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J. DAVID ARCHIBALD

STRUCTURE OF THE K-T MAMMAL RADIATION IN NORTH AMERICA: SPECULATIONS ON TURNOVER RATES AND TROPHIC STRUCTURE

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Preliminary results from Montana and New Mexico (USA) indicate that appearance rates for mammal species increase from the latest Cretaceous (Lancian) into the early Paleocene (Puercan) with a slight decline into the middle Paleocene (Torrejonian). Disappearance rates decline over the same interval and equal appearance rates by the Torrejonian. These results are the opposite of those found by Van Valen (1978). Some groups (condylarthrans) have more frequent speciation events and shorter species durations than suggested by Stanley (1979). The overall appearance rate for the K-T interval is very similar to that for the Paleocene-Eocene transition (both about 1 sp./10⁴ yrs.). The overall disappearance rate for the K-T interval (1.4 sp./10⁴ yrs.) is markedly higher than for the Paleocene-Eocene transition (0.5 sp./10⁴ yrs.). With the extinction of dinosaurs, "guilds" of small mammals are re-established and new "guilds" form after about 2.5×10⁵ years. Appearance rates are highest during guild establishment.

Key words: Mesozoic mammals, Cenozoic mammal radiation, Cretaceous-Tertiary boundary, turnover rates, trophic structure.

J. David Archibald, Department of Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, USA. Received: November 1981.

INTRODUCTION

The various radiations that have occurred during the history of life on this planet offer important opportunities to examine evolutionary patterns and processes. The class Mammalia has undergone a variety of radiations, but the radiation that began during the decline of dinosaurs some 65 to 66 million years ago stands out as one of the most important episodes. Recent studies, particularly those crossing the Cretaceous-Tertiary (K-T) boundary in northeastern Montana, now afford a prelimi-

nary examination of this radiation for western North America. The two major components of this radiation that have been examined are: 1) turnover rates and 2) trophic structure. Data used in this preliminary analysis come from latest Cretaceous (Lancian) through early Paleocene (Puercan) sites in Montana, and early (Puercan) through middle (Torrejonian) Paleocene sites in New Mexico (fig. 1a).

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TURNOVER RATES

Six biostratigraphic levels are recognized in northeastern Montana for purposes of this study (fig. 1b). The lower three—Bug Creek Anthills, Bug Creek West and Harbicht Hill—are latest Cretaceous (Lancian) in age based on the occurrence of dinosaurs. These levels yield Paleocene-aspect mammals and have been allocated to the Bug Creek faunal-facies (Sloan and Van Valen 1965, Archibald 1982). This faunal-facies was coeval with and was preceded by the Hell Creek faunal-facies which yields typical latest Cretaceous mammals (Archibald 1982). The upper three levels in Montana are Hell's Hollow, McKeever and Garbani. For purposes of this study, the faunally equivalent Purgatory Hill locality is included with Garbani, and Mantua lentil (from Wyoming) is included with McKeever. These upper three levels are early Paleocene (Puercan) in age (Van Valen and Sloan 1965, Clemens 1974, Van Valen 1978, Archibald 1982, Archibald *et al.* 1982).

In San Juan Basin, New Mexico, two levels are recognized, the classic Puercan and Torrejonian land mammal ages, which are approximately early and middle Paleocene in age (fig. 1b). Including the sites from New Mexico enables the sampling to extend into middle Paleocene, and also allows some degree of cross-checking between the early Paleocene localities of Montana and New Mexico.

In this study species-level taxonomy is employed to examine turnover rates and trophic structure. Theoretically, this approach has several

