

Mammalian evolution across the Cretaceous/Tertiary boundary: the contributions of survival, dispersal, and extinction

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Abstract. Currently the most detailed fossil record of mammalian evolution across the Cretaceous/Tertiary (K/T) boundary is derived from the Western Interior of North America. Recent discoveries in other areas, particularly South America, Africa, and Eurasia, are beginning to provide records of the changes in composition of contemporaneous terrestrial faunas. From a global perspective, Late Cretaceous and Paleocene terrestrial biotas are characterized by biogeographic provincialism, which appears to have had its origins in the differentiation of Gondwanan and Laurasian biotas earlier in the Mesozoic. During the transition from the Late Cretaceous into the Paleocene survival, dispersal, and extinction interacted to produce new patterns of biogeographic diversity.

Key words. Cretaceous/Tertiary boundary. Survival. Dispersal. Extinction. Mammals.

Introduction

The pattern of mammalian evolution across the K/T boundary in the North American Western Interior differs from those beginning to be documented on other continents. It does, however, provide data for testing hypotheses concerning the causal factors of the global mass extinctions marking this boundary and subsequent evolution of mammalian faunas. Differential survival and extinction of vertebrate lineages across the K/T boundary indicates evolution of the terrestrial biota was the product of interaction of both long-term and short-term causal factors. These included marine regression coupled with increased volcanism and effects of the impact of an extraterrestrial body. Mammalian lineages had begun to radiate prior to the end of the Cretaceous, and early Paleocene recovery of the terrestrial biota was the product of both local survival and extensive dispersal.

Growth of the record of mammalian evolution in the Late Cretaceous and Paleocene

G. G. Simpson's (1928, 1929) monumental catalogs provided a thorough inventory of most of the records of Mesozoic mammals discovered in the ninetieth and early twentieth century. Occurrences of Late Cretaceous mammals were essentially limited to small samples of mostly isolated teeth of latest

Cretaceous (Maastrichtian) age from the North American Western Interior (including the provinces of Alberta and Saskatchewan and the states of Montana, North and South Dakota, Wyoming, Colorado, and New Mexico). Discoveries of Cretaceous Mongolian mammals had been announced a few years earlier. Nothing was known of the latest Cretaceous mammals of South America, Europe, and Africa. Similarly, records of early Paleocene mammals were limited to a few areas in North America. The mammalian fossil record of the San Juan Basin, New Mexico, summarized and analyzed in a monograph by Matthew (1937), provided the majority of these data. Unconformities, related to marine regressions around the K/T boundary, contributed to gaps in the fossil record on other continents.

As a result of extensive application of the underwater screening technique after World War II, samples of mammals of Late Cretaceous and early Tertiary age were rapidly expanded. A survey of the Late Cretaceous mammalian record published in 1979 (Clemens *et al.*, 1979) documented North America mammalian local faunas of Judithian, "Edmontonian," and Lancian North American Land Mammal Ages (NALMA), approximately equivalent to the mid-Campanian-Maastrichtian interval (figure 1). A few mammalian remains were reported from Late Cretaceous localities in Peru, southern France, and Portugal. The Asian record was dominated by fossils from Mongolia, which are of Late but not latest Cretaceous age. Similar surveys of the early Paleocene record of mammalian evolution (see Archibald *et al.*, 1987; Savage and Russell, 1983) re-

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flected the strong bias in favor of the North American early Paleocene (Puercan NALMA) record. On other continents significant additions had been made to the record of mammalian evolution during the Paleocene; however, most of these local faunas are of middle or late Paleocene age.

The past decade has witnessed significant discoveries and expansion of the records of latest Cretaceous and early Paleocene mammalian evolution. To cite but a few of these welcome additions to our knowledge, South American local faunas from Argentina, Brazil, and Bolivia (Bonaparte, 1996; Pascual *et al.*, 1996) are greatly increasing documentation of both Late Cretaceous and Paleocene faunas of this continent. The European record has been expanded by discoveries of Cretaceous mammals in France (Buffetaut *et al.*, 1997), the Iberian Peninsula (Pol *et al.*, 1992), and other areas. In addition to many remarkably well preserved Late Cretaceous mammal skeletons from Mongolia (Novacek *et al.*, 1997), extensive discoveries document the Paleocene mammalian faunas of southern China. Records from India (Prasad *et al.*, 1994) and Madagascar (Krause *et al.*, 1999) have augmented our understanding of the Late Cretaceous mammalian faunas of the Southern Hemisphere.

