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Dinosaur Extinction: Past and Present Perceptions

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When I ask most schoolchildren what happened to the dinosaurs, they tell me that dinosaurs became extinct because a giant asteroid hit the Earth and instantly wiped them all out. When I then ask them if birds are related to dinosaurs, they most often answer yes, many saying that birds are dinosaurs. If they are then confronted with the quandary that if birds are dinosaurs and birds are alive today, how can dinosaurs be extinct, I am most often greeted with a stare or a grin. A very few respond that it was only the big dinosaurs on the ground that became extinct but birds did not. Although inelegant, these student answers are mostly correct.

Many adults do not grasp this distinction, mostly because they were raised to believe that dinosaurs and birds are not closely related, and that such a diverse group as birds that is unique in its mode of flight surely must be its own group. Most research and researchers have shown that birds and other dinosaurs are close kin; still, putting birds in a group with other dinosaurs is too much to swallow. What has happened in this apparent dilemma is that biological distinctiveness and evolutionary relationship have been confounded. Yes, birds are very distinct and in a number of ways unique, but we do not classify species on unique characteristics that they alone possess, but rather on derived characteristics they share uniquely with other species. For example, flight appears to be a character uniquely derived in birds, but feathers appears to be uniquely derived in birds as well as some of their nonflighted relatives that we call dinosaurs. This means that there is a group for birds, Aves; a more inclusive group, Theropoda, including Aves and a variety of both feathered and nonfeathered dinosaurs; and an even more inclusive group, Dinosauria, including theropods and other groups, such as sauropods, hadrosaurs, and ceratopsians.

This question of group, or more correctly, clade or lineage identification is an important issue for the study of extinction because we must precisely define a particular group of species, what biologists call a *taxon*, before we can study such issues as its demise. Thus, for Dinosauria we can say with considerable certainty that all onithischians (bird-hipped dinosaurs), all sauropods, and all theropods except for some uncertain number of bird species perished at or shortly following the Cretaceous/Tertiary (K/T) or Cretaceous/Paleogene (K/Pg) boundary. The rate at which this occurred, whether it was a global phenomenon, how many species were involved, and how other species were affected are all less well known and are the subjects of this chapter.

A final misconception that requires discussion is the quality of the fossil record immediately preceding and following the extinction of dinosaurs. One may believe that we possess a good global record of dinosaur extinction. This is unfortunately not the case. New studies in other parts of the world show promise, but in none of these do we have a good vertebrate fossil record up to and including the K/T boundary. The only region in the world where we do have good record is in the Western Interior of North America. Localities in New Mexico and Texas preserve some aspects of the K/T boundary fossil record, but by far the best records are from Alberta, Saskatchewan, Montana, and the Dakotas (Archibald, 1996, 2011).

Past Theories

Theories of the extinction of nonavian dinosaurs started appearing soon after they were discovered and named in the first half of the nineteenth century. Three of the better-known compilers of extinction theories were Glenn Jepsen in the 1960s, Alan Charig in the 1970s and 1980s, and Michael Benton in the 1990s. Depending on how one parses their lists, Jepsen (e.g., 1963) listed something like 48 theories in one long, paragraph-length sentence. The highest number of extinction theories claimed to have been complied were the 80 or so reported to Archibald (1996) by Alan Charig. Although Charig (1983, 1989) discussed various theories, an extensive list was not published. In 1990, Benton provided a much more methodically organized and referenced list of possible causes. He also provided opinions as to whether theories were "deliberate jokes," "speculative ideas," or "supported by some evidence." Table 43.1 is a slightly modified and updated version of Benton's tabulation. Again, exact numbers are somewhat difficult to compute, but Benton tabulates about 66 theories, not including 10 or so variations.

With so many theories, it is no wonder that dinosaur extinction remains one of the perennially hot topics concerning dinosaurs. I will not detail all the theories, but will provide a short synopsis of three of the more widely discussed. Even these three include a combination of factors listed in Table 43.1. Before turning to these current theories, it is worthwhile to examine what we know and what we think we know concerning the pace of dinosaur extinction--was it gradual, instantaneous, or something in between? The question of the pace of the extinctions has engendered debate second only to that surrounding the cause or causes of the extinctions.

