Chapter Seven

Victims and Survivors: Patterns of K-T Extinction and Survival

By the mid-1980s, the impact hypothesis had secured a strong foothold in both scientific circles and the public press. Proponents of the volcanic hypothesis were voiciferously raising their objections. Throughout this debate, however, there was a rather counterintuitive aspect to the problem of what decimated the dinosaurs and other groups at the K-T boundary. If one turns the question around, one is confronted with another basic but baffling mystery: How did the survivors survive?

Since the impact scenario was proposed, there was a kind of arms race to model its effects and generate enough potentially potent killing mechanisms to do the job. Indeed, that list is truly incredible--an earthquake one million times larger than any recorded in human history, a global inferno following the impact, a subsequent period of darkness lasting months, a interval of months on the continents when temperatures dropped below freezing, episodes of searing acid rain. Now, add to those presumably potent effects the enhancements contributed by the volcanic scenarios and one is really left wondering how anything survived. As Anthony Hallam put in 1989: "Even granted the evidence for impact, it is still by no means clear how many of the end-Cretaceous extinctions relate to it, and no really plausible, exclusively impact-based, 'killing scenario' has yet been put forward. Whether involving dust clouds blocking out sunlight, dramatic rise or fall of temperature, acid rain on a massive scale or spectacular wildfires on the continents, they are all too drastic in their environmental effects to account for the selectivity of the extinctions and the high rate of survival of many groups.[32]"

Hallam and several other scientists began to focus on this important point. If we were to gain a better understanding of how the K-T extinctions occurred, we would have to come to grips with the pattern of extinction and survival among different organisms. We would have to try to understand why some organisms perished while others survived--not just locally, but globally.

Explaining patterns of survival and extinction not only requires fairly complete fossil records but also an understanding of the physiology in these ancient organisms. For, we must specify which "killing mechanism" eradicated a particular group of animals or plants. Again, as the number of potential killing mechanisms increases and the scenario for extinction becomes more complex, it becomes that much more difficult to test and pinpoint which mechanism or combination of mechanisms was responsible for a particular group's extinction. Further, since the impact and volcanism could have generated many of the same "killing mechanisms" (ex. acid rain and the greenhouse effect), it becomes even more difficult to pinpoint which event was responsible.

Since early in these debates, the role of random chance has been occasionally invoked to explain the pattern of extinctions. The idea is that there really wasn't anything wrong with the organisms that went extinct, they were basically just unlucky[31]. Perhaps this is true, but this explanation does little to explain rigorously what "killing mechanisms" were responsible for the bad luck.

Extinction and Survival in the Oceans

Despite the complexity of the problem, some ideas regarding the selectivity of extinctions have been put forward. For example, in marine environments, many forms of microscopic organisms that live near the surface of the water column, such as planktonic foraminifera and coccolithophora, were apparently decimated at the boundary. Jan Smit has done a lot of this documentation in marine sections around the world[11]. Perhaps this was the result of acid rain, as the more acidic waters dissolved the calcium carbonate shells of these tiny but critical food sources[12]. These microscopic organisms formed the foundation of the food chain in ancient oceans just as they do in our modern oceans.

Calcium carbonate is the same chemical compound that makes up the shells of clams and snails. If you drop acid on these shells, a bubbling reaction is triggered. This reaction represents the acid dissolving the shell material. It takes a lot of strong acid to dissolve a whole clam shell. But because the shells of microscopic plankton are so small, it is much easier to dissolve the shell and kill the tiny organism.

The extinction of these tiny organisms could have set off an ecological chain reaction. Organisms that fed on these kind of plankton would have been the most vulnerable, especially those organisms that lived in the tropics. However, it is somewhat risky to infer what the diet of an animal that lived 65 million years ago was. One can only make guesses based on the diet of closest living relatives and interpretations based on the feeding apparatus of the extinct animal, which may or may not lead one to the correct answer.

It has further been suggested by Jennifer Kitchell and her colleagues that those kinds of plankton that have a method of reproduction that involves a dormant spore stage, such as dinoflagellates and diatoms, survived at higher rates than the forams and coccoliths which do not[13]. However, these statements do not really conclusively resolve the issue of which "killing mechanism" from which event was responsible.

Some workers, such as Gerta Keller Of Princeton University and Norman MacLeod of the British Natural History Museum have argued that many of the sections used by proponents of impact genrated extinction do not contain a complete fossil record of the events during the K-T transition[14]. Consequently, what appears to be an abrupt and catatstrophic extinction in the rock record actually happened more gradually. To give you a sense of how contentious this issue is, we need only take a look at the debate swirling around one relatively complete section at El Kef, Tunisia. Smit argues that almost all the late Cretaceous forams disappeared at the K-T boundary, whereas Keller argues that only about 1/3 did[15]. Independent tests are underway to try and resolve the dispute. However, disagreements extist about the species identification of many specimens. Furthermore, arguments abound about whether some of these microscopic fossils have been eroded out of Cretaceous sediments then redeposited in younger Tertiary sediments. This process is called reworking, and it greatly complicates attempts to interpret the sequence and pace of events in the fossil record.

Among other marine organisms, estimates for extinction of the nautilus-like ammonites reach 100%, whereas clams exhibit about 55% extinction, and snails about 35%[16]. Especially with ammonites, issues of reworking and the frequency at which specimens have been found at different levels in the sequence of rocks have been used to raise questions about whether these organisms actually went extinct before the K-T boundary. However, most workers now seem to accept the notion that ammonite extinction was part of the K-T event.

One Synthetic Explanation for the Victims and Survivors

There have been few attempts to generate an all-encompassing explanation for the patterns of survival and extinction on both land and sea. One such attempt was put forward by Anthony Hallam[33]. Hallam argued that the selectivity of the extinctions could be most logically explained by a combination of climatic and other environmental consequences related to falling sea levels and volcanism. He even attempted to attribute the extinction of particular groups to particular killing mechanisms.

First, Hallam compiled his list of victims. On land, dinosaurs perished, as well as pterosaurs--a group of flying reptiles. Some groups of mammals, such as the rodent-like multituberculates and the marsupials suffered high levels of extinction, along with some groups of land plants. Yet, many other land plants, freshwater fish, amphibians, snakes and placental mammals were not severely affected. In the oceans, the late Cretaceous extinctions completely eliminated ichthyosaurs, plesiosaurs, and mosasaurs--three groups of marine reptiles. Ammonites also went extinct. Microscopic marine organisms that lived near the surface of the ocean, such as coccoliths and forams, were almost completely decimated, as were relatives of modern squid called belemnites. Numerous groups of corals, clams, snails, and echinoderms (starfish, sea urchins and their relatives) were hard hit, along with bottom-dwelling forams and the microscopic radiolarians. But many kinds of marine invertebrates and microscopic organisms called dinoflagellates were not badly affected.

Examining this list of victims, Hallam correctlyly tried to use the environmental limits of the closest living relatives of these victims as a guide for interpreting what killing mechanism was responsible for their extinction. Much of his discussion of extinctions was based on the acidity of the seawater and freshwater. Scientists use a scale, called pH, to standardize these measurements. A pH of 1 is very acidic. A pH of 7 is perfectly balanced between acidic and alkaline. A pH of 7 is about the value for normal drinking water. A pH of 14 is highly alkaline. Slightly alkaline water is commonly called "hard" water, whereas slightly acidic water is commonly called "soft" water.

