozoic poles were forested, there is growing climatological and geological evidence that Mesozoic polar winters were cold enough to form heavy ice and even highland glaciers (Brouwers et al. 1987, Frakes and Francis 1988, Schneider 1987). The polar coastal areas known to be inhabited by dinosaurs had extended periods of little or no daylight, temperatures ranging perhaps as low as $-11°$ C, and possible snowfalls. During rainstorms, windchill factors and evaporation would have driven effective skin temperatures far below freezing. The giant deinosuchian crocodilians are absent from late Cretaceous sediments north of Montana, perhaps because these big ectotherms were unable to tolerate the winter conditions from Alaska to Alberta (the latter perhaps was just below the arctic circle).

It is important to note that polar winters last nearly half a year, and winters at the two poles occur in opposite seasons. So dinosaur populations at one pole would have been wintering over at the time of an impact, and conditions would have been changed only modestly. Already used to the dark and coolness and to feeding on a flora that had gone into dormancy, they may have been able to act as reserve populations during a meteoritic winter (Brouwers et al. 1987, Paul 1988a).

At the opposite extreme of temperatures, a severe long-term greenhouse effect would only serve to boost polar winter temperatures to more comfortable levels. Summer temperatures might have been raised to uncomfortable but probably not lethal levels. Coastal dinosaur populations, whether polar or more equatorial, would have experienced lesser temperature plunges than would inland populations in a false winter, so they may also have acted as reserve populations.

The flying pterosaurs certainly had high metabolic rates. There is no reason to believe they were any more susceptible to catastrophic extinction than were their archosaur relatives, the birds.

Differences between the K-T and earlier crises

Differences between conditions at the K-T boundary and earlier Mesozoic crises may have made survival at the K-T more difficult in some ways and easier in others. Despite a higher overall diversity, the latest Cretaceous dinosaur fauna may have been in a long-term decline, in contrast to the smaller but radiating late Triassic dinosaur fauna. If so, the late Cretaceous dinosaur fauna may already have been under stress and may have been overly vulnerable to a sudden, detrimental event. Ironically, many who support sudden, extraterrestrial-induced extinctions argue against the late Cretaceous dinosaur population being in decline (Russell 1984b, Leahy 1987), while many critics of the impact scenario tend to support a gradual decline.

Further, although the late Maastrichtian dinosaurs were fairly diverse in North America, where they formed three distinct, habitat-limited faunas (Lehman 1987), each of the three faunas seem less diverse than preceding faunas found in similar habitats (Archibald 1987, Carpenter 1983, Paul 1988b, Sloan et al. 1986). For example, the *Alamosaurus* fauna of the Maastrichtian, prefering seasonally dry habitat, consisted primarily of one sauropod species and one horned dinosaur species, fewer than the three or more sauropod and two stegosaur species common at most sites in the seasonally dry Morrison formation of the late Jurassic. Likewise, the coastal Maastrichtian *Triceratops* fauna was composed mainly of the one-horned form plus two less abundant duckbill species, well below the multitude of duckbill and horned dinosaurs that were common in the 75-million-year-old coastal Judith River formation of Alberta. If dinosaurs were in gradual decline in the late Cretaceous, the decline seems to have covered some 7–10 million years (Archibald 1987, Paul 1988b, Sloan et al. 1986), much longer than the 0.5–3 million years that comet showers or volcanic eruptions are supposed to last.

The Triassic–early Jurassic dinosaur fauna was a more globally uniform one than it was in the late Cretaceous because the latter period's continents were more separated and its faunas more isolated (Stanley 1986). The Cretaceous fauna may have been vulnerable to losing an isolated regional fauna to an impact and hence more liable to suffer disruption at the species-family level than would the Triassic–early Jurassic fauna.

On the other hand, a world fauna with high regional diversity should be less subject to total extinction than a more uniform one. The fact that the late Cretaceous fauna was more diverse than earlier ones could have made it less susceptible to disruption. Indeed, at 75 million years ago the world dinosaur fauna may have been at its all-time peak in diversity. Among other things it included tyrannosaurs, ostrich mimics, sauropods, little- to gigantic-horned herbivores, big duckbills and their smaller relatives, and assorted armored forms (Figure 6). Even at the K-T boundary 10 million years later, dinosaurs were more diverse than in the Triassic.

The late Cretaceous dinosaurs did not show drastic differences in survival abilities relative to earlier species. For example, small predatory dinosaurs of the late Cretaceous such as *Velociraptor* were similar to Triassic-Jurassic *Coelophysis* (Figure 3b) in basic form, except that the late Cretaceous predators were more closely related to birds that survived the end of the Cretaceous (Paul 1988b). Likewise, late Cretaceous segnosaurs were like the prosauropods that survived the Triassic-Jurassic events (Figure 3c, Paul 1984a).

