

Survival in the first hours of the Cenozoic

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ABSTRACT

For several hours following the Chicxulub impact, the entire Earth was bathed with intense infrared radiation from ballistically reentering ejecta. The global heat pulse would have killed unsheltered organisms directly and ignited fires at places where adequate fuel was available. Sheltering underground, within natural cavities, or in water would have been a necessary but not always sufficient condition for survival. Survival through sheltering from an initial thermal pulse is not adequately considered in literature about Cretaceous-Tertiary nonmarine extinctions. We compare predicted intense, short-term, thermal effects with what is known about the fossil record of nonmarine vertebrates and suggest that paleontological evidence of survival is compatible with theoretical results from bolide physics.

Keywords: bolide physics, Chicxulub, Cretaceous, evolution, extinction, extraterrestrial impact, infrared radiation, nonmarine, Paleocene, survival, Tertiary, vertebrates.

INTRODUCTION

The pattern of differential survival among nonmarine vertebrates across the Cretaceous-

Tertiary (K-T) boundary is one of the outstanding problems in paleontology. As Alvarez (1997, p. 14–15) stated, “Many smaller land animals survived, including mammals, as well as reptiles such as crocodiles and turtles. No one really understands why these animals escaped extinction.” Powell (1998, p. 174) noted, “No one has yet been able to explain under any theory why the crocodiles and turtles survived and the dinosaurs did not.” As Fastovsky and Weishampel (1996, p. 411) put it, “The pattern of selectivity—that is, who survived the extinction and who did not—becomes an important issue in understanding an extinction and determining its probable cause.” Clemens (quoted by Morell, 1993, p. 1519) asked, “The real question is, how did the others—how did any animal—manage to survive? [Impact theorists] have got to come up with a hypothesis that puts equal weight on survival. So many of these catastrophists want to kill the dinosaurs [that] they forget the rest of the biota. Birds, mammals, and amphibians managed to survive, and that tells you that there is something wrong with most of these hypothetical horrors.”

Many authors (e.g., Sheehan and Fastovsky, 1992; Archibald, 1996b; Dingus and Rowe, 1997) have tried to deal with the issue but have not adequately appreciated the selective qualities of an intense, short, worldwide barrage of heat that preceded longer-lived effects

of the Chicxulub impact. We argue that the stage for later evolutionary events was set by patterns of differential survival resulting from the short heat pulse caused by infrared (IR) radiation from reentering ballistic impact ejecta suborbitally lofted above the atmosphere by the Chicxulub K-T impactor. The IR pulse has been described by Melosh (1990, 2001), Vickery and Melosh (1990), Melosh et al. (1990), Toon et al. (1997), Kring (1995, 2000), and Kring and Durda (2002).

After discussing the initial worldwide thermal assault, we examine the full range of nonmarine vertebrate survivors of the initial devastating effects—and suggest the reason for their survival. We argue that sheltering underground, within natural cavities, or in water was the fundamental means to survival during the first few hours of the Cenozoic. Shelter by itself was not sufficient to guarantee survival, but lack of shelter would have been lethal. We integrate information from physics and paleontology to develop a hypothesis that can be tested through improved global documentation of biotic change in the nonmarine realm across the K-T boundary. The discussion here has a global scope even though, at present, it is only in a small part of western North America that the paleontological record is adequate for detailed analysis of floral and faunal reorganization within nonmarine settings of the earliest Cenozoic.

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TABLE 1. GLOBALLY CATASTROPHIC EFFECTS AND INDIVIDUAL MEANS FOR SURVIVAL IN THE NONMARINE REALM DURING AND IMMEDIATELY AFTER THE K-T IMPACT

Agents of stress	Mechanisms of damage	Relevant durations of effects	Means to survival
Intense overhead heat pulse	Lethal body temperature, incineration	Minutes to hours	Sheltering
Fires	Burns; pyrotoxins	Minutes to hours	Sheltering
Dust/soot/sulfate and NO _x loading; abnormal metals in soil; disruption of primary productivity	Cooling; cessation of photosynthesis; vision impairment; poisonous environment	Minutes or hours to many months	Sheltering; aestivation; ability to reduce metabolic rates; ability to locate food

Note: Data from Vickery and Melosh (1990); Melosh et al. (1990); Kring (1995, 2000); Kring and Durda (2002); Kieffer et al. (2002); Rampino (1999); Anders et al. (1991); Toon et al. (1997).

TABLE 2. NONMARINE VERTEBRATES THAT BECAME EXTINCT AT THE BEGINNING OF THE CENOZOIC

Vertebrate groups	Reasons for extinction
A few turtles: one species of aquatic baenid (<i>Theselus insiliens</i>), one aquatic species of subgenus <i>Trionyx</i> , one aquatic species of indeterminate dermatemydine, and probably the tortoiselike dermatemydid <i>Basilemys sinuosa</i> (known from one possibly reworked individual at Bug Creek, Montana) (Hutchison and Archibald, 1986)	Unknown; most turtle groups survived
Azhdarchid pterosaurs	Nonsheltering
Some lizards: e.g., most North American teiids; three of six other Maastrichtian species in part of western North America	Unknown
Crocodylians: one of six Maastrichtian species in Montana	Unknown; most crocodylians survived
Nonavian dinosaurs	Nonsheltering, except possibly the smallest, for which there is no evidence; loss of plant primary productivity
Archaic birds	Unknown
Some therian mammals: e.g., some eutherians (<i>Gypsonictops</i>) and most North American marsupials	Unknown