Provincialism of mammalian faunas

Detailed analysis of the expanding suite of Late Cretaceous and Paleocene mammalian faunas is beyond the scope of this article, but several significant points stand out. Broadly, a dichotomy in composition of Late Cretaceous mammalian faunas distinguishes those of Gondwanan continents, usually dominated by non-therians, and those of Laurasian continents, dominated by other groups of non-therians (cimolodontan multituberculates) and therians. Beginning in the Cretaceous and continuing into the Paleocene, some groups of mammals dispersed between Gondwanan and Laurasian continents (*e.g.*, note Gayet *et al.*, 1992). Secondly, increasing evidence from the Laurasian continents suggests significant inter- and intracontinental biogeographic differentia-

tion of mammalian faunas in the Late Cretaceous and early Paleocene (Weil and Clemens, 1998). This differentiation was not limited to the mammalian faunas but also characterized distribution of other vertebrates (*e.g.*, Clemens and Nelms, 1993) and terrestrial floras (Wing and Sues, 1992).

Mammalian evolution across the K/T boundary in the Western Interior of North America

The record of mammalian evolution during this period is particularly extensive as a result of decades of study of the Hell Creek and Tullock formations in northeastern Montana and correlative formations in adjacent areas (figure 1). In Montana, in 1903, Barnum Brown discovered the skeleton that would become the type specimen of *Tyrannosaurus rex* Osborn and in the following years added significantly to Lanciai vertebrate faunas. Starting in the 1960's fossils from the Hell Creek and Tullock formations provided increasingly detailed documentation of the course of mammalian evolution across the K/T boundary (see Archibald, 1982; Lofgren, 1995). The pattern of evolution of Paleocene mammals during the first ca. one million years after the K/T boundary has been calibrated through paleomagnetic analyses and $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric age determinations (Swisher *et al.*, 1993).

The hypothesis that the mass extinction of non-avian dinosaurs marking the K/T boundary was simply the product of an instantaneous, catastrophic event has been falsified (see Archibald, 1996, and Novacek, 1999, for discussions). During the close of the Cretaceous, marine regression probably drove a long-term trend of climatic cooling. Over a span of the last five to ten million years of the Cretaceous the diversity of the North American non-avian dinosaur fauna significantly decreased, particularly among the hadrosaurids and ceratopsids. Continental environments probably also were modified by the injection of aerosols and dust into the atmosphere by the long-term Deccan volcanism and short-term consequences of the impact of an extraterrestrial body. Patterns of

	Formation	NALMA	Ar/Ar age (in ma)	Polarity	
Tertiary	Tullock	Torrejonian	63.90	28r	
		Puercan	Pu2/3	64.11	29n
			Pu1	64.77	29r
		Hell Creek	Lanciai	65.16	
Cretaceous					

Figure 1. Correlation of North American Land Mammal Ages (NALMA, with subdivisions of the Puercan), (Archibald *et al.*, 1987), formations in northeastern Montana, and radiometric age determinations (Swisher *et al.*, 1993).

survival and extinction of mammalian and other vertebrate lineages across the K/T boundary support hypotheses invoking a complex set of long- and short-term environmental changes as causal factors of this mass extinction.

Evolution of the mammalian fauna of the Western Interior during the first million years of the Paleocene involved both radiation of lineages present in the area in the Cretaceous and immigration of mammals from other areas. Interaction of these factors is clearly documented in the local faunas from northeastern Montana. The local faunas of this area can be ordered stratigraphically from the Lancian (latest Cretaceous) into the Puercan (early Paleocene) with the approximately one million years of the Puercan subdivided into Pu1 (including Pu0) and Pu2/3 NALMAs. Mammalian species comprising the local faunas of these three periods of time have been categorized as either "residents" or "aliens" (Weil and Clemens, 1998). Species that carried through from one period to the next or species that have a closely related sister species in the preceding period were considered "residents." (Here close relationship was interpreted as presence of another species in the same genus, or possibly, another closely related genus). Species were classified as "aliens" when there was not a closely related species in the preceding period and their appearance probably documents immigration into what is now northeastern Montana.