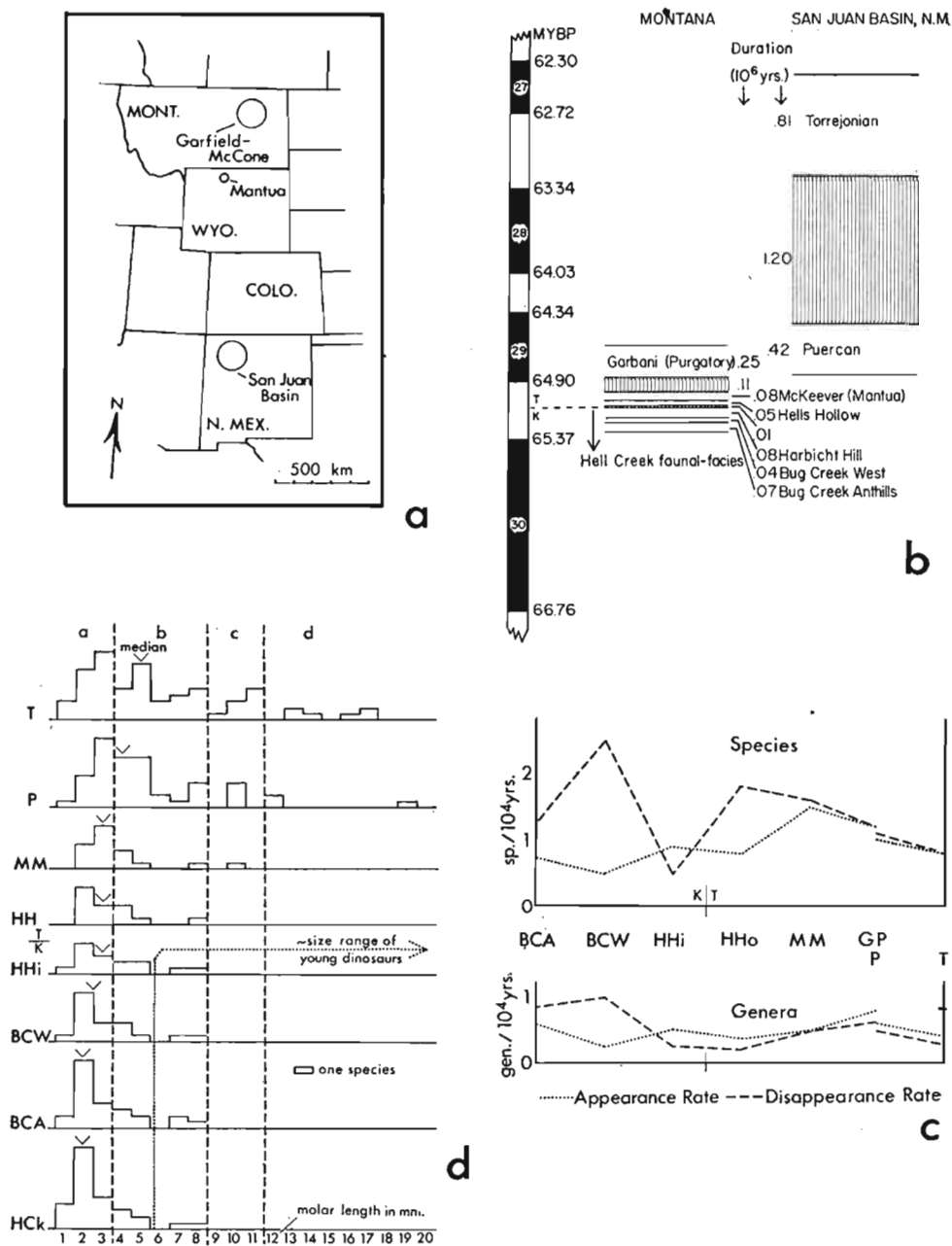


Fig. 1. *a* Areas under study in the western United States, *b* biostratigraphic position and duration of sampling levels in Montana and New Mexico with correlation to paleomagnetic polarity sequence of LaBrecque *et al.* 1977, *c* turnover rates for species and genera, *d* bar graph showing size distribution of mammals through sampling sequence. See text for further explanation. Abbreviations: *Hck* Hell Creek faunal-facies, *BCA* Bug Creek Anthills, *BCW* Bug Creek West, *HHi* Harbicht Hill, *HHo* Hell's Hollow, *MM* McKeever and Mantua, *GP* Garbani and Purgatory Hill, *P* Puercan (of New Mexico), *T* Torrejonian (of New Mexico), *K-T* Cretaceous-Tertiary boundary.

advantages. First, the species is much closer to the deme-level at which some ecological processes are thought to operate and second, as a biological entity a species is in principle the same in the latest Cretaceous as in the Recent. Neither of these attributes are true for higher taxonomic levels. Further, these local faunas are well enough known that even major systematic revision at the species-level will not greatly alter the number of recognized taxa. Again, this is not true for higher taxonomic levels where there is considerable debate concerning the recognition and number of such higher-level taxa.