TABLE 3. NONMARINE VERTEBRATE GROUPS WITH MEMBERS THAT PERSISTED INTO THE CENOZOIC

Vertebrate groups	Means for survival
Fishes	Shelter in water, burrows
Amphibians, lizards, amphisbaenians, snakes	Shelter in water, burrows in sediments, soil, wood, or beneath rocks
Turtles (nearly all aquatic lineages) (Hutchison and Archibald, 1986)	Shelter in water, burrows
Champsosaurs (Choristodera)	Shelter in water
Crocodylians	Shelter in water, burrow
Neornithine birds	Dive, swim, shelter in water, marshlands, burrows, nest in tree holes, termite nests
Monotreme mammals (Gelfo and Pascual, 2001)	Semiaquatic or burrowing
Gondwanatherian mammals (Sudamericidae, if separate from multituberculates; extinct later in Cenozoic)	Small size, possibly sheltering behavior
Multituberculate mammals (extinct later in Cenozoic)	Probably sheltering behavior (little known); known widespread distribution and rodent-like habits suggest ability to survive in polar darkness; probable abilities for torpor and food storage underground (Kielan-Jaworowska and Qi, 1990)
Dryolestoid mammals (extinct in early Cenozoic) (Gelfo and Pascual, 2001)	Small size, probably sheltering behavior
Marsupial mammals (some surviving, especially in some southern landmasses; one group in North America spread to Europe, Africa, and Asia but became extinct there later in Cenozoic)	None more than 1 kg in body mass until later in Puercan (early Paleocene) time and most less than that; potential burrowers or semiaquatic, based on closest living relatives
Placental mammals (some or all early placental mammals [a subset of eutherian mammals] present at close of Cretaceous; e.g., <i>Cimolestes</i> , <i>Protungulatum</i>) (Fox, 1989)	Same

We ask the obvious questions. What were the primary agents of stress? What were the mechanisms of the damage? What were the relevant durations of effects of the various

stresses? What common factors led to survival through the various kinds and durations of stress? Which nonmarine vertebrates were likely to have had significant numbers of in-

dividuals that sheltered underground or in water at the time of the Chicxulub impact? Do patterns of differential survival among nonmarine vertebrates match these expectations? Table 1 relates to the first four questions. Table 2 lists the nonsurvivors and Table 3 the survivors.

BASIC PHYSICS RELATED TO SURVIVAL

Assumptions

We accept that the K-T impactor was an asteroid 10–15 km in diameter (having a mass of $\sim 1-4 \times 10^{15}$ kg), arriving at tens of kilometers per second at an angle of perhaps 45° to Earth's surface (Kring, 1995), that produced a collapsed transient cavity $\sim 80-100$ km in diameter and a multi-ring basin 170–200 km in diameter (Melosh et al., 1990; Pope et al., 1997; Rampino, 1999; Kieffer et al., 2002) on the Yucatán peninsula of Mexico. Significant doublet (Bottke and Melosh, 1996) companion impactors, if any, are currently unrecognized. Kamensk crater in Russia dated at 65 ± 2 Ma (Rampino, 1999) and Silverpit crater in the North Sea dated at 65–60 Ma (Stewart and Allen, 2002) are of negligible size. However, impact of a companion 2-km-diameter doublet asteroid somewhere in the Pacific Ocean has been suggested on the basis of spinels and spherules cored at the K-T boundary at Deep Sea Drilling Project Site 577 (Robin et al., 1993). If such an impact occurred, its crater is either unrecognized or has been subducted, and in any case its effects would have been “local.” A larger, potentially highly significant, possible doublet-asteroid companion crater 300 km in diameter in the Colombian Basin southeast of Chicxulub has also been suggested (Hildebrand and Boynton, 1990a, 1990b, 1991) but is apparently now discounted or not investigated further. A double-impact event might help to explain some aspects of the K-T extinction problem raised by Keller et al. (1998) but is not necessary for the arguments developed here.

Local and Regional Effects of an Impact

Many authors (e.g., Anders et al., 1991; Boslough et al., 1996; Toon et al., 1997; Rampino, 1999) have examined specific aspects of environmental stresses following a large impact. Some stresses have effects only local or regional in scale, such as impact blast, earthquakes, a giant tsunami at coasts, chemical influences such as acid rain caused by NO_x and SO_2 production at impact, poisoned waters and soils, mutagenic pyrotoxins, temporary loss of primary photosynthetic productivity, and impact-caused volcanism above the antipodal asthenosphere heated by seismically focused energy. Local or regional stresses could not have produced global-scale nonmarine extinction, and general effects such as acid rain would have been locally neutralized by alkaline rocks and soils. A giant tsunami would have devastated some coasts and lowlands, but not all. Table 1 outlines some of the global stresses that have been hypothesized, including the thermal pulse that we focus on here.

A Short-Term Infrared Thermal Event

Our hypothesis centers on the differential probability of survival for terrestrial organisms through the hours-long, global pulse of intense IR flux that followed the Chicxulub impact. This intense IR flux was generated on a global scale by particles that were lofted into suborbital trajectories and became incandescent upon reentering the upper atmosphere (Melosh et al., 1990; Kring, 1995, 2000; Toon et al., 1997; Kring and Durda, 2002).

The worldwide, overhead, intense IR thermal radiation was the first significant stress after the Chicxulub impact (Melosh et al., 1990). It occurred during the first hours after the impact, prior to the atmospheric opacity that presumably led to "nuclear winter." This first event was stressful enough to kill all individual nonmarine macroscopic organisms except those protected in soils, underground, under rocks, or in water, in dense aquatic vegetation, or as sequestered eggs, pupae, spores, seeds, or roots.

