Acta Palaeontologica Polonica
Vol. 28, No. 1—2 pp. 55—61 Warszawa, 1983
Second Symposium on Mesozoic Terrestial Ecosystems, Jadwisin 1981

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MAMMALIAN EVOLUTION DURING THE CRETACEOUS-TERTIARY TRANSITION; EVIDENCE FOR GRADUAL, NON-CATASTROPHIC PATTERNS OF BIOTIC CHANGE

CLEMENS WILLIAM A.: Mammalian evolution during the Cretaceous-Tertiary transition; evidence for gradual, non-catastrophic patterns of biotic change. Acta Palaeont. Polonica, 28, 1—2, 55—61, 1983,

Hypotheses invoking catastrophic causal factors for terminal Cretaceous extinctions call for, 1) instantaneous, global extinctions, 2) resulting from a single or dominant causal factor. Currently available methods of correlation are not precise enough to test the first element of these hypotheses. Patterns of mammalian extinction and survival in northeastern Montana, USA — as well as records of other organisms — argue against the second element. In Montana most of the lineages of marsupials were decimated. Extinction of multituberculates was not as severe, while only one lineage of eutherians appears to have become extinct. Groups that apparently immigrated into northeastern Montana just prior to the end of the Cretaceous had a greater probability of survival than the residents. The probability of extinction was independent of individual body size. Different patterns of mammalian extinction in different environments also appear to defy explanation in terms of one common, catastrophic causal factor.

K e y w o r d s: Mammalia, Cretaceous, Tertiary, extinction, Montana, USA.

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INTRODUCTION

Scientific and popular publications continue to be flooded with articles concerning the causes of the extinction of dinosaurs and other organisms used to mark the end of the Cretaceous. These range from wild speculations to a few testable hypotheses. Currently many authors invoke some kind of catastrophic causal factor, for example increases in cosmic radiation or the impact of an extraterrestrial object that resulted in the instantaneous global extinction of these large reptiles. Although it is widely recognized that some dominant groups of marine invertebrates became extinct at approximately the same time 63 to 64 million years ago, the histories of extinction, survival, or diversification of lineages of other contemporaneous terrestrial animals frequently are not consider-

ed. The purpose of this article is not to suggest yet another causal factor for terminal Cretaceous extinctions, but to summarize data obtained from detailed studies of latest Cretaceous and Paleocene faunas of northeastern Montana, USA, and employ them, with information drawn from research on other groups, in tests of current hypotheses.

The sequence of continental strata documenting the transition from the Cretaceous into the Tertiary in northeastern Montana is divided into the Hell Creek and overlying Tullock Formations. The boundary between these formations is placed at the stratigraphically lowest, laterally continuous lignite of the sequence of well-stratified lignites, siltstones, and sandstones forming the Tullock Formation (Archibald, 1982). Outcrops of these strata along the Missouri River were first prospected in 1902 by Barnum Brown of the American Museum of Natural History. During that year and subsequent field seasons he recovered skeletons of *Tyrannosaurus* and other large, primarily latest Cretaceous vertebrates. Many years later, in the 1960's, Robert Sloan and Leigh Van Valen (1965) were the first to collect large samples of microvertebrate fossils, primarily from the Bug Creek Anthills locality in the Hell Creek Formation. Initiated over a decade ago by Harley Garbani's discovery of a rich Early Paleocene fossil locality in the Tullock Formation, University of California field parties have obtained samples of a sequence of local faunas of latest Cretaceous (Lancian) and Early and Middle Paleocene (Puercan and Torrejonian) ages. These collections and closely correlated geological analyses provide the first detailed record of change in the terrestrial fauna of a geographically limited area just prior to, during, and immediately after the local extinction of dinosaurs (Clemens and Archibald 1980).

The research in northeastern Montana has been and continues to be a cooperative project involving many colleagues whose help is greatly appreciated. Without necessarily implicating them with the conclusions presented here, I want to particularly acknowledge the considerable contributions of J. David Archibald, Lowell Dingus, Leo J. Hickey, and J. Howard Hutchison and call attention to their research papers cited in the bibliography. Financial support from the University of California, Museum of Paleontology, its Annie M. Alexander Endowment, and the Natural History Museum of Los Angeles County and grants from the National Science Foundation (DEB 77-24610) and the donors of the Petroleum Research Fund administered by the American Chemical Society (PRF 12487-AC2) are gratefully acknowledged.