Table 1

Specific and generic richness, turnover, and turnover rates. Duration for sampling levels given in fig. 1b

Sam- pling level	Species					Genera				
	Rich- ness	App.	App. rate (10 ⁴ yrs.)	Dis.	Dis. rate (10 ⁴ yrs.)	Rich- ness	App.	App. rate (10 ⁴ yrs.)	Dis.	Dis. rate (10 ⁴ yrs.)
T	70	68	0.8	61	0.8	52	36	0.4	24	0.3
P	47	43	1.0	45	1.1	36	26	0.6	20	0.5
GP	33	30	1.2	31	1.2	30	19	0.8	16	0.6
MM	16	12	1.5	13	1.6	14	4	0.5	4	0.5
HHo	13	4	0.8	9	1.8	11	2	0.4	1	0.2
HHi	15	7	0.9	4	0.5	13	4	0.5	2	0.3
BCW	17	2	0.5	10	2.5	12	1	0.3	4	1.0
BCA	24	5	0.7	9	1.3	17	4	0.6	6	0.9

App Appearances, *Dis* Disappearances

The method used for determination of turnover rates differs from those of most previous studies. Although it would be desirable to separate origination from immigration events, this is not possible for a majority of K-T mammals. Therefore, total appearance and disappearance rates were calculated. For example, appearances due to cladogenesis, anagenesis, and immigration are not differentiated.

In order to determine turnover rates, magnetostratigraphic sections in Montana and New Mexico (e.g. Archibald *et al.*, 1982) were correlated to those near Gubbio, Italy. LaBrecque *et al.* (1977) have calibrated the Cenozoic and Late Cretaceous paleomagnetic time scale (including the Gubbio section) providing for geochronologic estimates of polarity events. Archibald *et al.* (1982) found that the change from Lancian to Puercan faunas probably occurred during the same interval of reversed polarity in Alberta, Montana, and New Mexico. There is considerable controversy surrounding the intercontinental correlation of these paleomagnetic sec-

tions; however, I feel most evidence suggests that this is the reversed interval between anomalies 29 and 30 (but see Lindsay *et al.* 1981). The durations of each of the sampling levels given in fig. 1b were estimated from rates of sediment accumulation based on the thickness of the deposits representing the magnetostratigraphic intervals utilizing the geochronologic calibrations of LaBrecque *et al.* (1977).

For each of the sampling levels occurrences, appearances, and disappearances were tabulated. Utilizing these data and the estimated duration of each level, appearance and disappearance rates (species/10⁴ years) were calculated (Table 1). For species occurring in Montana (and Wyoming) the following sources were used: Sloan and Van Valen (1965), Van Valen (1978), Archibald (1982), Clemens (pers. comm.) and Sloan (pers. comm.). For species occurring in New Mexico the following sources were used: Matthew (1937), Russell (1967), Van Valen (1978), Taylor (1981), Tomida (1981), Tsentas (1981), Sloan (1981) and Archibald *et al.* (1983).

The plot of appearance—disappearance rates for species (fig. 1c) suggests that disappearance rates tend to decline into the middle Paleocene. It is not known whether the anomalously low disappearance rate for Harbicht Hill is real or an artifact. Many typical latest Cretaceous mammals (especially species of *Pedionmys*, see table 59, Archibald 1982) apparently make their last appearance in the Bug Creek faunal-facies at Bug Creek West. If this is correct then the low disappearance rate for Harbicht Hill (and the high rate for Bug Creek West) is real. However, if some of these species did last until Harbicht Hill, but at numbers too low to sample, the disappearance rate is artificially low for Harbicht Hill and artificially high for Bug Creek West. Appearance rates tend to increase into the earliest Paleocene and then decline into the middle Paleocene, although they do equal disappearance rates by this level. The Puercan of Montana and New Mexico have very similar turnover rates even though only 25—30% of species in the Puercan of Montana occur in the Puercan of New Mexico. Similar tabulations and computations were performed for genera (fig. 1c). The trends for genera are somewhat more subdued as might be expected. However, appearance rates overtake disappearance rates sooner and by a more noticeable amount for genera as compared to species. Thus the earlier increase in appearance rates beyond disappearance rates for genera as compared to species might be indicative of greater adaptive shifts going into the Paleocene. As will be seen, this appears to be born out by an analysis of species-level changes in the trophic structure.