Past and Present Evidence for and against Gradual Dinosaur Extinction

With the record of the extinction of dinosaurs currently limited to western North America, it is not surprising this is where researchers have most frequently turned to assess the speed at which dinosaurs became extinct. Two major questions are posed. The first question is whether the number of dinosaur species declined toward the later part of the Cretaceous, usually meaning the last 10 million years of the Cretaceous. The second is whether the number of species declined gradually, very rapidly, or somewhat in between during the time leading up to the end of the Cretaceous, usually the last days or months up to the last hundreds or tens of thousands of years of the Cretaceous.

In this section, I address what can be called the gradual arguments for these changes. Opinions vary on what happened to the number of dinosaur species during the last 10 million years of the Cretaceous (in the Western Interior). A widely held view is that the number of genera and

Table 43.1. Various theories of dinosaur extinction, mostly after Benton (1990) with modifications. Many of the sources for these theories can be found in Benton (1990).

I. Biotic causes
- 1. Medical problems
  - A. 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
      - ii. Malfunction of pituitary gland, leading 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
  - B. Diminution of sexual activity
  - C. Cataract blindness
  - D. Disease: caries, arthritis, fractures, and infections at maximum in Late Cretaceous reptiles
  - E. Epidemics
  - F. Parasites
  - G. AIDS caused by increasing promiscuity
  - H. Change in ratio of DNA to cell nucleus
  - I. Mental disorders
    - a. Dwindling brain and consequent stupidity
    - b. Absence of consciousness and ability to modify behavior
    - c. Development of psychotic suicidal factors
    - d. Paleo-weltschmerz
  - K. Genetic disorders: excessive mutation rate induced by high levels of cosmic rays or ultraviolet light, leading to a small population size burdened by a high genetic load, and consequent vulnerability to environmental shock
- 2. Racial senility (phylogeronty)
  - A. Evolutionary drift into senescent overspecialization, as evinced in gigantism, spinescence (e.g., loss of teeth, and degenerate form)
  - B. 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")
  - C. Increasing levels of hormone imbalance leading to ever-increasing growth of unnecessary horns and frills
- 3. Biotic interactions
  - A. Competition with other animals
    - a. Competition with the Asian mammals that invaded North America
    - b. Competition with caterpillars, which ate all of the plants
  - B. Predation
    - a. Overkill capacity by predators (carnosaurs ate themselves out of existence)
    - b. Egg eating by mammals, which reduced hatching success of the young and drained gene pools
  - C. Floral changes
    - a. Spread of angiosperms and reduction in availability of gymnosperms, ferns, etc., leading to a reduction of fern oils in dinosaur diets and lingering death by terminal constipation
    - b. Floral change and loss of marsh vegetation
    - c. Floral change and increase in forestation, leading to a loss of habitat
    - d. Reduction in availability of plant food as a whole
    - e. Presence of poisonous tannins and alkaloids in the angiosperms
    - f. Presence of other poisons in plants
    - g. Lack of calcium and other necessary minerals in plants
    - h. Rise of angiosperms and their pollen, leading to extinction of dinosaurs by terminal hay fever

II. Abiotic (physical) causes
- 1. Terrestrial explanations
  - A. Climatic change
    - a. Too hot because of high levels of carbon dioxide in the atmosphere and the "greenhouse effect"
      - i. High temperature and increased aridity
      - ii. Spermatogenesis inhibited
      - iii. Unbalanced male:female ratio of hatchlings
      - iv. Juveniles killed
      - v. Overheating in summer, especially if dinosaurs were endothermic
    - b. Too cold
      - i. Embryonic development inhibited
      - ii. Constant body temperature impossible to maintain by endothermic dinosaurs lacking insulation
      - iii. Hibernation during cold impossible due to size of dinosaurs
      - iv. Cold winter temperatures fatal even to inertial homeotherms (i.e., not endotherms)

c. Too dry
d. Too wet
e. Reduction in climatic equability and increase in seasonality

B. Atmospheric change
a. Changes in the pressure or composition of the atmosphere (e.g., excessive amounts of oxygen from photosynthesis)
b. High levels of atmospheric oxygen, leading to fires following an impact
c. Low levels of carbon dioxide, removing the "breathing stimulus" of endothermic dinosaurs
d. Excessively high levels of carbon dioxide, causing asphyxiation of dinosaur embryos in the eggs
e. Extensive vulcanism and the production of volcanic dust
f. Poisoning by selenium from volcanic lava and dust
g. Toxic substances in the air, possibly produced from volcanoes, causing thinning of dinosaur egg shells