The only nonelectromagnetic phenomenon that travels as fast as lofted suborbital impact ejecta (7–8 km/s) is seismic energy (8–14 km/s). Therefore, heat energy released from reentering ejecta would have affected large areas of the globe that had been perturbed by passing seismic waves but not yet by other agencies of mass destruction.

Despite uncertainties surrounding the details of the Chicxulub impact event (especially in mass and velocity of the impactor), there is

only a relatively small uncertainty about the thermal pulse itself. The existence, the magnitude, and the global extent of the thermal pulse are all strongly constrained by the evidence of the spherules in the boundary clay, which has not been completely sampled on a global basis. Spherules are formed from ejecta particles as they melt and incandesce on reentry. (But see Schmitz [1988] for a different interpretation of the origin of spherules.) The total mass of these spherules can be estimated from sample measurements, and their velocity must have been close to orbital velocity. The total kinetic energy of the spherules is therefore well established, and this kinetic energy must have converted to thermal energy upon reentry into the upper atmosphere. As Melosh et al. (1990, p. 252) wrote, "The arrival of the ejecta at any point on the Earth is accompanied by impressive amounts of energy: . . . a total energy of $1.3\text{--}5 \times 10^8 \text{ J}\cdot\text{m}^{-2}$ is deposited in the atmosphere. If most of the ejecta is in the form of condensate particles, this energy will be emitted as thermal radiation from altitudes in the neighborhood of 70 km. A standard tabulation of nuclear-weapons effects indicates that thermal energies of $2\text{--}4 \times 10^5 \text{ J}\cdot\text{m}^{-2}$ are sufficient to ignite dry forest materials, so thermal radiation from the reentering ejecta should be more than sufficient to start the global wildfires inferred from the soot in the [K-T] boundary layer." Melosh et al. (1990) estimated temperatures in the upper atmosphere (at ~ 70 km) in the range of 800–1100 K for several hours.

We suggest that the spherules are, in effect, the "smoking gun" of K-T nonmarine extinctions because they provide the critical evidence for the magnitude and the geographic extent of the heat pulse. The estimated cumulative global mass of spherules gives a lower bound on the total mass of the reentrant material (the process of converting reentering impact debris into spherules is not likely to have been perfectly efficient). The observed spherule mass from individual stratigraphic sections, extrapolated across the globe, allows us to estimate a lower bound on total kinetic energy of the reentrant material and thus a lower bound on intensity of the heat pulse, as noted in the paragraph above. The global distribution of spherules is therefore of central importance to the study of the impact. Spherules have been found in numerous locations in North America and Europe, but their distribution in more distant areas of the globe is not as well sampled. Nevertheless, Smit (1999) reported spherule layers in Tbilisi and New Zealand, and Smit and Romein (1985) showed spherules in drilling sites in the South

Atlantic. Smit (1999, p. 86–87) commented that "at sites more than 7000 km from the Chicxulub crater, the thickness of the ejecta layer, when properly reconstructed, is fairly constant at not more than 2–3 mm." We see from the soot evidence in New Zealand (see below) that the quantity of spherules was sufficient there to produce enough IR radiation to ignite fires. The global extent of the IR pulse therefore seems fairly well established. Ironically, in some cases the process of analyzing the boundary clay for iridium and other important impact indicators has destroyed the spherules.

Intensity and Duration of Thermal Flux

The several-hour duration of excessive energy flux released by reentering ejecta is essential to our argument. The normal zenith solar flux reaching Earth's surface is $\sim 1.4 \text{ kW}\cdot\text{m}^{-2}$. This value can be compared to the estimate by Melosh et al. (1990, p. 253) of global flux of thermal radiation reaching Earth's surface "of the order of $10 \text{ kW}\cdot\text{m}^{-2}$ over periods ranging from one to several hours after the impact. These power levels are comparable to those obtained in a domestic oven set at 'broil.'" Thermal energy at the Earth's surface would have been concentrated within 6000 km of the impact and concentrated again at its antipode (Melosh et al., 1990; Boslough et al., 1996). The amount of overhead thermal radiation everywhere, however, would have been sufficient to ignite terrestrial fuel except where Earth's surface was shielded by very dense cloud cover. Normal cloud cover would not have provided sufficient protection for exposed organisms; such cloud cover "is readily evaporated and may not [have provided] much protection to the forests beneath" (Melosh et al., 1990, p. 253). Power levels of that order would have been lethal to unprotected organisms.

Atmospheric Effects of Heat Pulse

The intense IR radiation would have originated from the entire sky. Darkness would have been eliminated worldwide for several hours and shadows curtailed. Shadowing effects would have been restricted to a direct proportion of the fraction of the sky blocked by a massive object. An organism at the foot of a lengthy vertical cliff, for example, would have been spared radiation from just under half the sky. It would not have been sufficient to shelter in a gully, under an isolated tree, or even under a sparsely forested canopy. Life confined to Earth's surface would have per-

ished well before incineration. After ignition temperature was reached, fires would not have spread from one area to another in the usual way. Rather, fires would have ignited nearly simultaneously at places having available fuel (Melosh et al., 1990; Wolbach et al., 1988; Jones and Lim, 2000; Ivany and Salawitch, 1993; Gilmour et al., 1989). The fires (on land with sufficient fuel) would have been especially intense because IR radiation coming from the entire sky continued to add heat even as the fires burned. But the focus in this paper is not on global fires but rather on their cause.