Modern surface-dwelling forams have difficulty living in seawater with acid levels below a pH of 7.6-7.8, and extant coccoliths die off in water with levels below 7.0-

7.3. Accordingly, Hallam reasoned that volcanic eruptions, such as those that formed the Deccan Traps, released almost 19 trillion tons (17 trillion tonnes) of hydrogen sulfate (H_2SO_4) and 270 billion tons (245 billion tonnes) of hydrochloric acid (HCl). As a result, tremendous amounts of acid rain would be dumped into the surface waters of the world's oceans--14 times the amount of acid rain generated by the burning of fossil fuels in Europe and the United States in 1976. In turn, the acidity levels of the surface waters in the ocean would drop to pH levels of 7.4 or lower, resulting in massive extinctions of planktonic forams and coccoliths. Since acidity levels in deeper levels of the ocean were less affected, the bottom-dwelling forams were reasoned to have fared much better. Similarly, living dinoflagellates can survive in water with pH levels as low as 4.0-5.0, and this group of microorganisms was one of the few to sail through the K-T crisis virtually unscathed.

In freshwater environments, the effects of acid rain were also implicated in the selective extinction of fishes. Hallam noted that in modern Canadian lakes, different kinds of fish can survive different levels of acidity: Walleye and lake trout, for example, disappear when pH levels reach 5.8-5.2, but yellow perch and lake herring can survive at levels less than 4.7. Consequently, if freshwater fish living during the K-T transition were similarly diverse in their tolerance of acidity, selectivity in extinction could be expected. Similarly, in the Canadian forests, different kinds of trees, such as red cedars and sugar maples are more tolerant of acid rain than white pine and white birch. Consequently, acid rain might be responsible for the selectivity seen in land plant extinctions at the end of the Cretaceous.

Many of the larger marine invertebrates that went extinct lived in near-shore environments such as reefs. Some kinds of corals, inoceramid clams, rudistid clams, some snails, and various echinoderms are exemplary. Hallam argued that these shallow-water animals were essentially left high and dry by the drop in sea level associated with the retreat of the shallow continental seaways at the end of the Cretaceous.

In part, he also attributed the extinction of dinosaurs to the increased climatic extremes that resulted from this regression of the seaways, but he also invoked an increase in ultraviolet radiation. This effect, he argued, was the result of the tremendous amount of hydrochloric acid injected into the stratosphere by the K-T volcanism, which depleted the ozone layer in the atmosphere. He asserted that the deleterious effects of this increased radiation would be especially acute on terrestrial animals that were unprotected or unable to hide in either their adult or reproductive stages. However, he was unable to explain precisely why dinosaurs were so affected while other terrestrial vertebrates such as placental mammals, birds, and freshwater amphibians were not. This is especially puzzling given the recent reports that increased ultraviolet radiation attributed to decreased ozone levels in our modern atmosphere may be reeking havoc on modern species of frogs and other amphibians.

Hallam's was a noble attempt to solve the murder mystery. But once again, given the fact that many of the same killing mechanisms that Hallam invoked as the result of volcanism have also been associated with the impact scenario, it becomes impossible to tease apart which event was responsible.

Were Extinctions More Severe Near the Equator Than at the Poles?

In the original formulation of the impact hypothesis, the dust cloud, which cut off photosynthesis, was implicated in the extinction of many species of plants. The role of seed, spore, and pollen reproduction has also been invoked to explain the pattern of extinction and survival among plants[20]. The idea is that species that had their reproductive structures sheltered underneath the soil would have been more protected from extinction. However, the picture of plant extinction and survival being developed on a global scale documents some interesting variations and complications.

Extinction rates for plants at mid-latitude sites, roughly half way between the equator and the poles, are relatively high. For example, Kirk Johnson of the Denver Museum of Natural History, Leo Hickey of Yale University, Doug Nichols of the U. S. Geological Survey, and Carol Hotton at the University of California at Davis have conducted studies on species of fossil pollen and fossil leaves that occur near the K-T boundary at mid-latitude sites in the western interior of North America[21]. As many as 30 to 50% of the fossil pollen species drop out at or near the boundary clay marked by the iridium anomaly. Among different kinds of fossil leaves, the extinction rate is even higher (fig. 7.06 and 7.07). Almost 80% of the latest Cretaceous leaf flora disappear at the boundary. Most researchers conclude that this pattern of changes is consistent with a sudden and catastrophic event such as the Chicxulub impact.

One specialist on fossil plants, Jack Wolfe of the U. S. Geological Survey, has even gone so far as to conclude that the impact occurred in early June. Wolfe based his interpretation on the reproductive stages exhibited by aquatic fossil plants preserved in the sediments and fall-out debris at the bottom of an ancient pond now located at Teapot Dome, Wyoming[22]. However, Nichols and Hickey have seriously questioned his identifications of the species present and his interpretive methodologies[23].

Near the South Pole, the rates of extinction for fossil pollen species seem to be much lower than those in the mid-latitudes of the northern hemisphere. On Seymour Island near the Antarctic Peninsula, only a few species disappear at the iridium anomaly according to Rosemary Askin and her colleagues[24]. Paleontologic studies on Seymour Island's marine invertebrate fossils by workers such as William Zinsmeister of Purdue University and his colleagues have generated are also[25]. In terms of typical marine invertebrates, such as clams, snails, lobsters, and ammonites, there is no abrupt change at the K-T boundary as marked by the iridium anomaly. Instead, there is a pattern of gradual extinction. The researchers argue that this is because this section is more complete than other marine K-T sections and thus preserves a more detailed picture of the sequence of extinctions. This pattern of extinctions has been used to argue against a single catastrophic extinction event caused by an impact. Not suprisingly, proponents of the impact hypothesis have argued in turn that the extinction was abrupt but that because of preservational gaps, sampling problems, and reworking, the pattern of extinctions appears gradual. In addition, studies of forams in sediments preserved on the sea bottom off the Antarctic coast are also thought to exhibit a gradual pattern of extinctions[26].

A gradual pattern of extinctions is also found for found for pollen species of plants in sections spanning the K-T boundary in New Zealand, which was much further south 65 million years ago than it is today. The rate of extinction is reported by Kirk Johnson to be much lower that that found in the Western Interior of North America[27]. In addition, the fossil record of microscopic marine organisms called radiolarians shows that all the late Cretaceous species survived the boundary events, then gradually became extinct above the K-T boundary, according to Chris Hollis[28].

These contrasts in extinction rates and patterns have led some paleontologists, such as David Archibald, Norman MacLeod, and Gerta Keller, to argue that the effects of the impact, if any, were greatly reduced at higher latitides than at mid-latitudes. This would make good intuitive sense, given that the impact occurred at a mid-latitude site near present-day Yucatan.