C. Oceanic and topographic change
a. Marine regression
b. Lowering of global sea level, leading to dinosaur extinction, assuming they were underwater organisms
c. Floods
d. Mountain building, for example, the Laramide Revolution
e. Drainage of swamp and lake habitats
f. Stagnant oceans caused by high levels of carbon dioxide
g. Bottom-water anoxia at start of transgression
h. Spillover of Arctic water (fresh) from its formerly enclosed condition into the oceans, leading to reduced temperatures worldwide, reduced precipitation, and a 10-year drought
i. Reduced topographic relief
j. Reduction in number of terrestrial habitats
k. Fragmentation of terrestrial habitats

D. Other terrestrial catastrophes
a. Sudden vulcanism
b. Fluctuation of gravitational constants
c. Shift of the earth's rotational poles
d. Extraction of the moon from the Pacific Basin
e. Poisoning by uranium sucked up from the soil

2. Extraterrestrial explanations
A. Entropy; increasing chaos in the Universe and hence loss of large organized life forms
B. Sunspots
C. Cosmic radiation and high levels of ultraviolet radiation
D. Destruction by solar flares of the ozone layer, letting in ultraviolet radiation
E. Ionizing radiation
F. Electromagnetic radiation and cosmic rays from the explosion of a nearby supernova
G. Interstellar dust cloud
H. Flash heating of atmosphere by entry of meteorite
I. Oscillations about the galactic plane
J. Impact of an asteroid, comet, or comet showers, causing extinction by a number of postulated mechanisms
a. Acid rain
b. Months or years of freezing temperatures
c. Global wildfires
d. Regional wildfires
e. Super hurricanes
f. Sudden increase in temperature
g. Airborne debris
h. Debris in freshwater streams
i. Months or years of darkness
k. Tsunamis

3. Multiple extraterrestrial or terrestrial factors
A. Bolide impact triggering or increasing volcanic activity with concomitant results
B. Volcanic activity, followed by marine regression and habitat fragmentation, and bolide impact with concomitant results.

Species declined considerably over this 10 million years (e.g., Sullivan 1998; Archibald 2011; Archibald and MacLeod, 2007). Usually, this comparison is based on the two best-studied Late Cretaceous dinosaur faunas in the Western Interior: the approximately 75-million-year-old (middle to late Campanian) fauna from Dinosaur Provincial Park ("Judith River" in Archibald

1996) southern Alberta and the approximately 66-million-year-old (late Maastrichtian) Hell Creek fauna of eastern Montana and western Dakotas. In 1996, Archibald indicated that the absolute generic diversity of dinosaurs decreased by 40 percent (dropping from 32 to 19) from the Judith River to the Hell Creek dinosaur fauna. Weishampel and colleagues (2004) provided a more recent taxonomic compilation, which included an intermediately aged fauna (early Maastrichtian) from the Horseshoe Canyon Formation, southern Alberta, which can be added to these computations. According to Weishampel et al. (2004), going from oldest to youngest, the Dinosaur Park Formation has yielded 32 named genera, the Horseshoe Canyon Formation has yielded 25 named genera, and the Hell Creek Formation has yielded 18. In each successive fauna there is turnover, but there is also a net loss of seven genera between each successive fauna. This translates to a 20 percent decline from the Dinosaur Park Formation fauna to the Horseshoe Canyon Formation fauna, and a 28 percent decline from the Horseshoe Canyon Formation fauna to the Hell Creek Formation fauna, for a total decline of almost 44 percent during the last 10 million years of the Cretaceous in at least the northern part of the Western Interior of North America. The often rarer nonavian saurischians (reptile-hipped dinosaurs), which at this time and place were represented by only theropods, declined by almost half during this interval (from eleven to six genera). Of particular interest was the dramatic reduction in numbers of species of the large, probably herding ornithischian ceratopsids (from five to two) and hadrosaurids (from seven to two) (Archibald 1996; Weishampel et al., 2004). Even most recent studies still continue to support the clear evidence for the decline of nonavian dinosaurs in the Late Cretaceous of North America (Archibald, 2011).