Instead of the dinosaurs being different at the K-T and earlier events, perhaps differences in postcrises conditions were the key factors. The entire Mesozoic was a period of relative global warmth, compared to the cooler climates prevalent before and after the era (Stanley 1986). Perhaps the most notable difference between Triassic-Jurassic and late Cretaceous climates was the greater extent of coastal climes in the latter because of its more separated continents and more numerous interior ocean basins and seaways (Stanley 1986). Because coastal conditions moderate both the temperature declines of a false winter and the increases of a greenhouse effect, a late Cretaceous crisis would appear more survivable in this regard. Rather than the earth being different, varying angles of meteorite impact and clustered versus single hits may have altered the final ecological consequences. Current data is insufficient to measure these factors.

Conclusions

If dinosaur and pterosaur species were readily susceptible to extinction by a meteoritic impact, comet shower, volcanic eruption, or a combination thereof, then one would expect to find repeated diversity and size bottlenecks among the dinosaurs when such events happened in the Mesozoic. The observation that the dinosaur faunas survived various impacts and eruptions with no discernible losses and with a relatively progressive increase in diversity acts as a natural test that casts serious doubt on the idea that the late Cretaceous dinosaurs and the pterosaurs were extinguished by K-T events of similar magnitude.

Potential survival mechanisms include cold- and dark-adapted polar dinosaurs acting as reserve populations, the large number of dinosaur species, the toughness of many species, and the abundant populations of some species. Although some conditions at the end of the Cretaceous may have made dinosaurs somewhat more vulnerable than on previous occasions, other K-T conditions appear to have been in their favor.

Those advocating extraterrestrial objects or subterranean upwellings as the primary causes of dinosaur extinction must explain why dinosaurs wholly failed to survive an event similar in scale to ones they had earlier survived so well, or what made the earlier events so much more survivable than the last one. The repeated claims that the K-T crisis was exceptionally intense are not supported by hard evidence. To say that the K-T crisis was exceptionally intense because it killed off the dinosaurs is circular reasoning; stronger evidence is required. In reality, some of the Mesozoic traps and craters are larger than those known so far from the K-T boundary.

Advocates also need to establish that the long-term environmental conditions after giant impacts were extraordinarily harsh, yet that they were compatible with the survival of other nonburrowing animals. Arguments that periodic comet showers are the major, or even partial, cause for the destruction and subsequent renewal of world land faunas on a 26–50-million-year schedule are similarly questionable.

It may be found eventually that nonexplosive earthbound causes were responsible for most or all of the extinctions (Stanley 1986, 1987). Ex-

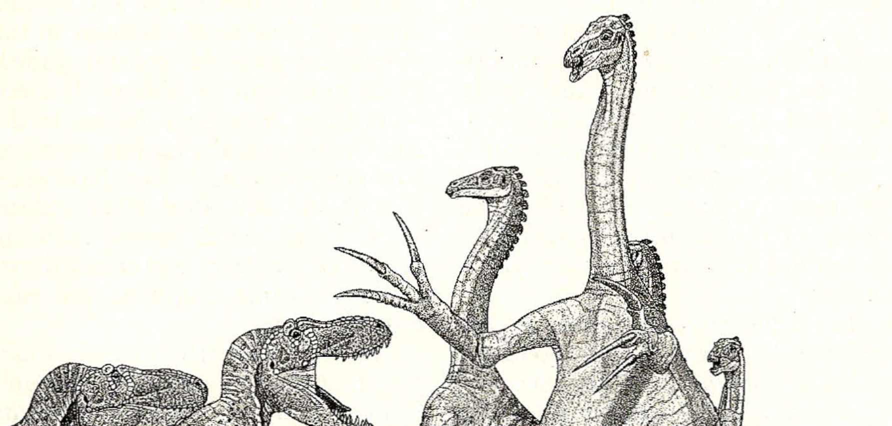

Figure 6. Two giants, *Tyrannosaurus bataar* and the segnosaur *Therizinosaurus cheliniformes,* were among the last dinosaurs in central Asia. Whatever the cause of their demise, no new dinosaurs replaced them.

tinction of dinosaurs and other species remains a poorly understood phenomenon, and the available data are often ambiguous and contradictory. Hence statements that one or another extinction scenario is the best are premature.

Recent press reports describe a 15-million-year-old meteorite crater 300 km in diameter in Czechoslovakia. If this crater exists, it raises further questions about the impact-extinction scenarios because a diverse assemblage of large mammals would have survived the enormous explosion creating the crater.

Most of the facts about dinosaur diversity and the Manicouagan and Puchezh-Katunki craters were known well before Alvarez et al. put forth their hypothesis in 1980. When the periodic comet showers were postulated as the reason for the dinosaurs' disappearance, there was no consideration of how little effect the showers had on earlier dinosaurs. Likewise, the Mesozoic basalt traps were documented long before it was suggested that one of them killed off the dinosaurs. The bones from Alaskan dinosaurs were discovered in 1961, although they did not receive attention until 1984, and reports of other polar dinosaurs were published in the early seventies. This critical evidence regarding the impact and eruptive extinction scenarios has been neglected by advocates and critics alike.

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