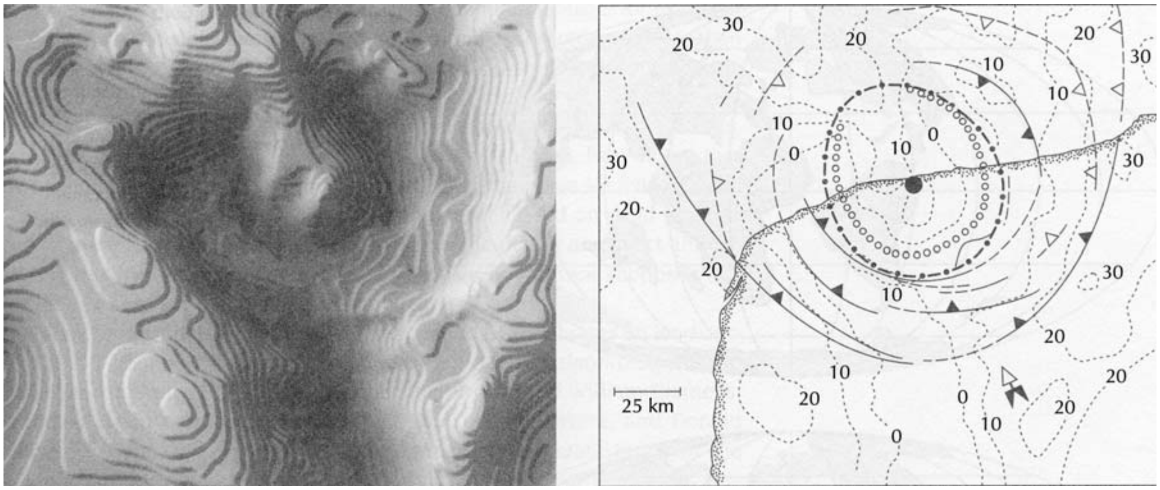


figure 7.01 Dots on these mapps show the location of Late Cretaceous dinosaur localities throughout the world. In A, all the Late Cretaceous dinosaur localities are shown. In B, those localities which span the K-T boundary are shown. Only these can be used to document the changes that occurred during the extinction event. (from Archibald, J. D., 1996, Dinosaur Extinction and the End of an Era, Columbia Univ. Press, New York, p. 15)

This idea also squares with a proposal made by Peter Schultz of Brown University and Steven D'Hondt of the University of Rhode Island. Based on asymmetry of the Chicxulub Crater, they hypothesized that the impacting body came in through the atmosphere at a low angle--not stright down[29]. The gravity maps of the crater appear to document a horshoe-shaped crater with a steep southeast side and a shallower northwest side (fig. 7.08). Such a configuration seems to indicate that the impacting body came in at an angle of only 20-30 degrees from the southeast. If so, the fireball resulting from the impact would spread directionally to the northwest over North America. The evidence from both the fossil and rock records is consistent with this scenario. Extinctions over the mid continent of North America are, as we have seen, especially severe. At some North American sites, there are two fallout layers, characteristic of oblique mpacts simulated in laboratory experiments. Also, the fragments of shocked quartz are larger in North America than in K-T sections from other parts of the world. This hypothesis will undoubtedly catalyze further tests to generate evidence that either confirms or refutes the scenario.

This scenario also seems to be consistent with tne research of David Jablonski and David Raup, who noted an apparent correlation between the geographic range of a group and its survival rate[30]. Those organisms that were geographically widespread fared better than those whose ranges were more restricted.

Nonetheless, for plants like for animals, it's still almost impossible to pinpoint one "killing mechanism" from one event. But what if we narrowed the scope a bit and focused just on vertebrates living on the continents, including the dinosaurs?

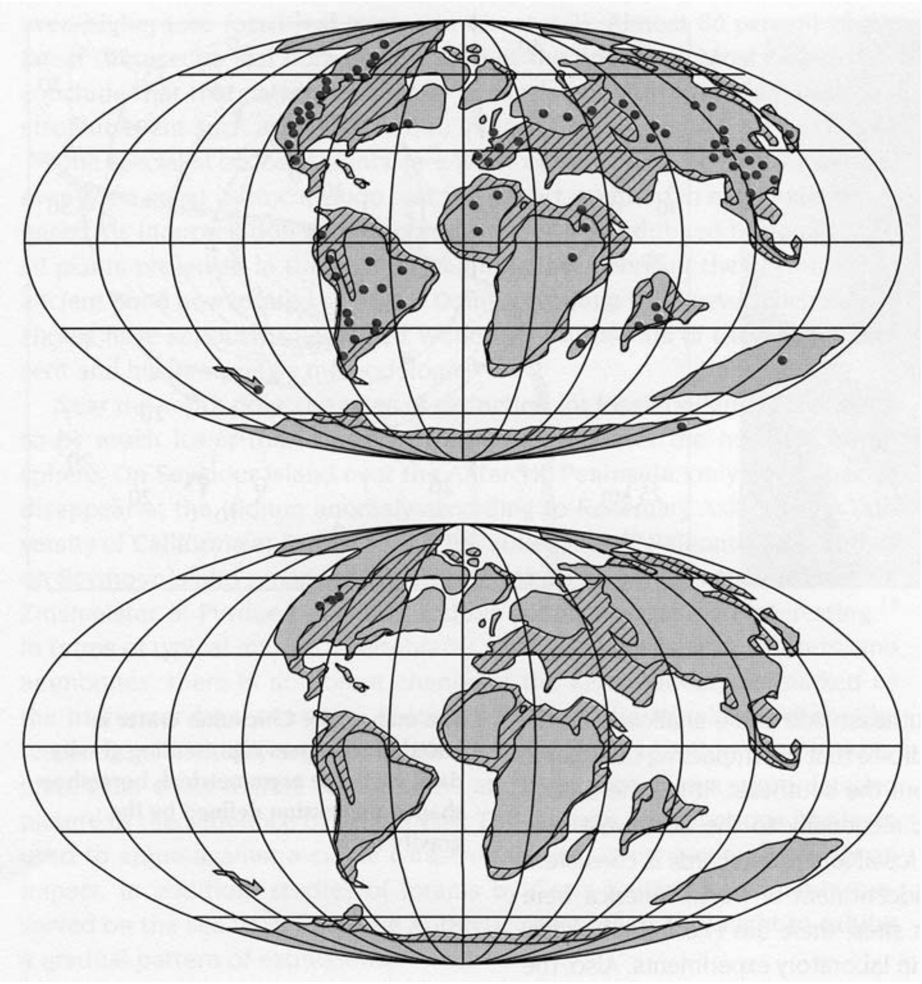


figure 7.02 Maps showing locations of latest Cretaceous and earliest Tertiary fossil localities throughout the world. In the first map (top), the dots indicate locations which span the K-T boundary. These localities can be used to document the changes that occurred during the extinction event

The Fossil Record of Dinosaurs Around the World

To document a global extinction of dinosaurs clearly requires having a late Cretaceous fossil record of dinosaurs from many areas around the world. Does such a fossil record exist?

Two vertebrate paleontologists have looked closely at this question, Peter Dodson of the University of Pennsylvania and David Archibald[1]. In assessing the late Cretaceous record, these workers have noted that only 26 localities of latest Cretaceous dinosaur localities have been discovered throughout the whole world (fig. 7.01). More importantly, all but six of these localities are found in the central interior of North America. In all, these 26 localities preserve remains of only 20 different genera of dinosaurs, and 14 of these 20 are restricted to North American localities. So, although we probably have a fairly good idea of what was happening in the interior of North America, we are almost totally ignorant of how dinosaurs were faring at the end of the Cretaceous in other parts of the world.

It's certainly possible that dinosaurs might have gone extinct in one geographic area but not in another area. Thus, the geographic incompleteness of the fossil record greatly hinders our ability to evaluate exactly what effect the volcanic eruptions and impact had on dinosaur faunas on different continents.

Patterns of Extinction and Survival of Vertebrates on the Continents

On land, reptiles larger than about 44 pounds (20 kilograms) suffered extinction at higher rates than smaller reptiles[17]. This accounts for most dinosaurs that lived at the end of the Cretaceous, such as the North American forms including *Tyrannosaurus, Triceratops, Anatotitan, Edmontosaurus,* and *Pachycephalosaurus*. It's certainly not, however, a foolproof guide. Take, for example, the crocodilian lineage, which apparently sailed right through, as mentioned earlier. Also, numerous kinds of reptiles smaller than 44 pounds became extinct, including some dinosaurs, such as *Dromaeosaurus* and *Troodon*.