As noted, the second issue related to the rate of dinosaur extinction is whether dinosaurs declined gradually, very rapidly, or not at all as one approaches the K/T boundary. Unlike the previous discussion that dealt with the last 10 million years of the Cretaceous, this interval of time is the last one million or so years of the Cretaceous. The last study to argue that there was gradual decline in the number of species of dinosaurs in the last few million years of the Cretaceous was that of Sloan and colleagues in 1986 in the area of Bug Creek in eastern Montana. They based this on an examination of the number and variety of isolated dinosaur teeth, which they argued decrease as one approaches the K/T boundary in eastern Montana. Later it was shown that much of the section they used in their analysis includes Paleocene channel deposits that had cut into underlying Cretaceous sediments (Lofgren 1995). Thus, dinosaur teeth in the Bug Creek sequence are usually regarded as having been reworked, and any decrease at subsequently higher localities would simply be the result of fewer and fewer reworked teeth. These were called *Zombie taxa* by Archibald (1996).

Past and Present Evidence for and against Catastrophic Dinosaur Extinction

Another view for the same 10-million-year interval suggests dinosaur diversity remained the same or even increased. Russell (1984) has been one of the major advocates of this idea. He argued that the Dinosaur Park Formation ("Judith River Formation" in Russell 1984) is much better sampled than the Hell Creek Formation. Thus, according to him, any apparent decline is the result of a discrepancy in sampling effort. Moreover, a comparison of faunas that preceded the Dinosaur Park fauna as well as those that succeeded it suggests that the Dinosaur Park fauna possesses an anomalously diverse dinosaur fauna. According to this reading of the fossil record by Russell, one would need to normalize for the number of localities in the Dinosaur Park Formation as well as the Hell Creek Formation to obtain meaningful comparative data between these fossil-bearing units.

More recently, Russell and Manabe (2002) provided evidence supporting the view that there is a decline in dinosaur taxa going from the approximately 75-million-year-old Dinosaur Park Formation to the 66-million-year-old Hell Creek Formation. Their numbers of named dinosaur genera differ somewhat from those cited in the previous section by Weishampel and colleagues (2004). Russell and Manabe (2002) recognized 30 named dinosaur genera from the Dinosaur Park Formation and 21 from the Hell Creek Formation. They indicated that the diversity of small dinosaurs was similar in the two faunas, but that the Hell Creek assemblage had less than half of the large dinosaurs found in the Dinosaur Park assemblage. These results indicate that Russell has modified his earlier views that there was no evidence for decline of dinosaurs in the last 10 million years of the Cretaceous in North America.

In 1990, Dodson quantified data on nonavian dinosaurs throughout their 160-million-year existence. He concluded that during the last 10 or so million years of the Cretaceous there was no evidence to indicate that dinosaurs were in decline, but also that the data do not support either gradual or abrupt extinction.

In addition to those arguing for a gradual decline of dinosaurs during the very last years of the Cretaceous, there are also those who argue that there was no such decline of dinosaurs during this interval. Thus, dinosaur extinction is commensurate with catastrophic events. In 1991, Sheehan and colleagues published a study purporting to show no decline in either kinds of dinosaurs or numbers of individuals as one approaches the K/T boundary. They wrote that they were tracking the diversity of eight families of dinosaurs vertically through the uppermost Cretaceous Hell Creek Formation. They argued that they were testing whether they could detect any change in the relative abundance of individuals or families of dinosaurs as one approaches the K/T boundary. They reasoned that if there were no change, the diversity of dinosaurs did not decrease when approaching the K/T boundary. If, however, change were detectable in the relative abundances, there was a diversity change approaching the K/T boundary. The study concluded that there was no discernible change, which they argued is compatible with theories of catastrophic extinction.

Unfortunately, their methodology precluded them from addressing the question they wished to ask--whether there was discernible change. According to these authors, the eight families of dinosaurs that they included in their study represent 14 genera. They used familial-level data in their analysis rather than the 14 genera because they felt that generic-level data could be misleading and that many fossils must be excluded because they were not identifiable to generic level. This means genera could become extinct within the Hell Creek without being detected by the authors. The distribution of genera in families used in this study shows that six of the 14 genera could have become extinct without any drop in familial diversity. This is a 43 percent generic extinction without the loss of a single family. Thus, this study used a taxonomic level (family) that is far too coarse to detect any decline in dinosaur diversity as one approaches the K/T boundary, if there were such a decline. There were other problems with this study. As shown by Hurlbert and Archibald (1995), the statistical approaches used in the Sheehan et al. (1991) study were not capable of detecting whether there was a decline, an increase, or no change in dinosaur diversity. Also, most of the specimens identified in the field in the Sheehan et al. (1991) study were not collected, so it is impossible to verify identifications (Pearson et al. 2002).