Air Temperature at Earth's Surface

The atmosphere itself would have been largely transparent to IR radiation from the re-entry of ejecta coming from Chicxulub. Therefore, the air temperature at ground level at points distant from the impact (and lacking fuel for combustion-related, local temperature rise) would have been elevated by only ~ 10 K (Melosh et al., 1990). The biological implications of these distinctions from common experience are profound. Vertebrates at or near the surface of the ground or water would have been able to breathe without searing their respiratory membranes. But unless they were sheltered from direct surface (skin) exposure to the IR pulse, they would have perished quickly from absorption by their surficial tissues of intense thermal radiation coming from the entire visible sky. This absorbed heat would have been transported to the nervous system with lethal results. The worldwide fire or likely subsequent reignition of dead trees by lightning would have been secondary effects that are irrelevant to our hypothesis.

Similarly expected effects on plant tissues lead to a potential test of our hypothesis. We predict that at the base of the K-T fallout layer on preimpact vegetated ground (above the water table), there should be no remains or impressions of leaves where the fallout settled. Most of the surface vegetation and dry litter should have burned off prior to the settling of most of the K-T fallout. In contrast, unburned leaves are often found at the base of volcanic ash beds deposited above the water table. In strata deposited under quiet waters in coal swamps and lakes, preserved leaves would be expected at the base of fallout from both impact debris and volcanic ash. Thus, our hypothesis satisfies criteria for testability suggested by Williams (1994).

A complete burning of the Cretaceous terrestrial biomass would have reduced the total oxygen content in the air by less than 1% (under the assumption of a maximum biomass

carbon density of 1.5 g/cm^2 (Wolbach et al., 1988, p. 668) and the present atmospheric oxygen mass of $1.1 \times 10^{21} \text{ g}$). However, there might have been local oxygen deficiencies near or under the fire, as in firestorms over burning cities in war. This possibility would not have affected vertebrates that were able to spend extended periods of time underwater (fishes, amphibians, champsosaurs, crocodilians, many turtles), but might have affected certain tropical and temperate burrowing animals. If oxygen deprivation was a problem, then survivorship in burrows might have been concentrated in environments that had relatively little fuel, such as desert, alpine, or polar ecosystems or near oceans where convective winds blowing from the sea toward the fire would have helped to replenish oxygen.

Physics Related to Prime Habitats for Sheltering

Under Soil

Soil is essentially opaque to IR radiation; radiant thermal energy is dissipated in its top millimeter or so. Absorbed thermal energy can be carried to greater depths only by conduction. The measured thermal conductivity of soil ranges from 0.0024 to $0.024 \text{ W/(m}\cdot\text{K)}$, the specific heat capacity of rock and soil minerals is $\sim 710 \text{ J/(kg}\cdot\text{K)}$ (Mitchell, 1993), and the density of soil is $\sim 1500 \text{ kg/m}^3$. If we take the extreme assumption that the surface of the soil during the K-T event was in thermal equilibrium with the IR flux from the upper atmosphere at $\sim 1000 \text{ K}$ (the temperature would have been lower than this through limited shadowing and cooling by evaporation of soil moisture), then between 2 and 20 h would have been needed to raise soil temperature by $\sim 1 \text{ K}$ at a depth of 10 cm below the surface. Therefore, a burrow deeper than 10 cm beneath the surface would have provided adequate shelter from incident thermal radiation during the critical hours.

As Pyne et al. (1996, p. 190) commented on the shielding effect of soil in normal-scale, modern fires, "There is general consensus that fires are responsible for small or insignificant levels of direct vertebrate mortality, although faunal mobility, fire size, and seasonality influence animal survival. For rodents that nest underground, sometimes several feet below the surface, in-place survival is high because soil is an excellent insulator." But, as we reiterate, it was the initial thermal pulse coming from the entire sky that is most important to the present discussion—not the subsequent, global firestorms.

Under Water

Shelter in water from intense, worldwide IR radiation is a more complex problem, although water is also opaque to incident thermal radiation. IR radiation at $1000\text{--}1200 \text{ K}$ would have a spectral peak at wavelengths of $2500\text{--}3000 \text{ nm}$, and IR absorption coefficients for water range as high as $13,000 \text{ cm}^{-1}$ at these wavelengths (Zolotarev et al., 1969). Most incident radiant energy, therefore, would have dissipated in the top few micrometers of water as latent heat of vaporization of surface water. Thin layers of heated surface water would have been stable against convection, but some heat might have been carried to minor depths by wind-driven currents or turbulence.

SOOT AND CHARCOAL

Globally distributed thermal radiation accounts for the widespread occurrence of soot associated with the Cretaceous-Tertiary boundary. Soot deposits amounting to 11 mg/cm^2 are widespread at the boundary (Anders et al., 1991; Boslough et al., 1996; Toon et al., 1997; Wolbach et al., 1988; Rampino, 1999; Kring, 2000; Kring and Durda, 2002). According to Wolbach et al. (1988, p. 665), "Cretaceous-Tertiary (K-T) boundary clays from five sites in Europe and New Zealand are $10^2\text{--}10^4$ -fold enriched in elemental C (mainly soot), which is isotopically uniform and apparently comes from a single global fire." This soot layer is often discussed regarding climatic effects (while the ash remained aloft) and as a source of pyrotoxins. The soot layer coincides with the Ir layer, suggesting that the fire was triggered by meteoritic impact and began before the ejecta had settled. But we note that the most fundamental cause of the fire itself is rarely considered in discussions of the selectivity of the K-T extinctions.