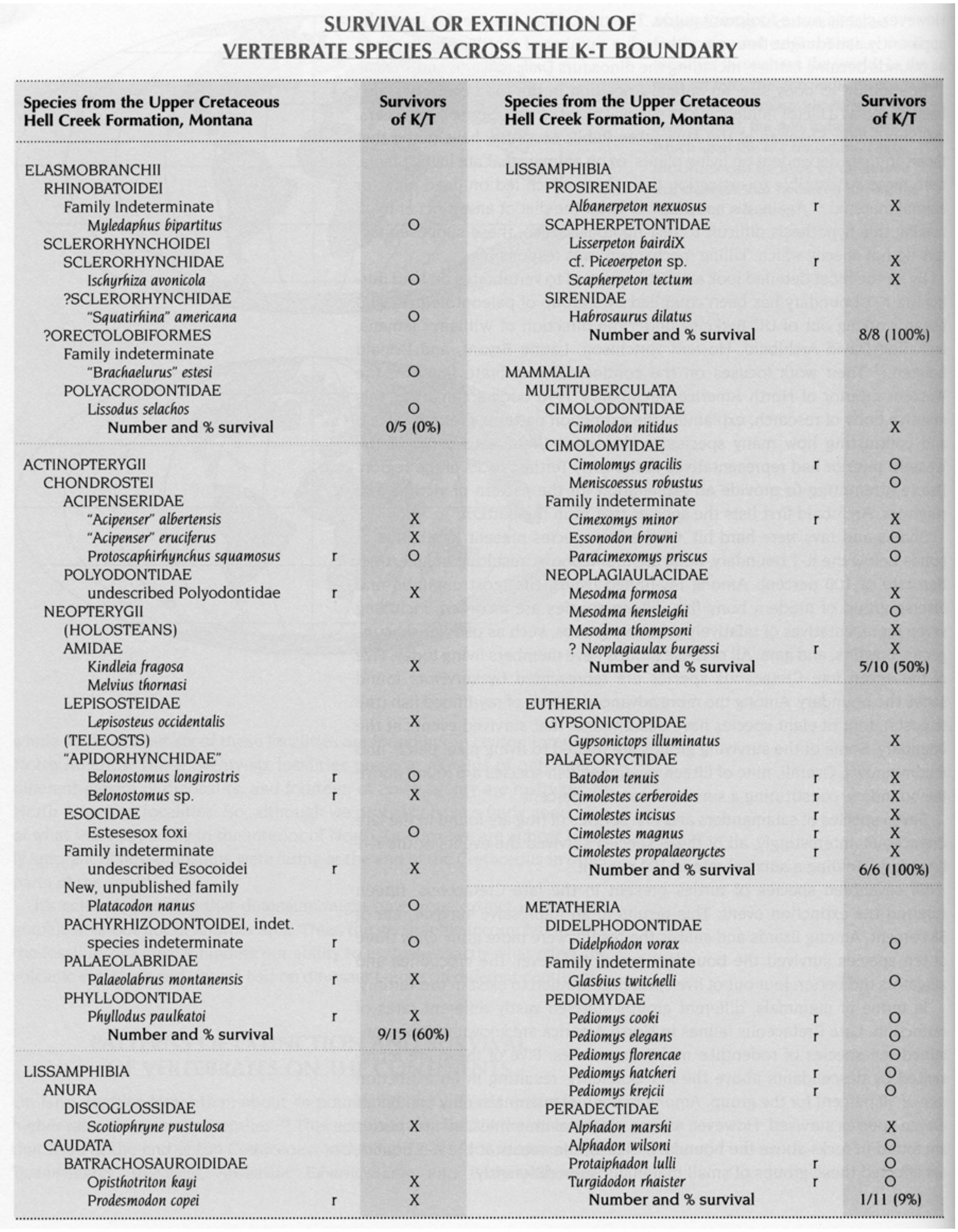
In addition to body size, an animal's position in the food chain has also been raised as a factor influencing survival or extinction. Some reseachers, including Peter Sheehan at the Milwaukee Public Museum, have noted that those animals dependent on living plants or on animals that ate living plants were most susceptible, whereas those which fed on dead plant or animal material were less susceptible[19]. Again, it's not possible to be certain what the diet of an extinct animal was, which makes this hypothesis difficult to test rigorously, and these supposed factors do not specify which "killing mechanism" was responsible.

By far the most detailed look at what happened to vertebrates on land during the K-T boundary has been compiled by a group of paleontologists who began working out of UC Berkeley under the direction of William Clemens, including David Archibald, Howard Hutchison, Laurie Bryant and Donald Lofgren[18]. Their work focuses on the continental vertebrate fauna in the Western Interior of North America. Arcibald's 1996 book summarizes this massive body of research. The problem of explaining the extinction patterns was approached group by group by contrasting how many species in the latest Cretaceous rocks of the Hell Creek Formation had representatives in the early Tertiary rocks of Tullock Formation (fig. 7.04 and 7.05).

Sharks and rays were hard hit. Of the five species present in streams or ponds below the K-T boundary, none are found above, resulting in an extinction rate of 100%. Among ray-finned fishes, the most common and diverse group of modern bony fish, fifteen species are recorded, including seven representatives of relatively primitive groups, such as paddlefish, sturgeons, bowfins, and gars. All of these groups have members alive today, and five of the seven species found in the Hell Creek are represented by survivors found above the boundary. Among the more advanced groups of ray-finned fish (the teleosts), four of eight species have descendants that survived events at the boundary. Some of the surviving groups are related to living pike, perch, and mudminnows. Overall, nine of fifteen ray-finned fish species are found above the boundary, constituting a survival rate of 60%.

The Hell Creek also preserves remains of seven species of salamanders and one species of frog. Interestingly, all of these species survived the events at the K-T boundary, yielding a survival rate of 100%.