The turnover rates presented here differ from those of previous authors. Van Valen (1978) indicated that origination rates for species and genera of condylarths declined by an order of magnitude between Bug Creek Anthills and Puercan. These results are the opposite of the general trend for an increase in appearance rate for species I estimated between

Bug Creek Anthills and Torrejonian. Although the methodologies of Van Valen and those presented here do differ, they are not enough to account for such a discrepancy in rates. I believe the rates calculated by Van Valen are in error because geochronologic time was underestimated by an average factor of three between Bug Creek Anthills and Harbicht Hill and overestimated by a factor of five between Mantua and Puercan.

Stanley (1979) concluded that there were not an unusually high number of speciation events during the early Cenozoic radiation of eutherians. Further, the rates of morphological change during these speciation events would have been high. These conclusions were based upon a comparison with seven later Cenozoic mammalian families. Borrowing the standard exponential equation for population growth from demography, $\frac{dn}{dt} = RN$, and integrating to $N = N_0 e^{Rt}$, Stanley found that the seven mammalian families had an average $R = .22/10^6$ years (where R is a fractional increase per unit time, t is time, N is the number of species after time t , N_0 is the original number of species, and e is a constant, the base of natural logarithms). The above conclusions regarding rates of speciation for early Cenozoic eutherians were drawn by Stanley even though he notes that his $R = .39/10^6$ years for early Cenozoic eutherians is 75% higher than the average $R = .22/10^6$ years for the seven later Cenozoic families. An R value of $.36/10^6$ years calculated for all K-T transition mammals considered in this study is quite close to Stanley's R value of $.39/10^6$ years for early Cenozoic eutherians. However, for condylarths during the K-T transition I calculated an R value of $1.16/10^6$ years, which is over 400% greater than Stanley's later Cenozoic average of $.22/10^6$ years.

Stanley (1979) also feels an average species duration of 1 million years for later Cenozoic mammals applies to early Cenozoic mammals as well. He found that only 1% of later Cenozoic European mammals lasted less than 3.5×10^5 years. Since the lower boundary (and thus the duration) of the Lancian cannot be estimated an analogous estimate cannot be calculated for the K-T transition in North America. However, a minimum percentage of mammals existing less than 3.5×10^5 years during the K-T transition is 30%, which is obviously much greater than Stanley's 1% figure.

These results suggest that (contrary to Stanley 1979) some early Cenozoic mammalian groups such as condylarthrans had more frequent speciation events and shorter species durations than did later Cenozoic mammals. Further, such data cannot be used to address the issues of punctationalism *versus* gradualism since the rates of morphological divergence are either unstudied or unknown for these groups.

Although it would be worthwhile to compare turnover rates for the K-T transition with other early Cenozoic transitions, such data are not readily available. However, utilizing Rose's (written comm. 1981) data

for the late Paleocene and early Eocene of the Bighorn Basin, Wyoming, I obtained an overall appearance rate of 1.0 sp./10⁴ years and an overall disappearance rate of 0.5 sp./10⁴ years. For the K-T transition these overall rates are 0.9 sp./10⁴ years and 1.4 sp./10⁴ years, respectively. It is dangerous to draw conclusions from only two samples, but the approximately 1 sp./10⁴ year appearance rate for both the K-T and Paleocene-Eocene transitions suggests that the K-T transition is not unique in its rate of appearances. The disappearance rate of 0.5 sp./10⁴ years for the Paleocene-Eocene transition may be low relative to the rest of the Tertiary. This is consistent with Lillegraven's (1972) finding that the highest ordinal diversity and second highest familial diversity of mammals, in North America occurs in the early Eocene. This was a time of considerable overlap between archaic and newly appearing orders of mammals. The disappearance rate of 1.4 sp./10⁴ years for the K-T transition is probably quite high relative to the rest of the Tertiary, but as of now I have no strong evidence to support this thesis. However, the general pattern of faunal reorganization and extinction during the K-T transition lends credence to this supposition.

Another trend that would be interesting to track during this interval is standing taxonomic richness. However, there is no satisfactory method at present that can convincingly compare sampling levels that vary substantially in duration. This is the case for this exercise. The geochronologically older sampling levels in this study sample time intervals on the order of tens of thousands of years. They are probably closer to representing standing taxonomic richness than are the Puercan and Torrejonian levels, which sample hundreds of thousands of years. However, Taylor's (1981) report of 45 species-level taxa from the Kutz Canyon local fauna (which he feels represents only the early Torrejonian) *versus* the 70 species recognized for the whole of the Torrejonian in the present study suggests standing taxonomic richness is not being overestimated by more than a third.