A more recent study published by Pearson and colleagues (2002) collected over 10,000 vertebrate specimens from microsites, and parts of 41 dinosaur skulls from most of the stratigraphic extent of the Hell Creek Formation, western Dakotas. As in most other studies (e. g., Archibald 1996), they found that the uppermost two meters is essentially devoid of fossils. Using a rarefaction analysis, they found no evidence for "a decline in vertebrate diversity through the formation or dinosaur diversity in the three meters below the K/T boundary" (145). They argued that their results are not commensurate with gradual vertebrate extinctions at the end of the Cretaceous. In this study, they recovered some 61 vertebrate taxa, only about two-thirds of which were identified to a least the generic level. This contrasts with the next most recent study that identified at least 107 vertebrate taxa to at least the generic level (Archibald 1996). This earlier study, however, lacked the stratigraphic completeness of the Pearson et al. (2002) study. When all 61 vertebrates are considered, the Pearson et al. (2002) study is quite convincing as to the relative stability of the fauna throughout the Hell Creek Formation. When dinosaurs alone are considered, however, the picture is somewhat different. Of the 13 nonavian dinosaurs recognized in this study, only eight are identified below the family level. Thus, the same taxonomic coarseness found with the Sheehan et al. (1991) study might also pertain here. Second, the actual pattern of the disappearance of these 13 taxa below the K/T boundary are as follows (Pearson et al. 2002, fig. 4): seven disappear between 5 and 0 m below (one is in fact found above 0 m, but still in Cretaceous aged rocks), three disappear between 10 and 5 m, and two disappear between 15 and 10 m, while the final two are gone between 40 and 35 m below. Thus, the disappearances of nonavian dinosaurs show a more stepped pattern than the overall more static pattern for all vertebrates combined. Whether this should be read literally as a gradual or stepwise extinction or can be treated statistically as indistinguishable from a simultaneous extinction remains an open question. The vertebrate fossil record, especially of large, rare taxa such as dinosaurs, is certainly poorer than the marine record of invertebrates. Yet even for invertebrates at the K/T boundary, Payne (2003) found "that the data are not always sufficient to rule out either stratigraphically simultaneous extinctions or a literal reading of extinction rate as representing gradual or episodic extinction" (37). The Pearson et al. (2002) study shows that the vertebrate fauna of the Hell Creek Formation appears to have been stable throughout most of its deposition. It does not, however, address the question of whether the disappearances of nonavian dinosaurs and other vertebrates were gradual or sudden.

Coda on the Rates of Dinosaur Extinction

The previous two sections examined past and present evidence concerning the diversity of dinosaurs during (1) the last 10 million years of the Cretaceous and (2) the waning one million years or so before and at the K/T boundary. For the longer-term pattern, the evidence continues to support a decline of 30 to 45 percent generic diversity of dinosaurs. For the shorter-term pattern, better support is emerging that vertebrate diversity held steady in the waning days of the Cretaceous, but the evidence for gradual versus catastrophic dinosaur extinction remains unclear. Both of these patterns are biased in that they are from the northern Western Interior of North America.

Current Theories

Here I examine three of the major causes proposed for the extinction of dinosaurs--asteroid (or more generally, bolide) impact, marine regression and habitat regression, and massive eruptions of flood basalts. None of these are mutually exclusive, and a number of scenarios have been proposed that combined parts of each of the three. In general, the three causes, in the order listed above, range from very short to very long term in both duration and effect.

The most catastrophic of the three causes is the asteroid impact theory (Alvarez et al. 1980) that argues that a 10-km (6-mi) asteroid struck the Earth 66 mya, producing ejecta and a plume reaching far enough into the atmosphere to spread around the globe, blocking the Sun. The cessation of photosynthesis resulted in death and extinction of many plants, the herbivores that fed on them, and the carnivores that fed on the herbivores (but see Pope 2002). The probable crater, named Chicxulub, has been located near the tip of the Yucatan Peninsula (e. g., Hildebrand 1993). At 180 km (110 mi) across, it is one of the larger such structures on Earth. In addition to the crater, two other important pieces of physical evidence supporting an impact are an increase in the element iridium at the K/T boundary, and minerals, especially quartz grains, showing shocked lamellae in two directions. A high level of iridium at the Earth's surface and double lamellae are both more indicative of an impact than volcanism. Some of the more proximate effects of an asteroid impact include acid rain, globe wildfire, sudden temperature increases or decreases, infrared radiation, tsunamis, and super-hurricanes (e.g., Archibald, 2011; Archibald and Fastovsky, 2004).