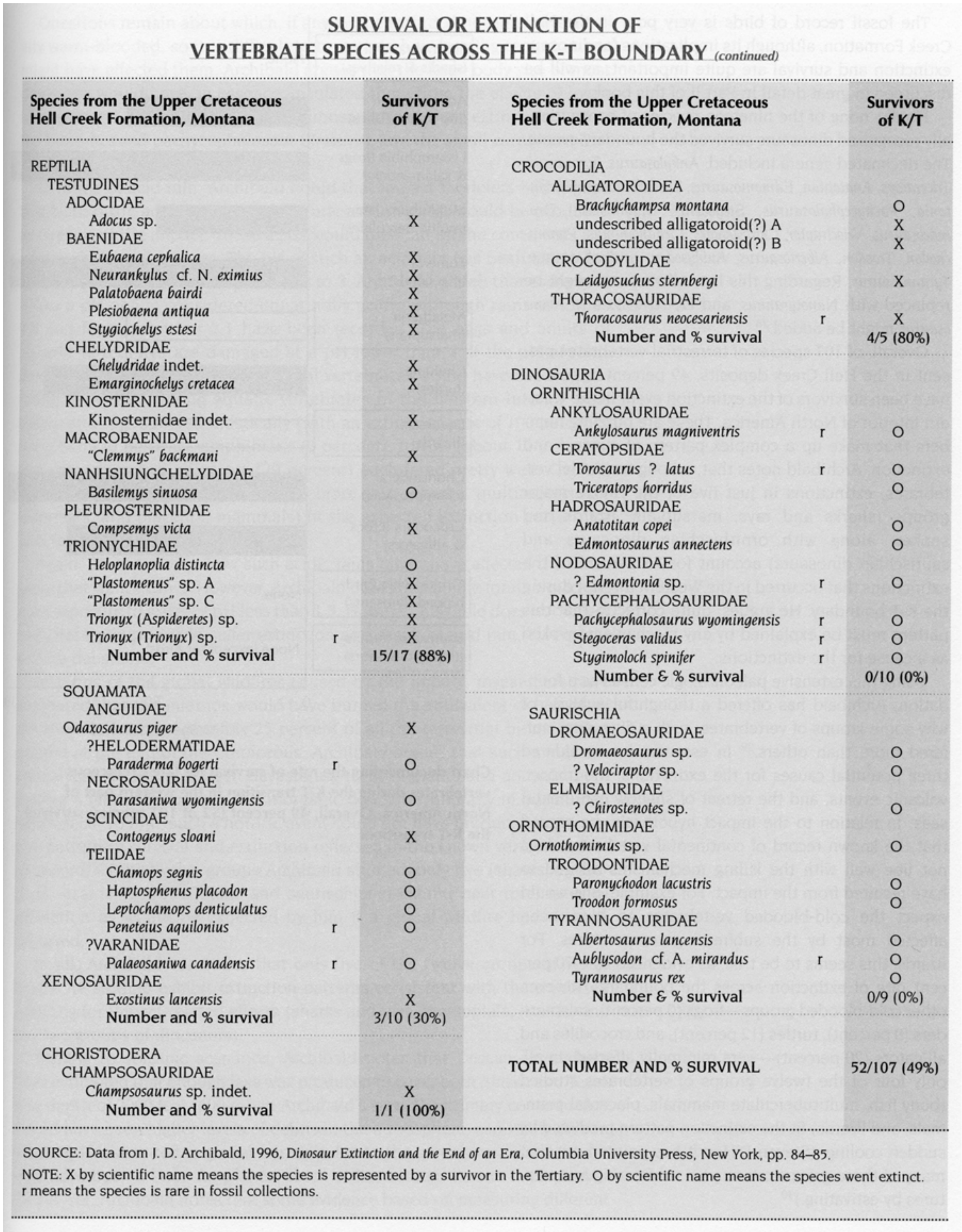
Of seventeen species of turtles present in the Hell Creek Formation, fifteen survived the extinction event. This results in an impressive survival rate of 88%. Among lizards and snakes the results were more grim. Only three of ten species survived the boundary events. However, the crocodiles and allagators did better. Four out of five species continued to exist after the K-T transition.



SURVIVAL OR EXTINCTION OF VERTEBRATE SPECIES ACROSS THE K-T BOUNDARY

Species from the Upper Cretaceous Hell Creek Formation, Montana		Survivors of K/T
ELASMOBRANCHII		
RHINOBATOIDEI		
Family Indeterminate		
Myledaphus bipartitus		O
SCLERORHYNCHOIDEI		
SCLERORHYNCHIDAE		
Ischyrhiza avonicola		O
?SCLERORHYNCHIDAE		
"Squatirhina" americana		O
?ORECTOLOBIFORMES		
Family indeterminate		
"Brachaelurus" estesi		O
POLYACRODONTIDAE		
Lissodus selachos		O
Number and % survival		0/5 (0%)
ACTINOPTERYGII		
CHONDROSTEI		
ACIPENSERIDAE		
"Acipenser" albertensis		X
"Acipenser" eruciferus		X
Protoscaphirhynchus squamosus	r	O
POLYODONTIDAE		
undescribed Polyodontidae	r	X
NEOPTERYGII		
(HOLOSTEANS)		
AMIDAE		
Kindleia fragosa		X
Melvius thornasi		
LEPISOSTEIDAE		
Lepisosteus occidentalis		X
(TELEOSTS)		
"APIDORHYNCHIDAE"		
Belonostomus longirostris	r	O
Belonostomus sp.	r	X
ESOCIDAE		
Estesesox foxi		O
Family indeterminate		
undescribed Esocoidei	r	X
New, unpublished family		
Platacodon nanus		O
PACHYRHIZODONTOIDEI, indet.		
species indeterminate	r	O
PALAEOLABRIDAE		
Palaeolabrus montanensis	r	X
PHYLLODONTIDAE		
Phyllodus paulkatoi	r	X
Number and % survival		9/15 (60%)
LISSAMPHIBIA		
ANURA		
DISCOGLOSSIDAE		
Scotiophryne pustulosa		X
CAUDATA		
BATRACHOSAUROIDIDAE		
Opisthotriton kayi		X
Prodesmodon copei	r	X
LISSAMPHIBIA		
PROSIRENIDAE		
Albanerpeton nexuosus	r	X
SCAPHERPETONTIDAE		
*Lisserpeton bairdi*X		
cf. *Piceoerpeton* sp.	r	X
Scapherpeton tectum		X
SIRENIDAE		
Habrosaurus dilatus		
Number and % survival		8/8 (100%)
MAMMALIA		
MULTITUBERCULATA		
CIMOLODONTIDAE		
Cimolodon nitidus		X
CIMOLOMYIDAE		
Cimolomys gracilis	r	O
Meniscoessus robustus		O
Family indeterminate		
Cimexomys minor	r	X
Essonodon browni		O
Paracimexomys priscus		O
NEOPLAGIAULACIDAE		
Mesodma formosa		X
Mesodma hensleighi		O
Mesodma thompsoni		X
? *Neoplagiaulax burgessi*	r	X
Number and % survival		5/10 (50%)
EUTHERIA		
GYPSONICTOPIDAE		
Gypsonictops illuminatus		X
PALAEORYCTIDAE		
Batodon tenuis	r	X
Cimolestes cerberoides	r	X
Cimolestes incisus	r	X
Cimolestes magnus	r	X
Cimolestes propalaeoryctes	r	X
Number and % survival		6/6 (100%)
METATHERIA		
DIDELPHODONTIDAE		
Didelphodon vorax		O
Family indeterminate		
Glasbius twitchelli		O
PEDIOMYDAE		
Pediomys cooki	r	O
Pediomys elegans	r	O
Pediomys florencae		O
Pediomys hatcheri	r	O
Pediomys krejcii	r	O
PERADECTIDAE		
Alphadon marshi		X
Alphadon wilsoni		O
Protaiphadon lulli	r	O
Turgidodon rhaister	r	O
Number and % survival		1/11 (9%)

Chapter 7 from: *The Mistaken Extinction - Dinosaur Evolution and the Origin of Birds*, by Lowell Dingus and Timothy Rowe, 1998. W. H. Freeman, New York.