DISCUSSION

Although the specific causal factors implicated in hypotheses of catastrophic extinction of dinosaurs and other organisms used to mark the end of the Cretaceous vary greatly, these speculations have at least

two common attributes. They call for essentially instantaneous, global extinctions occurring within periods of a few days, months, or possibly years in duration. Also, they usually invoke either a single or a dominant causal factor, for example see Alvarez *et al.* (1980). In contrast, what can be termed gradualistic hypotheses suggest that the global biotic changes marking the close of the Cretaceous occurred over geologically instantaneous but biologically significant periods of time, possibly tens or hundreds of thousands of years, and were the result of changes in a nexus of physical and biological relationships.

An obvious mode of testing these contradictory classes of hypotheses would be to make precise comparisons of times of extinction of organisms in terrestrial and marine environments in different parts of the world. However, this type of test cannot be conducted. In most sedimentary basins the boundary between rocks containing records of Cretaceous biotas and those documenting the Tertiary is marked by an unconformity indicating loss of part of the record of biological change through nondeposition or erosion (Matsumoto 1980). Even though there are a few areas where the sections of sedimentary rocks appear to lack major gaps, biostratigraphic, radiometric, and magnetostratigraphic methods of correlation applied to rocks deposited 60 to 70 million years ago do not have the resolution to distinguish between events that occurred within an interval of a few weeks or months and those that took place hundreds of thousands of years apart (see Archibald *et al.* 1982).

Analysis of patterns of extinction and survival of various lineages of plants and animals during the transition from the Cretaceous to the Tertiary provides an indication of the nature of the causal factors that were operative and, thereby, a possibility of testing catastrophic and gradualistic hypotheses. Focusing attention on dominant groups of Cretaceous organisms, such as dinosaurs and ammonites whose extinctions are used to mark the end of the Period, biases the analysis in favor of catastrophic hypotheses, but does not reject the gradualistic. An adequate test of the contradictory hypotheses requires that equal weight be given to consideration of lineages that survived and formed the earliest Tertiary biotas.

As a result of extensive field work employing techniques favoring recovery of microvertebrate fossils a detailed record of the evolution of latest Cretaceous and early Paleocene mammalian faunas of western North America is beginning to emerge. Most known latest Cretaceous mammalian faunas were composed of representatives of three major groups, the Multituberculata, Marsupialia, and Eutheria (see Lillegraven *et al.* 1979). All were mammals that by modern standards would be classified as being of small body size, ranging from species as small as mice to those approximately the size of a fox terrier. Analysis of the functions of their dentitions and what little is known of their skeletons suggests that

multituberculates occupied a wide spectrum of ecological niches available to omnivores and herbivores. The marsupials of the latest Cretaceous are best interpreted as small omnivores similar to the modern members of the opossum family Didelphidae. Different patterns of dental morphology of contemporaneous eutherians suggest the beginnings of specializations for carnivorous or herbivorous diets, but probably most of these animals were basically omnivores.

The first study of the pattern of extinction of latest Cretaceous mammalian lineages based on a large sample of one fauna was an analysis of the lineages represented in the fauna of the type area of the Lance Formation in eastern Wyoming (see Clemens 1973). This revealed that all but one of the twelve or so species of marsupials in the Lance fauna probably became extinct at about the time the dinosaurs perished; only a species of *Alphadon* appeared to have Paleocene descendants. Approximately three-quarters of the lineages of multituberculates were thought to be directly related to Paleocene species. None of the few known eutherians were thought to lack Paleocene descendants, but now it appears that *Gypsonictops* became extinct at the close of the Cretaceous. A similar pattern of extinction and survival in these three groups of mammals emerged from an analysis of the mammalian fauna of the "upper part of the Edmonton Formation" (now designated the Scollard Formation — see Clemens *et al.* 1979) of Alberta, Canada (Lillegraven 1969). Both studies were flawed by the lack of earliest Paleocene (Puercan) mammalian faunas in the same stratigraphic sections. Comparisons had to be made with Puercan faunas in Montana and western Wyoming, which were known from much smaller samples, and the type Puercan fauna from New Mexico, which had not been adequately sampled by techniques adapted to the recovery of microvertebrate fossils.