TROPHIC STRUCTURE

The K-T transition in North America was also examined in terms of faunal composition and trophic structure. A simple plot for K-T mammals by order shows that from a taxonomically equally balanced fauna in the latest Cretaceous, one group, the condylarthrans, emerge by the mid-Paleocene comprising almost 50% of species richness (fig. 2a). This dominance may be unique for the K-T transition in North America, but is probably not unique for radiations in general or the K-T transition in particular. A similar sort of dominance by other mammalian groups may have occurred in other parts of the world during this same interval.

A more detailed analysis of the K-T mammal transition can be done by estimating and tracing guilds (ecologically similar species) through this interval. Estimates of size and food preference were made utilizing dental size and morphology (and cranial and postcranial morphology for a few of the species). As a crude approximation of size, the length of the first lower molar for multituberculates and fifth lower post canine tooth for therians were plotted through the K-T interval (fig. 1d).

Utilizing the four size groups (*a-d* fig. 1d) in tandem with estimates of food preference I have attempted to establish and trace guilds through the K-T interval. These guilds are by necessity somewhat arbitrary: however, it is the relative change and timing of these changes of guild structure that are important. Five numbered groups with similar dental morphology or assumed dietary preference were recognized and were further divided according to which of the four size categories they belong. Group one includes forms with medium to low-cusped, usually non-sectorial dentitions. Multituberculates are somewhat difficult to categorize, but forms with large P/4-blades were placed in group 1. Smaller members were insectivorous, granivorous, or frugivorous while large members were more strictly herbivorous. Group two includes multituberculates with small P/4 blades and often gliriform incisors (the taeniolabidoids). Members may have been more strictly herbivorous even at small-size, but possibly this group should be included with the first. Group three includes forms with high-cusped and/or sectorial or trenchant dentitions. As size increases diet shifts from insectivory to carnivory. Group four includes the larger and more specialized taeniodonts. Here the enlarged tusks and clawed manus are indicative of a probably quite specialized "rooting" habit. Group five includes the order Pantodonta. The North American forms were probably herbivorous and here we see the first development for crests for "slicing" food stuffs.

When these guilds are traced through the K-T interval several patterns can be observed (fig. 2b). In the latest Cretaceous, mammals were limited to small size and filled many of the ecological roles small mammals fill today. Towards the end of the Cretaceous condylarths appear and begin to replace marsupials. Following a probable decrease in species richness near the K-T boundary, an increase in species richness occurs in some of the guilds, suggesting a refilling of these pre-existing guilds before the establishment of new ones. By Puerco time new guilds appear and by the Torrejonian there is some tendency towards taxonomic evenness within some guilds. Not too surprisingly, as the rate of establishment of new guilds accelerates the rate of appearances reaches its highest levels. During these episodes disappearances are low (but not at their lowest) which is also not surprising because the mammals are expanding into relatively empty ecological space.