SURVIVAL OR EXTINCTION OF VERTEBRATE SPECIES ACROSS THE K-T BOUNDARY *(continued)*

Species from the Upper Cretaceous Hell Creek Formation, Montana		Survivors of K/T
REPTILIA		
TESTUDINES		
ADOCIDAE		
Adocus sp.		X
BAENIDAE		
Eubaena cephalica		X
Neurankylus cf. N. *eximius*		X
Palatobaena bairdi		X
Plesiobaena antiqua		X
Stygiochelys estesi		X
CHELYDRIDAE		
Chelydridae indet.		X
Emarginochelys cretacea		X
KINOSTERNIDAE		
Kinosternidae indet.		X
MACROBAENIDAE		
"*Clemmys*" *backmani*		X
NANHSIUNGCHELYDIDAE		
Basilemys sinuosa		O
PLEUROSTERNIDAE		
Compsemys victa		X
TRIONYCHIDAE		
Heloplanoplia distincta		O
"*Plastomenus*" sp. A		X
"*Plastomenus*" sp. C		X
Trionyx (*Aspideretes*) sp.		X
Trionyx (*Trionyx*) sp.	r	X
Number and % survival		**15/17 (88%)**
SQUAMATA		
ANGUIDAE		
Odaxosaurus piger		X
?HELODERMATIDAE		
Paraderma bogerti	r	O
NECROSAURIDAE		
Parasaniwa wyomingensis		O
SCINCIDAE		
Contogenys sloani		X
TEIIDAE		
Chamops segnis		O
Haptosphenus placodon		O
Leptochamops denticulatus		O
Peneteius aquilonius	r	O
?VARANIDAE		
Palaeosaniwa canadensis	r	O
XENOSAURIDAE		
Exostinus lancensis		X
Number and % survival		**3/10 (30%)**
CHORISTODERA		
CHAMPSOSAURIDAE		
Champsosaurus sp. indet.		X
Number and % survival		**1/1 (100%)**

Species from the Upper Cretaceous Hell Creek Formation, Montana		Survivors of K/T
CROCODILIA		
ALLIGATOROIDEA		
Brachychampsa montana		O
undescribed alligatoroid(?) A		X
undescribed alligatoroid(?) B		X
CROCODYLIDAE		
Leidyosuchus sternbergi		X
THORACOSAURIDAE		
Thoracosaurus neocesariensis	r	X
Number and % survival		**4/5 (80%)**
DINOSAURIA		
ORNITHISCHIA		
ANKYLOSAURIDAE		
Ankylosaurus magniventris	r	O
CERATOPSIDAE		
Torosaurus ? *latus*	r	O
Triceratops horridus		O
HADROSAURIDAE		
Anatotitan copei		O
Edmontosaurus annectens		O
NODOSAURIDAE		
? *Edmontonia* sp.	r	O
PACHYCEPHALOSAURIDAE		
Pachycephalosaurus wyomingensis	r	O
Stegoceras validus	r	O
Stygimoloch spinifer	r	O
Number & % survival		**0/10 (0%)**
SAURISCHIA		
DROMAEOSAURIDAE		
Dromaeosaurus sp.		O
? *Velociraptor* sp.		O
ELMISAURIDAE		
? *Chirostenotes* sp.		O
ORNOTHOMIMIDAE		
Ornothomimus sp.		O
TROODONTIDAE		
Paronychodon lacustris		O
Troodon formosus		O
TYRANNOSAURIDAE		
Albertosaurus lancensis		O
Aublysodon cf. A. *mirandus*	r	O
Tyrannosaurus rex		O
Number & % survival		**0/9 (0%)**
TOTAL NUMBER AND % SURVIVAL		**52/107 (49%)**

SOURCE: Data from J. D. Archibald, 1996, *Dinosaur Extinction and the End of an Era*, Columbia University Press, New York, pp. 84–85.

NOTE: X by scientific name means the species is represented by a survivor in the Tertiary. O by scientific name means the species went extinct. r means the species is rare in fossil collections.

In terms of mammals, different groups suffered vastly different rates of extinction. Late Cretaceous faunas in North America are known to have contained ten species of rodentlike multituberculates. Five of these are represented by descendants above the K-T boundary, resulting in an extinction rate of 50% for the group. Among marsupials, only one out of eleven species survived. However, among placental mammals, all six species are found in rocks above the boundary. Clearly, the events at the K-T boundary affected these groups of small mammals quite differently.

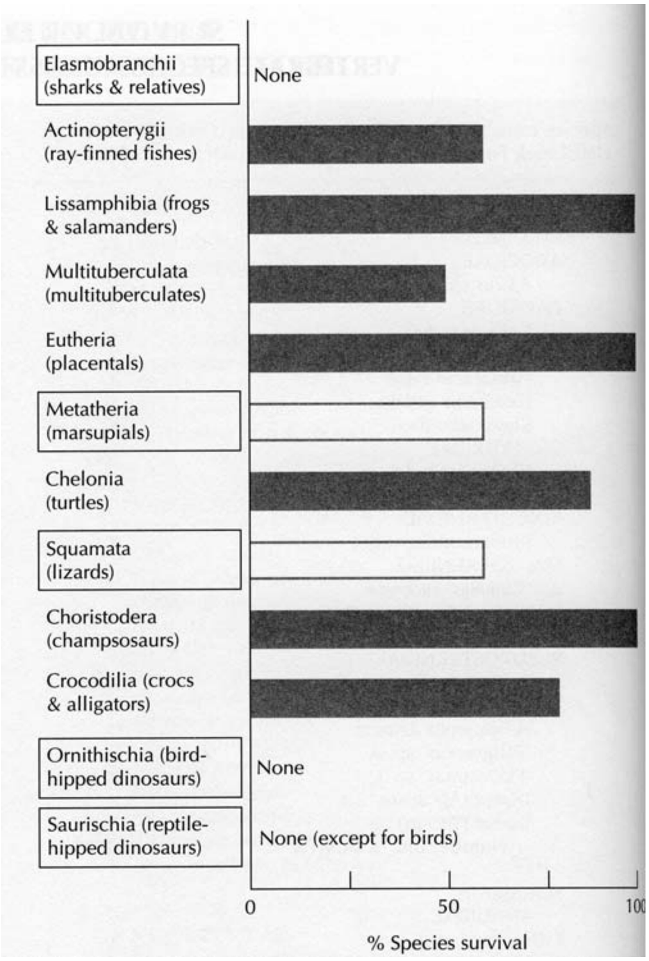


figure 7.03 This chart documents the rate of survival for late Cretaceous vertebrates during the K-T transition in the western part of North America. (from Archibald, J. D., 1996, Dinosaur Extinction and the End of an Era, Columbia Univ. Press, New York, p. 126)

The fossil record of birds is very poor in the Hell Creek Formation, although its implications for dinosaur extinction and survuval are quite important, as will be discussed in great detail in Part 2 of this book.

Finally, none of the nineteen species of conventionally recognized dinosaurs survived the boundary events. The decimated genera included: *Ankylosaurus, Torosaurus, Triceratops, Anatotitan, Edmontosaurus, Thescelosaurus, Edmontonia,* *Pachycephalosaurus, Stegoceras, Stygimoloch, Dromaeosaurus, Velociraptor, Chirostenotes, Ornithomimus, Paronychodon, Troodon, Albertosaurus, Aublysodon, and of course, Tyrannosaurus.*

Overall, of 107 species of terrestrial vertebrates present in the Hell Creek deposits, 49% appear to have survivors of the extinction event in the Western Interior of North America. If one accepts that some rarely preserved species survived but have not been found yet in rocks above the boundary, the overall survival rate could increase to over 60%. These are puzzling numbers that make up a complex pattern of survival and extinction. Archibald notes that, among terrestrial vertebrates, extinctions in just five of the twelve major groups (sharks and rays, marsupials, lizards and snakes, along with ornithischian dinosaurs, and saurischian dinosaurs) account for 75% of the extinctions that occurred in the Western Interior during the K-T boundary. He argues, quite correctly, that this pattern must be explained by any mechanism invoked as a cause for the extinctions.