The next cause, marine regression and habitat fragmentation, occurred over a longer interval of time, from tens to hundreds of thousands of years. *Marine regression* refers to draining of epicontinental seas. One of the greatest such regressions is recorded in rocks near the end of the Cretaceous Period some 66 mya. Estimates suggest that 29 million square km (11.2 million square mi) of land were exposed during this interval (Smith et al. 1994), more than twice the next largest such addition of land during the past 250 million years. This land mass is approximately the size of Africa. There were marked proximate effects of this regression--major loss of low coastal plain habitats, fragmentation of the remaining coastal plains, establishment of land bridges, extension of freshwater systems, climatic change with a general trend towards cooling on the newly emerged landmasses.

Massive eruptions of flood basalts, the Deccan Traps, on the Indian subcontinent occurred over a much longer interval than marine regression, perhaps millions of years surrounding the K/T boundary (Courtillot 1999). The volume of material estimated to have been erupted over this 4-million-year interval would cover both Alaska and Texas to a depth of 610 m (2000 ft). Proximate causes resulting from such massive volcanism have not been as well studied as those for marine regression or asteroid impact, but newer studies are underway (Keller et al. 2008). Proximate causes, however, have been argued to be similar for both impact and volcanism. Climatic changes caused by massive eruptions would have been longer term.

The Pattern of K/T Vertebrate Extinctions

To test these three causes, one must examine what happened not only to dinosaurs, but also to other species that lived with these creatures. Such a study (Archibald and Bryant, 1990; Archibald, 1996, 2011) examined the best-known K/T sections located in eastern Montana. The assemblage included 107 well-documented species of vertebrates belonging to 12 major monophyletic lineages. Of these species, only 19 are nonavian dinosaurs. Because of a poor fossil record, pterosaurs and birds (a clade of saurischian dinosaurs) could not be included in this sample. Although there has been debate as to whether a number of major clades of modern birds appeared before the K/T boundary, Chiappe (2007) argued that unquestioned members of modern bird clades are not known in the fossil record until the early Tertiary, whereas Lindlow (2011) supports the appearance of some modern clades before the K/T boundary. Pterosaurs, however, had dwindled to at most one family (Archibald 2011). Of the 107 species of vertebrates, 52 (49 percent) survived the K/T boundary. This level of survival is only about 10 percent lower than that for similar intervals before and after the K/T boundary. The amount of survival at the K/T boundary for vertebrates in the Western Interior appears to have been higher than that for a number of other major groups of plants and animals. Nevertheless, the effects on vertebrates were profound. Whether the extinction of nonavian dinosaurs was gradual or catastrophic, nonavian dinosaurs, the large land vertebrates for much of the Mesozoic Era, were replaced by mammals in probably only a few thousands or tens of thousands of years. Mammals, including our own clade, Primates, rapidly diversified, filling niches left by dinosaurs and creating new ones.

The most obvious pattern of extinction among these 12 major vertebrate clades is that extinctions were concentrated in five of the clades, sharks and relatives, lizards, marsupials, ornithischians, and saurischians. Species in these five clades account for 75 percent of the extinctions. This demonstrates that the K/T extinctions were highly selective; any theory of extinction must account for this selectivity.

Comparing the K/T Vertebrate Record to the Possible Causes

Using the vertebrate fossil record, we cannot test directly whether the seas underwent a major regression, whether there were major volcanic eruptions, or whether an asteroid struck Earth. We can instead test the various proximate causes that have been proposed as the result of these ultimate causes. Starting with the asteroid impact, we can test the suggestions of acid rain, sharp temperature decrease, and global wildfire. (Because the biotic effects of volcanic eruption have not been explored as extensively and are considered similar to the effects of impact, this will not be discussed further.) We know from work on extant species and habitats that among vertebrates acid rain hurts aquatic organisms most. Except for sharks and relatives, however, aquatic species did very well through the K/T transition. If a sharp, short temperature spike occurred, we know from modern vertebrates that wholly or partially terrestrial ectotherms should have been most affected. Once again, most of these, except lizards, did well through the K/T boundary.