Wolbach et al. (1988, p. 668–669) further stated that "[t]he global amount of K-T carbon, $(7 \pm 4) \times 10^{16} \text{ g}$, is very large: $\sim 10\%$ of the present (above-ground) biomass carbon. In present-day forest fires, soot yields range from 0.1 to 2%." Such a massive amount of soot is commensurate with burning virtually all of the above-ground biomass, even if that biomass was significantly greater than that which exists today. Kring and Durda (2002) suggested that the fires were less than global in extent. However, their calculations show that global distribution of IR radiation causing such fires still would have been lethal to unsheltered organisms, even if it was slightly less than what would be needed to ignite fires everywhere. Unprotected organisms would

have succumbed well before the point even of partial incineration.

Jones and Lim (2000) discounted the results of Melosh et al. (1990) on the basis that “decayed and charred” wood occurs stratigraphically above the K-T impact debris, but we consider their argument irrelevant. Charred (or merely oxidized) wood is common in sediments (personal observations based on field screening for bones and teeth) and can occur at many stratigraphic levels. Moreover, any resulting charred wood from an initial global conflagration (as well as from other causes) would continue to accumulate (and be redeposited) for some time after the initial hours of the global heat pulse and the abnormally intensified fires.

We emphasize that the central point of this paper is that initial mortality among terrestrial organisms was caused largely by the thermal pulse that ignited these fires. The fires themselves also would cause some mortality but only among survivors of the thermal pulse. The principal importance of evidence from fossil soot is to provide significant circumstantial corroboration for the magnitude of the thermal pulse, simply noting that it was sufficiently intense to ignite widespread fires.

SELECTIVITY IN PATTERN OF SURVIVAL

Effects of Initial Heat Pulse vs. Longer-Term Global Fire

Archibald (1994, p. 385) argued that “[d]uring a global wildfire, terrestrial vertebrates would be baked or fried and the aquatic environment choked with debris, killing most life. Like the global bolide impact scenario, the global wildfire is so broad in its killing effects that it explains everything and nothing.” Later he argued (1996a, p. 385) that “[t]he global wildfire scenario is so broad in its killing effects that it could not have been selective.” Then he tempered these claims (1996b, 2000) but restricted his list of bolide effects (mainly to months of atmospheric opacity), arguing that the bolide provided the coup de grâce in a time near the close of the Maastrichtian in which long-term stresses held more important negative influences. Archibald did not mention a brief but intense, worldwide thermal pulse associated with a large bolide impact.

Contrary to Archibald’s viewpoint, we argue that the effects of intense overhead thermal radiation delivered for several hours at 10 or more times the power coming from the Sun would have been highly selective in determin-

ing which lineages of nonmarine vertebrates survived. Individuals small enough to shelter in soils, underground, deep in rock piles, or possibly in holes in very large trees would have been favored. We are mindful that not all sheltered organisms would have been guaranteed ultimate survival; further effects of the impact were yet to transpire. But the first selective cut would have been entirely dependent upon shelter from the enormous flux of incoming thermal energy.

Probability of Survival Linked to Body Size and Specific Habitats

Several authors have commented on differential extinction of nonmarine vertebrates without providing adequate explanation for it. From Table 1 and our discussion it is clear that certain body sizes and occupations of specific habitats would have favored initial survival. Being too large to find a hole to hide in would have been a death sentence. Another obvious factor is that small creatures, normally sheltering or hunting underground or deep enough in rock piles, likely would have survived an overhead thermal pulse coming from the entire visible sky. But there also exist more broadly based, evolutionary advantages of small body size (<3 kg) in mammals were summarized by Bourlière (1975). Principal advantages according to Bourlière include: (1) ready concealment from predators and low energy expenditure needed for escape; (2) wide variety of potential foods; (3) wide variety of available microhabitats; (4) potentially high rates of population increases in response to favorable environmental conditions; and (5) high potential for rapid evolutionary change in adaptation to prevailing conditions through splitting into small, localized populations.” Almost all of these features would apply to small vertebrates generally, and they might also be considered as preadaptations in the context of survival through the heat pulse in the earliest Cenozoic.

Regardless of body size, living in a lake, stream, or marsh would have been advantageous also. Cold-blooded vertebrates that did not need to come to the surface frequently (e.g., fishes, crocodiles, champsosaurs, most turtles, amphibians) easily could have survived the intense but short period of worldwide overhead thermal radiation simply by remaining underwater. Many warm-blooded,

semiaquatic mammals and birds could have survived in lakes, marshes, or swamplands having dense sheltering vegetation unlikely to burn fully. Some of these endotherms may have been capable of remaining underwater, surfacing only occasionally to breathe.

The Fossil Record

With the exceptions of a few avian, crocodylian, and turtle lineages, the extinct groups listed in Table 2 had no obvious large members known to have been present up to the K-T boundary that employed a burrowing or swimming lifestyle. We do not address the question of how many lineages of nonavian dinosaurs were still present to suffer the effects of the Chicxulub impact (Sheehan and Fastovsky, 1992). In any case, however, it is difficult to imagine a burrowing *Triceratops* or a swimming tyrannosaur. Moreover, even hadrosaurs are now thought to have been primarily terrestrial (Weishampel et al., 1990).

No evidence has been offered that late Maastrichtian pterosaurs or nonavian dinosaurs could burrow, swim, or dive (Padian, 1983). That some of the smallest nonavian dinosaurs may have survived is possible, but we know of no valid occurrences of dinosaurs in Cenozoic rocks other than reworked nonavian remains and birds. Whether airborne or on land, a Maastrichtian pterosaur would soon have been “broiled.” Some dinosaurs are known to have brooded eggs in nests (Norell et al., 1995) where the eggs might have been sheltered from overhead IR radiation by a dead parent’s body. We do not know if the young were precocial, but there are many reasons to expect that any nonavian dinosaur eggs or hatchlings still alive in the immediate aftermath of the bolide impact would not have survived long. Even large, precocial hatchlings in modern birds (a dinosaurian subset) almost always require care after they leave the nest.