Using this extensive paleontologic census as a foundation, Archibald has offerred a thoughtful analysis of why some groups of vertebrates, such a dinosaurs, suffered worse than others[34]. In essence, he considered three potential causes for the extinctions, the impact, volcanic events, and the retreat of shallow continental seas (fig. 7.09). In relation to the impact hypothesis, he argued that the known record of continental vertebrates does not jibe well with the killing mechanisms alleged to have resulted from the impact. For example, one would expect the cold blooded vertebrates to have been affected most by the subfreezing temperatures. For lizards, this seems to be true, as evidenced by a 70% rate of extinction across the boundary. However, other cold-blooded groups--frogs (0%), salamanders (0%), turtles (12%), as well as crocodiles and alligators (20%)--were minimally affected. In all, only four of the twelve groups of vertebrates studied (bony fish, multituberculate mammals, placental mammals, and lizards) fit the extinction pattern predicted by sudden cooling.

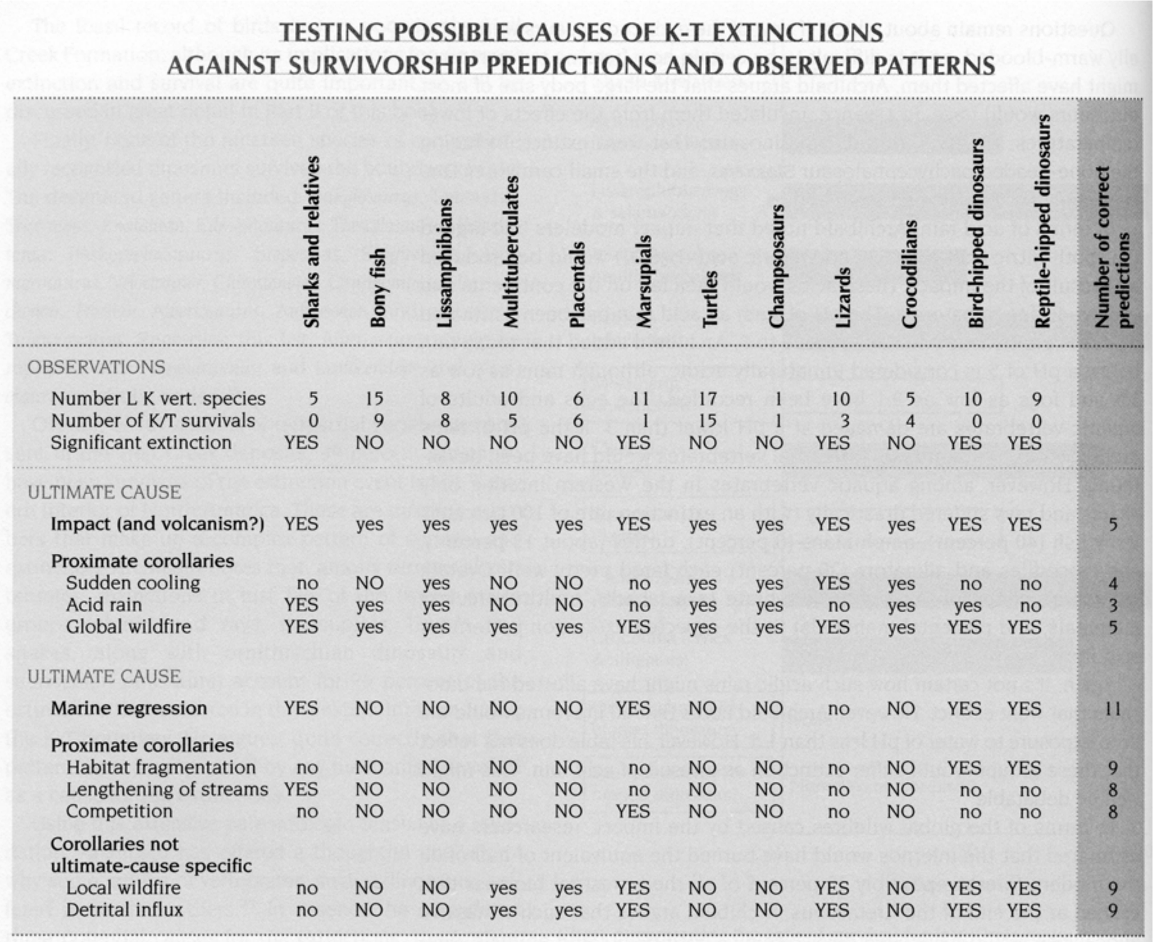
Questions remain about which, if any, of the extinct dinosaurs were acutally warm-blooded, so it is difficult to be certain how freezing temperatures might have affected them. Archibald argues that the large body size of most dinosaurs would have, in essence, insulated them from the effects of lower temperatures. However, not all the dinosaurs that went extinct, including the bone-headed pachycephalosaur*Stegoceras,* and the small carnivores *Dromaeosaurus and Troodon,* had large bodies.

In terms of acid rain, Archibald noted that impact modelers had argued that both nitric acid (HNO_3) and sulfuric acid (H_2SO_4) would be produced as a result of the impact. These would then fall on the continents and oceans during rain storms. The pH of such rains has been estimated by modelers to have been as low as 0-3. Archibald noted that in modern environments rain below a pH of 5 is considered unnaturally acidic, although rains as low as 3.8 and fogs as low as 2.1 have been recorded. The eggs and adults of aquatic vertebrates are damaged at a pH lower than 3. If the pH of rains dropped to 0, the results on terrestrial vertebrates would have been devestaing. However, among aquatic vertebrates in the Western Interior, only sharks and rays suffered drastically, with an extinction rate of (100%). Bony fish (40%), amphibians (0%), turtles (about 12%), and crocodiles/alligators (20%) fared pretty well. Overall, only three of the twelve major vertebrate taxa (sharks, multituberculate mammals, and placental mammals) fit the expected pattern for acid rain.

Again, it's not certain how such acidic rains would have affected the dinosaurs that went extinct.   However, Archibald notes that all life forms would die from exposure to water of pH less than 1.5. However, his table does not reflect that these groups would suffer extinction as a result of acid rain. This might well be debatable.

In terms of the global wildfires caused by the impact, researchers have estimated that the infernos would have burned the equivalent of half of all the modern forests, possibly 25% of all the terrestrial biomass that existed at the end of the Cretaceous. Archibald argues that such a massive apocalypse would have been devestating to to both plants and animals, generating a fall-out of organic an inorganic debris beyond any in our human experience. To him, such a horific event could not have produced the selective pattern of survival and extinction reflected in the known vertebrate fossil record. Of the twelve groups Archibald studied, only five (sharks, marsupials, lizards, ornithischians and saurischians) exhibit near total rates of extinction as would be expected by him if a global wildfire had actually occurred.

In all, Archibald concludes that only five of the twelve groups of vertebrates he studied exhibit extinction patterns consistent with the predicted patterns for impact related effects (sharks and rays, marsupials, lizards, and the two groups of dinosaurs).