Whether dinosaurs should be considered endotherms, ectotherms, or another kind of physiology remains controversial. Finally, global wildfire, which is argued to have consumed 25 percent of all above ground biomass, should have been a nearly equal opportunity killer, outright burning many creatures and suffocating others in aquatic systems with a hyper-influx of detritus. In addition to the lack of substantial amounts of charcoal at the K/T boundary (Belcher et al. 2003), the fossil record is highly selective, rendering global wildfire a very unlikely scenario. A global fire had been suggested as a result of a thermal pulse, which also would have outright killed all unprotected plants and animals (Robertson et al., 2004) until it was realized that much of such a pulse would have been blocked by any incoming material (Goldin and Melosh, 2009).

Of all of these proximate causes of an asteroid impact, what seems most important is the blocking of sunlight, causing a cessation of photosynthesis. This had been considered enough to kill and cause the extinction of up to 80 percent of the plants species in at least some areas of North America. By 2004, it was argued (Wilf and Johnson 2004) that the plant extinction rate in at least the middle portion of North America would have been only 57 percent. Even this lower level would have had a devastating effect on large herbivores, especially if already stressed by other events, such as marine regression and habitat fragmentation.

As global marine regression began in the last few million years of the Cretaceous, tremendous new tracts of dry land were added. But all known dinosaur-bearing vertebrate localities near the K/T boundary are from coastal plain habitats that were being drastically reduced during marine regression. This reduced dramatically the size of these habitats, stranding dinosaurs in ever-smaller areas, much as humans are doing to the habitats of large mammals in Africa today.

This stressed dinosaur populations, setting them up for the final biotic insult caused by even a smaller asteroid impact and massive volcanism. At the same time, the coastlines were retreating away from the Western Interior, taking the sharks and relatives with them. They could traverse freshwater courses up to a few hundreds kilometers, but not thousands of kilometers. The marine connection was severed. Although low coastal streams disappeared, the total freshwater systems held their own and, in many cases, increased in length as the coastline retreated. Thus, freshwater species did very well, with descendants such as paddlefish, sturgeon, and gar still plying the Missouria–Mississippi river systems.

The lowering of sea level also reconnected once separated landmasses, such as eastern Asia and western North America. The earliest ungulate relatives, first known from North America, appear at this time. A very rare occurrence of the early archaic ungulate, *Protungulatum*, is definitely known from the Hell Creek Formation in Montana some 300,000 years before the K/T boundary (Archibald et al., 2011). Possibly latest Cretaceous archaic ungulates are also reported from sites in Canada (Fox, 1989) These new ungulates have a dental morphology that resembles that of the opossum-like marsupials, which arose in North America some 100 mya and had been very common for at least the 20 million years leading up to the K/T boundary, 66 mya. It seems likely that the appearance of these ungulates in North America spelled competitive doom for the marsupials. Interestingly, when they both appear in South America a few million years after the K/T boundary, they have spilt the difference, with the ungulates becoming more strictly herbivores while the marsupials became omnivores and carnivores, including large saber-toothed marsupial cats. The one group that cannot be explained by this globally testable hypothesis is the drastic reduction of lizards in the Western Interior. A more local, ad hoc explanation is that the suggested climatic shift to a wetter, rainier climate in areas such as eastern Montana following the K/T boundary may have driven out the more dry-adapted lizards.

Summary

Clearly, among the public, asteroid impact is the most widely recognized cause of dinosaur extinction. It is also popular among scientists, but there remain many unanswered questions regarding its killing mechanisms. For some time after the impact theory was purposed in 1980, impacts by various bolides were argued to have caused cyclic extinctions, including the five mass extinctions in the past 550 million years. More analysis, however, has caused the idea of cyclical episodes of extinction to fade. Although impacts on Earth are quite common, the evidence now indicates that such impacts do not correlate well with episodes of mass extinction, while both marine regression and massive volcanism do correlate well with such episodes (MacLeod 2004). All three of these events occurring at the K/T boundary provided a unique set of events in the history of planet Earth.

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