Studies by Sloan and Van Valen (1965) in northeastern Montana revealed the presence of latest Cretaceous mammalian faunas with compositions distinctly different from those that had come to be regarded as typical for this time in western North America. The faunas, the so-called Bug Creek faunas (or latest Cretaceous faunas of Paleocene aspect) were dominated by multituberculates and eutherians, including forms such as the multituberculate *Catopsalis* and the condylarth (eutherian) *Protungulatum* that are thought to be immigrants. Most of the species common in "typical" latest Cretaceous faunas are present in the oldest of the Bug Creek faunas (Bug Creek Anthills local fauna) but appear to gradually drop out in later faunas. Subsequent analyses by Archibald (1981) and others, suggest that in northeastern Montana the Bug Creek faunas (the Bug Creek faunal facies) occupied areas along a major river system flowing eastward from highlands in the west into the Western Interior Sea, which connected the Arctic Ocean with the Gulf of Mexico and bisected the North American continent throughout much of the Late

Cretaceous. It is now hypothesized that the "typical" latest Cretaceous mammalian faunas (the Hell Creek faunal facies of Archibald (in press) and the mammalian faunas of the type area of the Lance Formation and the Scollard Formation) probably inhabited the broad coastal and interior floodplains and only a few of their members found their way into the major river valleys (Clemens and Archibald 1980).

The pattern of mammalian evolution documented in the faunas of the floodplains is one of stasis, persistence of lineages until the abrupt extinction of many species at approximately the same time as the demise of the dinosaurs (Archibald 1981). In contrast, mammalian evolution in the Bug Creek faunal facies is characterized by diversification of eutherians, particularly the condylarthrs; survival of many lineages of multituberculates; and loss of records of almost all lineages of marsupials (see Sloan 1976, Van Valen and Sloan 1977).

Recent studies of the histories of plants (Hickey 1981 and in press) and marine invertebrates (Kauffman 1979) during the Cretaceous-Tertiary transition are pertinent for they also reveal biogeographically complex patterns of extinction and survival. Samples of pollen floras from many parts of the world indicate that the highest levels of extinction occurred in the *Aquilapollenites* province, a region including western North America and a large part of eastern Eurasia. Floras in other areas at middle and higher northern latitudes suffered much less through extinction. Hickey (*op. cit.*) noted even lower levels of extinction in tropical and lower latitude southern floras. In definite contrast, Kauffman (1979) emphasized that in the marine realm extinctions were greatest among groups with predominantly tropical, Tethyan or marginal Tethyan ranges.

CONCLUSIONS

We lack methods of correlation with sufficient resolution to determine whether global extinctions of organisms used to mark the end of the Cretaceous occurred essentially instantaneously, within a period of a few weeks or months, or gradually over a period of hundreds of thousands of years. However, the conflicting catastrophic and gradualistic hypotheses can be tested by analysis of local and regional patterns of extinction. Detailed analyses of mammalian evolution in northeastern Montana during the Cretaceous-Tertiary transition demonstrate that the lineages that became extinct cannot be categorized by body size. Both large and small species of mammals became extinct. Extinction was most severe among marsupials. Multituberculates and, especially, eutherians suffered much less. Also it is becoming apparent that the patterns of extinction and evolutionary diversification of mammals in the floodplain and river

valley biotas differed greatly. On the floodplains the latest Cretaceous fauna exhibits an evolutionary stasis until the abrupt extinction of the dinosaurs and many mammalian lineages. In contrast, the fauna of the river valleys (the Bug Creek faunal facies) appears to undergo a gradual change with the appearance and diversification of several immigrant groups. Studies of the changes in floras and marine faunas in various parts of the world show patterns of regional differences in severity of extinction. This regional variation argues against catastrophic hypotheses calling for instantaneous global extinctions resulting from a single or a dominant causal factor. To the contrary, the paleobiological data strongly suggest terminal Cretaceous extinctions were the product of changes of complexly interrelated physical and biological factors over a period of earth history of geologically short but biologically significant duration.

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