TESTING POSSIBLE CAUSES OF K-T EXTINCTIONS
AGAINST SURVIVORSHIP PREDICTIONS AND OBSERVED PATTERNS

	Sharks and relatives	Bony fish	Lissamphibians	Multituberculates	Placentals	Marsupials	Turtles	Champsosaurs	Lizards	Crocodilians	Bird-hipped dinosaurs	Reptile-hipped dinosaurs	Number of correct predictions
OBSERVATIONS													
Number L K vert. species	5	15	8	10	6	11	17	1	10	5	10	9	
Number of K/T survivals	0	9	8	5	6	1	15	1	3	4	0	0	
Significant extinction	YES	NO	NO	NO	NO	YES	NO	NO	YES	NO	YES	YES	
ULTIMATE CAUSE													
Impact (and volcanism?)	YES	yes	yes	yes	yes	YES	yes	yes	YES	yes	YES	YES	5
Proximate corollaries													
Sudden cooling	no	NO	yes	NO	NO	no	yes	yes	YES	yes	no	no	4
Acid rain	YES	yes	yes	NO	NO	no	yes	yes	no	yes	yes	no	3
Global wildfire	YES	yes	yes	yes	yes	YES	yes	yes	YES	yes	YES	YES	5
ULTIMATE CAUSE													
Marine regression	YES	NO	NO	NO	NO	YES	NO	NO	no	NO	YES	YES	11
Proximate corollaries													
Habitat fragmentation	no	NO	NO	NO	NO	no	NO	NO	no	NO	YES	YES	9
Lengthening of streams	YES	NO	NO	NO	NO	no	NO	NO	no	NO	no	no	8
Competition	no	NO	NO	NO	NO	YES	NO	NO	no	NO	no	no	8
Corollaries not ultimate-cause specific													
Local wildfire	no	NO	NO	yes	yes	YES	NO	NO	YES	NO	YES	YES	9
Detrital influx	no	NO	NO	yes	yes	YES	NO	NO	YES	NO	YES	YES	9

figure 7.04 This table from Archibald's 1996 book attempts to correlate the potential killing mechanisms resulting from impact, volcanic activity and seaway retreat with the pattern of extinctions and survival in vertebrates of the Western Interior in North America. (from Archibald, J. D., 1996, Dinosaur Extinction and the End of an Era, Columbia Univ. Press, New York, p. 128.

Turning to volcanic scenarios, Archibald notes that Deccan researchers have estimated that enough lava was produced to cover both Alaska and Texas to a depth of 2000 feet. In Archibald's view, the primary consequence would have been higher levels of debris in the atmosphere, especially carbon dioxide. This resulted in global warming due to the greenhouse effect, and it may have been a boon for plants, which utilize carbon dioxide in photosynthesis. Yet, Archibald notes that some evidence based on measuring different forms of oxygen atoms in marine sediments off of Africa suggest that the temperature of the ocean actually decreased by about 8 degrees C during the K-T transition. He suggests that because of the long-term nature of this temperature change, most organisms, especially those with short generation times, would have been able to adapt successfully. Those with longer generation times, such as dinosaurs, might not have been able to.

Curiously, Archibald does not address potential effects of acidic rain generated by volcanic eruptions, an effect prominently discussed by proponets of the volcanic scenario for extinction. However, in his table summarizing his results (6.1) he lumps the effects of impacts and volcanism together, so presumably his conclusions would mirror those argued for impact-based acid rains. If volcanism is assumed to have caused sudden cooling and acid rain, but not global wildfires, the the table can be used to estimate how many of the twelve groups fit the expected pattern of extinction. Four of the twelve groups fit the expected pattern (sharks and rays, multituberculate mammals, placental mammals, and lizards).

Finally, Archibald discusses how the fossil record of vertebrates fits the potential effects resulting from the retreat of contiental seas back into the major ocean basins at the end of the Cretaceous. As noted previously, the retreat of these seaways is probably related to plate tectonic motions and may even be related to the plumes of magma that created the large episode of volcanic activity at the end of the Cretaceous.

Archibald, citing work by a group of British scientists, first presents the case that the retreat of the continental seas at the end of the Cretaceous was among the most extensive in the history of the Earth[35]. As the seaways pulled back, the land surface of the planet is thought to have increased by more than 25%--an increase equal to adding a continent the size of modern-day Africa. He notes three resulting potential causes for extinction: habitat fragmentation, lengthening of streams and competition from invading species across land bridges.

Archibald argues that the retreat of the seawys generated a reduction in the area of coastal plains, where most of our evidence of late Cretaceous vertebrates is found. He reasons that such a reduction of habitiat would affect large vertebrates, such as most dinosaurs, first because these require the most habitat area per animal to satisfy their needs. As evidence for such a effect, Archibald cited the deleterious effects of habitat loss on today's large mammals in the Rift Valley System of East Africa. He goes on to discuss another effect of the marine regressions--habitat fragmentation. He notes that some paleontologists have argued that the concept of habitat fragmentation is not testable with geographically incomplete fossil records. But citing the work of modern ecologists, Archibald states that, if a habitat is broken up into many pieces, the ability of animals to move from one area of the habitat to another will be impeded. Consequently, it may not be possible to maintain populations of animals large enough to assure a species' reproductive viability, especially for large organisms, like dinosaurs.

Comparing this prediction to the fossil record, Archibald notes that only eight of 30 large vertebrate species present in the late Cretaceous survived the extinction events. All eight survivors were at least partially aquatic, including two fish, one turtle, and a number of crocodiles and alligators. The extinguished species include one turtle, one lizard, one crocodilian, and 19 dinosaurs. He argues that nine of the 12 groups he studied fit the expected extinction pattern for habitat fragmentation (all but sharks, marsupial mammals, and lizards).

Second, Archibald notes that with the retreat of seaways, river systems must have become longer, increasing the area of these freshwater aquatic habitats. Freshwater vertebrates, including ray-finned fish, salamanders, aquatic turtles, crocodiles and alligators, did pretty well. However, the sharks and rays, with their ties to marine environments, disappeared from the area. In all, Archibald feels that eight of the twelve vertebrate groups studied fit the extinction pattern predicted by lengthened rivers and reduced coastal marine environments (all but marsupial mammals, lizards, and the two groups of dinosaurs).

Finally, Archibald argues that the drastic reduction of marsupial mammals across the K-T boundary was due to the immigration and resulting competition of archaic hooved mammals from Asia. The fossil record shows that about 15 species of marsupials were present in the Western Interior just before the K-T boundary. That number dropped precipitiously to one after the extinction events. As the seaways retreated, the Bering Land Bridge between Alaska and Asia became exposed above sea level. Within a million years of the K-T boundary, 30 species of archaic hooved mammals, thought to have originated in Asia between 80 and 85 million years ago, reached North America. It's this coincidence that led Archibald to suggest that the archaic hooved mammals out competed the marsupials. This is certainly possible, but competition in the fossil record is a very difficult proposition to test because we cannot observe the populations interact. Despite this, Archibald argues that eight of the 12 groups have extinction patterns consistent with the expected effects of competition (all but sharks, lizards, and the two dinosaur groups).

In all, Archibald argues that the fossil records for eleven of the twelve groups of vertebrates studied fit the anticipated patterns for the three extinction mechanisms related to marine regression. Only lizards do not. Accordingly, Archibald concludes that marine regression the most evidence available in the fossil and rock records.

At the time of this writing, Archibald's study has just been published. It's clearly the most comprehensive effort of its kind and will undoubtedly generate a great deal of further discussion from advocates of all the different extinction hypotheses.

Thus, there is good geological evidence for a monumental impact, a massive volcanic event, and the retreat of shallow continental seaways at the end of the Cretaceous. The "killing mechanisms" ascribed to each event could have taken their respective tolls on the Earth's biota. Since many of those killing mechanisms were associated with more than one event and since different killing mechanisms from different events could have killed off a particular group of organisms, it is difficult to associate the extinction of particular groups with a particular event. This is especially true since the period of volcanism and seaway retreat overlapped in time with the period of impact(s).

If we could assure ourselves that the extinctions occurred very quickly at the end of the Cretaceous, rather than over a longer period of time, that might help us decide which event was responsible. This is because the effects of the impact are thought to have operated over a period of only months to a few thousand years, whereas those associated with volcanism and seaway retreat are generally thought to have operated over tens or hundreds of thousands of years. How well can we really distinguish the durations of these kinds of events in the geologic record at the end of the Cretaceous? That question is the focus of the next chapter.

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