Survival in the first hours of the Cenozoic

Douglas S. Robertson
Department of Geological Sciences and Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Colorado 80309, USA

Malcolm C. McKenna
Department of Geology and Geophysics, University of Wyoming, Laramie, Wyoming 82071-3006, USA, and University of Colorado Museum, Boulder, Colorado 80309, USA

Owen B. Toon
Program in Atmospheric and Oceanic Sciences and Laboratory for Atmospheric and Space Physics, University of Colorado, Boulder, Colorado 80309, USA

Sylvia Hope
Department of Ornithology and Mammalogy, California Academy of Sciences, San Francisco, California 94118, USA

Jason A. Lillegraven
Department of Geology and Geophysics and Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071-3006, USA

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, 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.
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 individuals 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.

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

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

**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).
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 NOX and SO2 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 1.3–5 × 1018 J·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 2–4 × 1017 J·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 sowe 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 ~1.4 kW·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 kW·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/cm² (Wolbach et al., 1988, p. 668) and the present atmospheric oxygen mass of 1.1 x 10²¹ 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, crocodylians, 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 W/(m·K), the specific heat capacity of rock and soil minerals is ~710 J/(kg·K) (Mitchell, 1993), and the density of soil is ~1500 kg/m³. 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 ~1000 K (the temperature would have been lower than this through limited shading and cooling by evaporation of soil moisture), then between 2 and 20 h would have been needed to raise soil temperature by ~1 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 1000–1200 K would have a spectral peak at wavelengths of 2500–3000 nm, and IR absorption coefficients for water range as high as 13,000 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/cm² 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 10–100-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 ± 4) x 10⁶ g, is very large: ~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 determining 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 that would apply to the catastrophe of the earliest Cenozoic. Discussing mammals specifically, Lillegraven et al. (1987, p. 287) stated, “Ecological evolutionary advantages and disadvantages 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, crocodilian, 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. 
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, protected those birds sheltering under rocks or overhangs. Nesting in cavities or termite

**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. Dividing seabirds (normally inhabiting deeper nearshore 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 owls. 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 cornorants 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 many 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 restructured 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.

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