The patterns shown in figs. 1d and 2b argue against the hypothesis

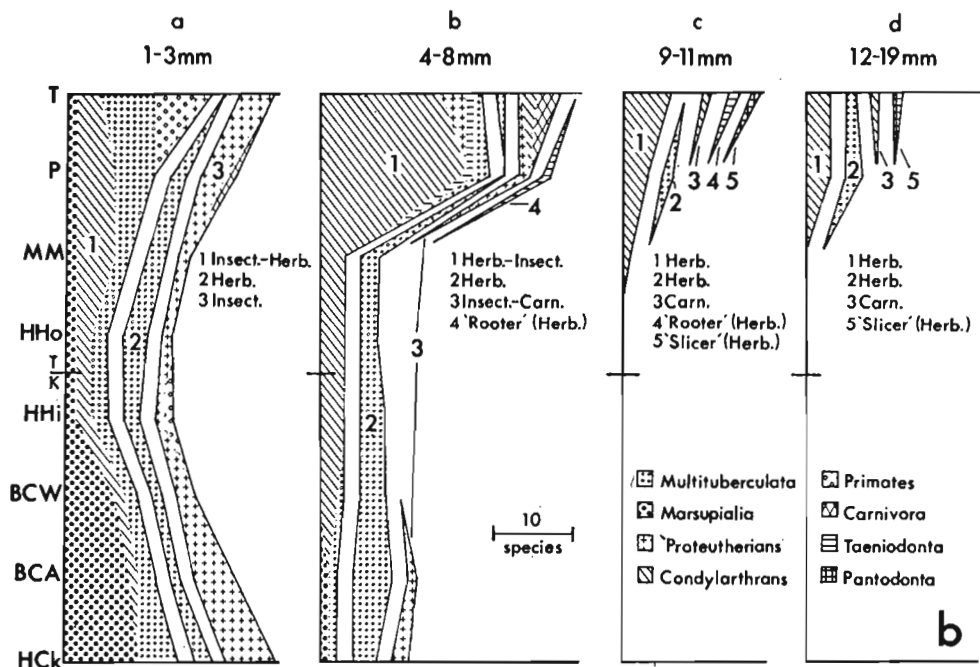
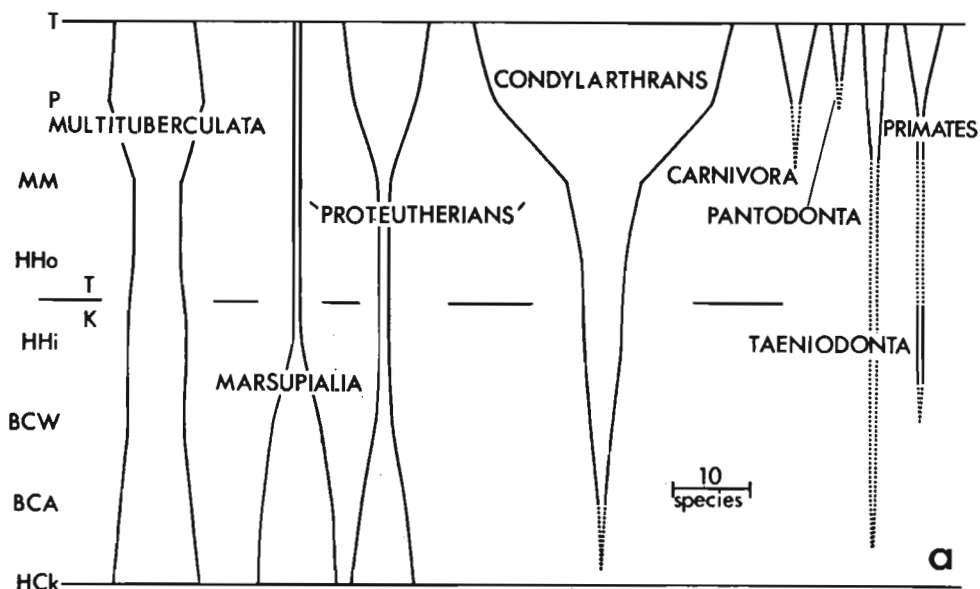


Fig. 2. *a* Species richness through the sampling levels grouped by orders or equivalent taxonomic groups, *b* guilds (by size and dietary preference) through the sampling levels. See text for further explanation. Abbreviations: *Insect.* insectivorous, *Herb.* herbivorous, *Carn.* carnivorous. Other abbreviations as in fig. 1.

that mammals contributed to the demise of dinosaurs through some sort of competition (Van Valen and Sloan 1977). First, the size distribution pattern in fig. 1d persisted for almost 130 million years and it was only after the extinction of dinosaurs that mammals increased in size. Second, with the ecological release that occurred after dinosaur extinction there is a time lag of almost 2.5×10^5 years, before mammals radiate (including size increase). Third, if competition were a factor one might have expected more mammal species to have been decimated; yet with the introduction of the supposed competitor, the condylarthans, only the marsupials were decimated while all dinosaurs disappeared.

SUMMARY

There are certainly realized and unrealized biases in this type of study. Nevertheless, there are several implications for the K-T transition in particular and possibly for radiations in general. 1) The overall appearance rate for the K-T transition is not high, at least compared to the Paleocene-Eocene transition. However, the overall disappearance rate may be high for the K-T transition. 2) Condylarths are a dominant taxonomic group in the radiation in North America but this may not be true elsewhere. 3) After perturbations to the system, some pre-existing guilds are re-established before new guilds form. 4) Not surprisingly, appearance rates reach maxima during times of guild establishment. 5) A considerable time lag between dinosaur extinction and extensive mammalian radiation suggests mammal-dinosaur competition was not a major factor in dinosaur extinction. Such time lags may be common in radiations, as they have also been observed in the marine record (Carr and Kitchell 1980).

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