In contrast to those species that went extinct, most of the terrestrial vertebrate groups that survived into the early Cenozoic include members or have close relatives that were at least semiaquatic then or are so today, or nest, den, or forage underground. Some hibernate or lie dormant for extended periods underground, underwater, or both (e.g., turtles and most amphibians) or lay eggs underground or in water. In western North America, amphibians apparently lost no lineages (possibly because of too few data), and turtles suffered relatively minor K-T extinction, with a loss of perhaps 4 genera out of 19 known to have existed during the Maastrichtian in Montana

(Hutchison and Archibald, 1986). All surviving vertebrates not able to shelter in water were of relatively small body size (Hutchison and Archibald, 1986), and certainly some individuals or pairs were not prevented from occupying burrows for a few hours at the critical time, in contrast to the larger, latest Cretaceous, nonavian dinosaurs.

Mammals

Mammals surviving the K-T event were generally rat-sized or smaller, and they did not produce descendants with masses of more than 10–100 kg until hundreds of thousands to several million years later (Alroy, 1998). Small insectivorous/carnivorous cimolestids (related to later carnivores, ungulates, taeniodonts, tillodonts, pantodonts, pantolestids, and apatemyids) did survive the K-T event with little more than species-level change. Although extrapolation from Holocene to Maastrichtian time is admittedly a source of pitfalls, we note that there are semiaquatic monotremes, didelphid marsupials, and tenrecoid, soricoid, and talpoid placentals today, as well as burrowers and “sand-swimmers” like Australian *Notoryctes* and African chrysochlorids. Armadillo-like early edentate ancestors, if present in the Cretaceous, could have survived through burrowing, as their descendants do today.

We see no reason to think that these general lifestyles did not exist among various vertebrate lineages in the pre-Cenozoic world. Not all of the extant members of groups that survived the K-T debacle still shelter underground, in soils, or in water, but we suggest that all of the survivors of the immediate aftermath of the Chicxulub impact did. Most living mammals, large and small, are capable of briefly entering water, especially when stressed. It is not necessary to postulate that mammals sheltering in water in the first few hours of the Cenozoic were “semiaquatic” in the sense of pinnipeds, platypuses, or even water shrews. We simply mean that they could have alternated emersion with secretive behavior in partially sheltered habitats long enough to maintain an adequate, heat-protective film of water within their pelage. That some lineages of small Cretaceous vertebrates did not survive does not test our hypothesis because some would be expected to have succumbed to later effects of the impact. Regarding the diversification of mammalian clades, we favor the “long fuse” model of Archibald and Deutschman (2001) and Springer et al. (2003) whereby a few lineages success-

fully survived the K-T event and then rapidly diversified.

Birds

Phylogenetic Considerations

Paleontologists have yet to determine what birds were present at the time of the K-T event. Although giant terrestrial birds had evolved by the Late Cretaceous, there is no paleontological evidence for their survival across the K-T boundary (Buffetaut, 2002). Enantiornithines and most other archaic birds disappeared before the end of the Maastrichtian in the fossil record of the single complete and well-studied terrestrial section (Stidham and Hutchison, 2001). Others, including Clarke and Chiappe (2001) and Dyke et al. (2002), have described rare, late survivors elsewhere. Enantiornithines are not obviously adapted for swimming, although they have been recovered from lacustrine, riverbank, and one marine site (Chiappe and Walker, 2002). Small, diving hesperornithiforms are found in mixed, reworked uppermost Cretaceous–lowermost Paleocene river gravels in western North America but are not known in later, clearly Paleocene sites (Stidham, 2002). These distributions are not yet studied in detail but are compatible with K-T extinctions. Archaic birds remain unknown from younger, clearly Paleocene sites.

Only neornithines (the phylogenetically distinct, extant birds) seem to have persisted into the Cenozoic. Feduccia (1995) proposed that an evolutionary bottleneck in bird diversity developed at the K-T boundary, through which only a few lineages of neornithine shorebirds similar to charadriiforms passed. However, support for this view is weakening. The idea that only shorebirds survived the end-Cretaceous event may well be due to taphonomic bias. Very old, delicate bird bones are rarely preserved. The settings that best preserve them are quiet estuaries and calm, upwelling, shore margins rich with nutrients, also preferred habitats for shorebirds—hence their abundance in early collections. More diverse latest Cretaceous sites now known record not only shorebirds but also waterfowl related to modern ducks; highly aquatic seabirds including stem-lineage cormorants, loons, and possibly petrels; terrestrial birds related to modern galliforms; and possibly parrots (reviewed by Hope [2002] and see Appendix). Collateral “ghost” lineages, bracketed phylogenetically by this diverse record, indicate that many more lines of extant birds existed during Cretaceous time than have yet been found as fossils. As Cracraft

(2001) suggested, these ghost lineages must include the most basal group, the paleognaths (ratites, tinamous), although no fossil record has been found of them in Cretaceous deposits.

Recent molecular studies also are compatible with high diversity of neornithine birds late in the Cretaceous (Cooper and Penny, 1997; Paton et al., 2002; Ericson et al., 2002). Nevertheless, all of the fossils that are expected on the basis of either molecular or ghost lineage data are extrapolations that have not been tested adequately.

