

DEVASTATION OF TERRESTRIAL ECOSYSTEMS AT THE K-T BOUNDARY IN NORTH AMERICA: THE FIRST CALIBRATED RECORD OF PLANT AND ANIMAL RESPONSE TO THE CHICXULUB IMPACT. Kirk Johnson¹, Douglas Nichols², Conrad Labandeira³, and Dean Pearson⁴, ¹Denver Museum of Natural History, 2001 Colorado Blvd., Denver, Colorado 80205, kjohnson@dmnh.org, ²U.S. Geological Survey, MS 939, Box 25046 DFC, Denver, Colorado 80225, nichols@usgs.gov, ³Paleobiology Department, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, labandeira.conrad@nmnh.si.edu, ⁴Pioneer Trails Regional Museum, Bowman, ND 58623, pearson@bowman.ctctel.com.

Introduction: Extensive collection of leaves, many with insect damage; palynomorphs; and vertebrates from the uppermost Cretaceous (upper Maastrichtian) and lowermost Paleocene (Puercan) formations in western North America has resulted in a combined database of unparalleled density. These data are derived from sites from New Mexico to Canada with a strong focus on the excellent record of the northern Great Plains of the United States. These latter sites and samples have been correlated within a lithostratigraphic framework calibrated by magnetostratigraphy, radiometric dates, and the geochemical and physical indicators of the Cretaceous-Tertiary (K-T) boundary. This integrated record documents major devastation of terrestrial ecosystems as a direct consequence of the Chicxulub impact.

Plants: Plant fossils are studied as megafossils or palynomorphs. While both are derived from the same original vegetation, they have different taphonomic pathways and taxonomic resolution. We use both types of fossils to take advantage of their relative strengths. Leaf megafossils are suitable for extinction studies because of their high taxonomic resolution and low potential for reworking. Palynomorphs have great abundance and broad distribution allowing high stratigraphic resolution and the recognition of continent-wide patterns.

The plant megafossil record. The most densely sampled K-T leaf flora in the world exists in our Great Plains research area in the Bighorn, Powder River, and Williston Basins (parts of Wyoming, Montana, and North and South Dakota) where more than 30,000 leaves from 306 localities demonstrate an 80 percent extinction across the K-T boundary. The 180-m-thick section that spans the K-T boundary (K = 100 m, T = 80 m) in southwestern North Dakota has yielded a diverse megaf flora (based on 13,500 voucher specimens) of more than 385 morphotypes from 171 quarry sites. The uppermost Cretaceous flora is dominated by angiosperms, with ferns, fern allies, cycads, ginkgos, and conifers representing less than ten percent of total taxa and specimens. The Cretaceous sequence can be divided into three distinct floral zones. The uppermost zone begins roughly 20 m below the K-T boundary

and corresponds approximately to the beginning of magnetic polarity subchron C29R. This flora is significantly more diverse than that of the lower floral zones and is characterized by leaf physiognomy that suggests a significant climate warming in the final 350,000 years of the Cretaceous. Floral extinction at the K-T boundary is extensive, effectively eliminating all dominant plant taxa in non-mire facies. The overlying depauperate Paleocene flora, preserved in a variety of facies, is dominated by taxa that were previously restricted to Cretaceous mires. We interpret this to be a post-catastrophe recovery flora that spread onto the early Paleocene landscape from mires and wetlands that, for unknown reasons, served as refugia during the terminal Cretaceous event. Recent work on more than 70 quarries spanning the K-T in the more southerly Denver Basin in Colorado is still in progress but preliminary results also suggest major floral extirpation at the K-T boundary.

The record based on palynology. Palynomorphs from 23 K-T boundary or near-boundary sections in southwestern North Dakota indicate 30 percent extinction at the boundary. The palynological database for this area includes 110 palynomorph taxa for which relative abundance or presence/absence data were recorded in more than 230 samples based on surveys of more than 450,000 specimens. With a single exception, extinction in this area occurred exclusively among angiosperm taxa. By their nature, palynomorphs represent higher-level taxa, so this extinction involved not just species but genera or families of plants. Additional data originate from detailed investigations in five other research areas in the western United States and adjacent southern Canada (27 additional sections). Palynostratigraphy at all these localities is calibrated by the iridium anomaly and shocked minerals. Results from these areas show similar effects on palynofloras of somewhat differing compositions. On a continent-wide basis (16 study areas; 225 palynomorph taxa), about 45 percent of the late Maastrichtian palynoflora was destroyed by the terminal Cretaceous event. This regional database covers some 5000 km from north to south; results reflect strong variation with latest Maastrichtian and earliest Paleo-