Analysis of these records (Weil and Clemens, 1998) reveals that the multituberculates, marsupials, and eutherians comprising the Lancian local faunas of northeastern Montana were almost entirely "residents" with closely related species in older "Edmontonian" or Judithian local faunas. The extinctions at the K/T boundary reduced the total diversity of the mammalian fauna of northeastern Montana to about 60% of its Lancian level (from 28 to 17 species). Most of the Lancian lineages of marsupials became extinct. Several lineages of multituberculates became extinct, as did a few eutherian lineages, but for the most part survival was high. Almost two-thirds of the Pu1 mammalian fauna of this area was made up of "alien" species, which highlights the significant role of immigration in recovery of the fauna after the K/T boundary.

What were the homelands of these immigrants? The limited Late Cretaceous fossil record from outside the northern Western Interior offers some clues. One of the abundantly represented eucosmodontid multituberculates in Pu1 faunas of the Western Interior is *Stygimys kuszmauli* Sloan et Van Valen. This eucosmodontid is not represented in earlier faunas of the northern Western Interior. The earliest known record of the genus is in the Campanian of Baja

California del Norte, suggesting that the appearance of *Stygimys* at the beginning of the Paleocene in the northern Western Interior was the product of immigration from western regions of North America. Another example of the importance of immigration in reconstitution of the mammalian fauna of the Paleocene in the Western Interior is the locally abrupt appearance of species of the early ungulates *Protungulatum*, *Oxyprimus*, *Baioconodon* (= *Ragnarok*), and *Mimatuta*. Except for a report of *Protungulatum* in the Lancian Fr-1 local fauna of southern Saskatchewan, where it is accompanied by another probable Pu1 "alien," the multituberculate *Catopsalis*, these ungulates are unknown in Lancian local faunas in the Western Interior. Their ancestry is unclear, but recent field work (Nessov *et al.*, 1998) revealed the presence of a diverse group of primitive ungulatomorphs, the zhelestids, in the Late Cretaceous faunas of Uzbekistan.

Additional examples of the importance of immigration in recovery of the mammalian fauna of northeastern Montana are apparent in a comparison of the compositions of Pu1 and Pu2/3 faunas. Stressing that systematic study of the Pu2/3 fauna from northeastern Montana is still underway, a significant proportion, probably 30 to 40% of the Pu2/3 fauna, is made up of immigrants.

Conclusions

Increasing collections add support to previous analyses that highlight patterns of differential survival and extinction of vertebrate lineages across the Cretaceous/Tertiary boundary. The latest Cretaceous came to an end with long-term, global trends for marine regression coupled with increased volcanism. The short-term effects of the impact of an extraterrestrial body added to modification of the terrestrial environment. In different ways all produced extensive changes in the physical environment that were reflected in evolution of the terrestrial biota. The available paleontological data supports and does not falsify the hypothesis that evolution of the terrestrial biota across the K/T boundary was the product of the interaction of long-term and short-term causal factors.

During the transition from the latest Cretaceous into the early Paleocene, terrestrial faunas of the North American Western Interior were subdivided into a complex of biogeographic units. Recent discoveries are beginning to add data documenting biogeographic heterogeneity on other continents. Also, increasing documentation of the important role of immigration in the Late Cretaceous and during the early Paleocene recovery of the terrestrial fauna of the Western Interior is indirect evidence of this biogeographic heterogeneity.

Acknowledgments

I thank Prof. J.F. Bonaparte for his invitation to present this paper at the 7^o International Symposium on Mesozoic Terrestrial Ecosystems. In addition to valuable discussions with Profs. J.F. Bonaparte, R. Pascual, and A. Weil, I acknowledge with thanks the helpful comments on drafts of this manuscript by Dr. N.C. Arens and G.P. Wilson as well as those of two anonymous reviewers. This is University of California Museum of Paleontology contribution no. 1739.

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Accepted: December 4th, 2000.