Avian Semiaquatic and Sheltering Habits Today

Semiaquatic behavior and sheltering underground are widespread today in bird groups that are known (Hope, 2002) or probable (Ericson et al., 2002; Cracraft, 2001; Edwards and Boles, 2002) survivors from the Cretaceous. Dense marsh vegetation common in the Cretaceous probably did not burn completely and would have sheltered some individuals of many of the anseriforms and shorebirds. Diving seabirds (normally inhabiting deeper near-shore waters) survived despite the need to surface frequently for breathing, as considered above. Breathing would not have posed problems for birds emerging from dives into intense IR radiation. Most diving birds today stay down only 30 s to 1 min and then surface for about the same length of time between dives. Respiratory membranes would not have been threatened by such a brief stay in the range of air temperatures projected. The exposed feather coat, however, would have been vulnerable. The outer feathers of most seabirds today do not become structurally wetted; water is repelled during a dive by the smooth hydrofoil surface. When such birds emerge, not even a thin film of water remains. Thus, under conditions of intense IR radiation, feathers soon would have been singed, allowing water to penetrate to the downy underfeathers. The wet plumage itself would have protected those birds sheltering under rocks or in agitated shallow water.

Among birds, the most common form of sheltering now, and probably the most effective way for birds to survive extreme thermal stress arriving from the entire visible sky, would have been the same as that for small vertebrates in general—shelter in a rock pile, a burrow, or an insulated cavity. Many of the smaller arboreal birds today, as varied as woodpeckers, kingfishers, and owls, roost or nest in natural cavities, burrows, or rocky crevices or in nests sheltered under rocky overhangs. Nesting in cavities or termite

mounds is virtually universal in the large group of coraciiforms. Passeriform habits include most of the above, carried to an extreme in the 2–3-m-long tunnels dug by some ovenbirds. Even a deep nest cavity in a large tree might have provided shelter for a brief interval before the tree burned deeply. Subterranean sheltering is widespread even in seabirds. Auks, petrels, and some penguins nesting on Antarctic coasts or barren oceanic islands find or dig burrows. It would seem that a critical difference between birds that survived and pterosaurs that did not is that, from what is known of their anatomy, pterosaurs did not swim, dive, or burrow (Colbert, 1980).

Avian Exceptions to Expectations for Survival

The sparse and controversial early record of birds (see Appendix) is mostly compatible with the sheltering hypothesis—but it also raises a few questions. The advanced swimming and diving adaptations of hesperornithiforms suggest that they would have survived, as did diving neornithine cormorants and loons. Perhaps hesperornithiforms are a case of extinction from other impact-related causes after the primary event, but the cause is unknown. Conversely, the terrestrial, nonburrowing habits and large body size of most paleognaths (e.g., ostrich, rhea, emu) and many galliforms today (e.g., pheasant, turkey) predict that their ancestors would have suffered extinction. The phylogenetically earliest paleognaths were much smaller (Houde, 1988), suggesting they might have burrowed, as the smallest of living ratites do today (kiwis). Living galliforms, however, muddy the prediction because even the smallest galliforms today (some quail) are not known for burrowing or swimming.

EXTENSIONS OF THERMAL-SHELTERING HYPOTHESIS

Our thermal-sheltering hypothesis for nonmarine vertebrates also can be extended to many survivors among the invertebrates and plants. Many nonmarine plants have roots, seeds, and other energy-rich, vegetative parts capable of propagation underground. Nonmarine invertebrates, such as insects having populations that lived in water or burrows or that had eggs and pupae underground, could have survived thermal stress within their normal habitats.

Although we have emphasized sheltering during the initial IR pulse as the key to survival of nonmarine vertebrates through the first few hours of the Cenozoic, it is clear from

Table 1 that some of the same behaviors could have been used to cope with other stresses that followed. For example, burrowing protects from cold as well as from heat. Moreover, small creatures that could burrow or aestivate may have had special capacities for lowering metabolic rates, and probably they were adapted to finding stored or underground food in many environments that had been burned out at the surface and had lost capacities for primary productivity.

Oceanic extinctions at the K-T boundary or in the months or years immediately thereafter would have had different impact-related causes, such as food-chain collapse caused by reduced light levels or various chemical effects. Marine organisms and some nonmarine ones may have been lost because of these kinds of secondary effects. Subsequent greenhouse warming in the first 2 m.y. after the Chicxulub impact (Liu and Schmitt, 1996) would have favored dispersal through polar regions. We do not address those issues here but focus rather on terrestrial environments.

EVOLUTIONARY IMPLICATIONS

The thermal-sheltering hypothesis provides a simple explanation, within the context of bolide physics, that reasonably accounts for much of the pattern of nonmarine differential survival observed at the K-T boundary. Paleontological observations combined with knowledge of the behavior of modern adaptive counterparts are consistent with the hypothesis. Moreover, the observed rapid, early Paleocene burst of evolutionary diversification (Lillegraven and Eberle, 1999), opportunities for niche filling (Alroy, 1998), and dispersal would have resulted from small, isolated populations of sheltered survivors. Much early Paleocene dispersal, which would be recognized within the fossil record as new immigrations (Clemens, 2002), would have been expected within the first few centuries following the impact.