cene floras that was related to paleolatitude. Extinction was varied within major groups of plants continent-wide: 51 percent among angiosperms, 36 percent among gymnosperms, and 25 percent among ferns and fern allies. Because total continent-wide extinction levels are larger than local extinction levels, we suggest that locally endemic taxa were more affected by the terminal Cretaceous event than were widespread taxa. Earliest Tertiary palynofloras are characterized not by new appearances but by loss of the dominant elements of the Cretaceous vegetation. Unique palynomorph assemblages (such as fern-spore abundance anomalies) in close proximity to ejecta deposits show regional effects of impact-related devastation of terrestrial ecosystems. These short-lived plant communities consisted almost exclusively of opportunistic survivor species of ferns in most areas investigated. Repopulation of post-impact landscapes evidently was from local refugia.

Insects: Previous studies have indicated no evidence for mass extinction among insects at K-T boundary. These studies were based on global, family-level compilations of body-fossil data that indicated no deviation from background rates of extinction. In contrast, the palynologic and megafloreal evidence cited above demonstrates a major extinction of plant taxa at the K-T boundary. To test these opposite conclusions, we examined insect-mediated plant damage on 6,000 leaves in a succession of 78 of our megafloreal localities in southwestern North Dakota from a section that spans a 2.0 m.y. interval of the late Maastrichtian Hell Creek Formation and earliest Puercan Ludlow Member of the Fort Union Formation. All characterizable leaf hosts from these floras were assigned to morphotypes and/or Linnean taxa, providing explicit recognition of plant hosts. We identified 42 types of insect damage, representing insect herbivory from four functional feeding groups: external foliage feeders, leaf miners, gallers, and piercer-and-suckers. For the Hell Creek megaflorea, 41 types of damage were identified, including several conspicuous examples of galls and scales on primary veins, serpentine mines, and diagnostic slot-hole feeding, each occurring monospecifically and abundantly on separate species of Lauraceae, Platanaceae, and Cannabaceae. For the Fort Union megaflorea, only 17 types of damage were identified; abundance levels were found to be significantly lower; and the associations were more generalized, lacking host-specific associations. These data demonstrate that at local scales insect herbivory suffered dramatically during the terminal Cretaceous event, with no evidence of subsequent recovery. Levels of herbivore diversity remained depressed

until pronounced vegetational shifts in the Western Interior of North America during the Early Cenozoic Thermal Maximum in latest Paleocene to early Eocene time.

Vertebrates: Recent surveys of the uppermost Cretaceous Hell Creek Formation in southwestern North Dakota have yielded a total of 10,034 identified vertebrate fossils from 42 sites and dinosaur skulls or skeletons from 41 additional sites. This Lancian fauna is composed of 67 taxa of fish (including sharks and rays), amphibians, lizards, turtles, crocodylians, champsosaurs, dinosaurs, pterosaurs, birds, and mammals. The 83 sites span the entire 100-meter thickness of the formation. Most vertebrate sites in the lower part of the Hell Creek Formation are in channel deposits; those in the upper part of the formation are more common in floodplain deposits. Dinosaurs are found in the highest vertebrate sites in the Hell Creek Formation and one ceratopsian partial skeleton was found in the overlying Fort Union Formation (1.4 m below the K-T boundary). Other significant finds include pterosaur fossils 8.4 m below the boundary, and sharks within 4 m of the boundary. The former is the world's youngest occurrence and the latter suggests that the Western Interior seaway was still present in the area near the end of the Cretaceous. Sample size, rather than stratigraphic position, appears to be the primary factor that determines the presence of taxa at these sites. All dinosaur taxa that occur at more than two sites also occur at the highest well-sampled (>500 specimens) site, 8.4 m below the K-T boundary. Dinosaurs also occur in the highest sites that preserve vertebrate fossils. Common vertebrate taxa range throughout the Hell Creek Formation and Lancian faunal extinction appears to be coincident with plant extinctions at the end of the Cretaceous.

Summary: In general, this multidisciplinary examination of K-T ecosystem change documents a dramatic loss of Cretaceous species richness. The ecological landscape of North America was fundamentally altered by the disappearance of major groups of plants and animals and the early Paleocene terrestrial biota was markedly depauperate. Twenty years ago, the Alvarez hypothesis posed the unexpectedly difficult challenge for paleontologists to evaluate abrupt extinction in the terrestrial realm. The challenge has been met for western North America using multidisciplinary methods that provide a standard for future work. A complete understanding of the global effects of the Chicxulub impact on terrestrial ecosystems awaits similar research on other continents.