It will never be possible to know the full effects of the Chicxulub (or any other) impact or linked impacts (Wolfe, 1991). The exact intensity and extent of the IR heat pulse may reasonably be disputed, particularly when the sampling of the spherule evidence is far from being globally complete. It is not impossible that, under some of the lower estimates of impact effects, distant parts of the globe might have been spared some of the worst of the effects. This idea provides another way to test the hypothesis through field work that achieves a more complete sampling of the spherule evidence, especially in fragments of

Gondwana that were far from the impact site. Claeys et al. (2002, p. 66) reported that their database “demonstrates that a significant effort is needed to improve our knowledge of K-T boundary sites in South America, Africa, Australia, and the high latitudes (>60°).” It will also be important to explore the terrestrial biotic evidence in more detail. Yet the hypothesis presented here establishes a *prima facie* case for significantly higher probability of survival through the initial global heat pulse and subsequent fires among terrestrial vertebrates that dwelt in soils, used burrows, or bathed or swam in water. Despite the various inherent biases in documentation of the biotic record across the K-T boundary, the observed patterns of differential survival do match this increased survival probability. None of the previously advanced extinction hypotheses (e.g., acid rain, global cooling or warming, poisoning, and tsunamis) explains so well these patterns of survival in the nonmarine realm.

Sheltering behavior among survivors of the intense thermal stress that began on a global scale within minutes of the Chicxulub impact shaped the composition of nonmarine ecosystems for millions of years into the Cenozoic. Other processes subsequent to the heat pulse would have modified the initial survival patterns, and undoubtedly they too were selective. Differential survivals documented from the fossil record are becoming increasingly consistent with the overall picture expected from the physics of the K-T impact. Physics and paleontology are compatible because they deal with a single history.

APPENDIX. MAJOR TAXA OF EXTANT NEORNITHINE BIRDS KNOWN IN THE CRETACEOUS

Listed here are major taxa (here used in the stem sense) of extant neornithine birds that are known in the Cretaceous from fossil records (*) or are assumed to have been present on the basis of ghost lineage requirements, or of well corroborated basal phylogeny and biogeography (phylogeography) that together indicate a Cretaceous evolutionary radiation. Within major taxa, Cretaceous and Cenozoic families of birds are listed only if they are known to wade, swim, or dive, or to shelter in a burrow or tree hole, or to nest in a termite mound. Cretaceous ghost lineages are assumed if the sister group is known in the Cretaceous fossil record. Sister groups are reconstructed from a provisional phylogeny presented by Cracraft (2001); polytomous ghost lineages are excluded unless they are

otherwise well supported. Additional major groups of neornithine birds may have been present in the Cretaceous, but the fossil record and knowledge of basal phylogeny in Neornithes are too limited to support further reconstructions.

PALAEOGNATHAE—Apterygidae (kiwis), Cassowariidae (cassowaries), Dromidae (emus). **GALLIFORMES***. **ANSERIFORMES***—Anhimidae (screamers), Anseranatidae (magpie geese), Presbyornithidae, Anatidae (ducks, geese, swans). **GRUIFORMES**—Heliornithidae (sungrebe), Eurypygidae (sunbittern), Aramidae (limpkin), Gruidae (cranes), Rallidae (rails). **CHARADRIIFORMES**—Rostratulidae (painted snipe), Hematopodidae (oystercatchers), Phalaropodidae (phalaropes), Recurvirostridae (avocets), Charadriidae (plovers), Dromadidae (crab plovers), Chionidae (shearwaters), Stercorariidae (skuas, jaegers), Laridae (gulls, terns, skimmers), Jacanidae (jacanas). **PROCELLARIIFORMES**—Hydrobatidae (storm petrels), Procellariidae (shearwaters, petrels), Diomedidae (albatrosses), Pelecanoididae (diving petrels). **GAVIIFORMES*** (loons). **PELECANIFORMES*** (if monophyletic, e.g., Sibley and Ahlquist, 1990)—Phaethontidae (tropicbirds), Pelecanidae (pelicans), Fregatidae (frigatebirds), Limnofregatidae, Sulidae (boobies, gannets), Plotopteridae, Phalacrocoracidae (cormorants), Anhingidae (snakebirds), Pelagornithidae. **PASSERIFORMES**—Acanthussittidae (New Zealand wrens), Eurylaimidae (broadbills), Tyrannidae (tyrant flycatchers), Rhinocryptidae (tapaculos), Dendrocolaptidae (woodcreepers), Furnariidae (ovenbirds), Cotingidae (cotingas), Corvidae (jays and crows; hole nesting in jackdaws only), Grallinidae (torrent larks), Paradisaeidae (birds of paradise), Dicaeidae (flower peckers, pardalotes; hole nesting in pardalotes), Passeridae (weavers—some nest in holes), Climacteridae (Australian tree creepers), Sittidae (nuthatches), Troglodytidae (wrens), Paridae (titmice, chickadees), Motacillidae (wagtails and pipits), Sturnidae (starlings, mynahs), Turdidae (thrushes), Muscicapidae (Old-World flycatchers), Cinclidae (dippers), Hirundinidae (bank and rough-winged swallows in holes), Prunellidae (hedge-sparrows), Meliphagidae (honeyeaters), Icteridae (troupials, American blackbirds and orioles; a few nest in holes), Tersinidae (swallow-tanagers), Drepanididae (Hawaiian honeycreepers, some nest in lava tubes), Fringillidae (finches). Among these, passeriform family-group taxa are oversplit but can be viewed as a tritomy (Acanthussittidae, suboscines, oscines) (Ericson et al., 2002); all three branches contain sheltering

members and probably were separate before the Cenozoic.

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Note added in proof: Belcher et al. (2003) reported quantities of charcoal that are about an order of magnitude below background levels in six North American K-T boundary clay layers. They interpreted the diminished levels of charcoal as evidence against the existence of a global firestorm at the end of Cretaceous time. We have argued instead that the reduction from ordinary charcoal levels is better explained in terms of the destruction of background charcoal by a fire of unusual intensity (Robertson et al., 2004).

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