

## Paleogene vertebrates and their response to environmental change

Philip D. Gingerich, Ann Arbor

With 7 figures and 1 table

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**Abstract:** The global standing diversity of Vertebrata is relatively constant through the Cretaceous at 200-300 families but it approximately doubles following the Cretaceous-Paleogene (K-P) extinction event to reach a new Cenozoic level of about 600 families. This increase is greatest in the late Paleocene and early Eocene, and the Paleocene-Eocene transition is thus of special interest for vertebrate evolution. The diversity of Reptilia decreased substantially across the K-P boundary as global temperature declined more gradually, but the diversity of Teleostei, Aves, and Mammalia all increased greatly through the Paleocene and early Eocene, advancing against the temperature trend. The dominant pattern in these groups appears to be one of stabilization following environmental disturbance rather than continual biotically-driven evolution independent of environmental change. This is true on the 5-6 million-year time scale of stratigraphic stages across the K-P boundary, but it is most clearly seen in the abrupt response and subsequent stability of mammals on a 10 to 100 thousand-year time scale during and immediately following the Paleocene-Eocene thermal maximum. The Paleogene is important for understanding both vertebrate history back to the deeper past and vertebrate evolution forward to the present.

**Zusammenfassung:** Die globale "standing diversity" der Wirbeltiere liegt während der Kreide konstant bei 200-300 Familien, erreicht jedoch nach dem Aussterbeereignis an der Kreide-Paleogen (K-P)-Grenze das neue kainozoische Niveau von ungefähr 600 Familien. Diese Zunahme ist am größten während des späten Paläozäns und dem frühen Eozän. Der Übergang vom Paläozän zum Eozän ist daher für die Evolution der Wirbeltiere von besonderer Bedeutung. Die Diversität der Reptilien nimmt mit dem schrittweisen Sinken der globalen Temperatur im Bereich der K-P-Grenze stark ab, während diejenige der Knochenfische, Vögel und Säugetiere während dem Paläozän und dem frühen Eozän gegenläufig zur Entwicklung der Temperatur zunimmt. Bei diesen Gruppen entspricht das vorherrschende Muster eher der Stabilisierung nach einer Störung der Umwelt als demjenigen einer biotisch getriebenen, von Veränderungen der Umwelt abhängigen Evolution. Dies trifft für die 5-6 Millionen Jahre im Bereich der K-P-Grenze zu, ist aber am deut-

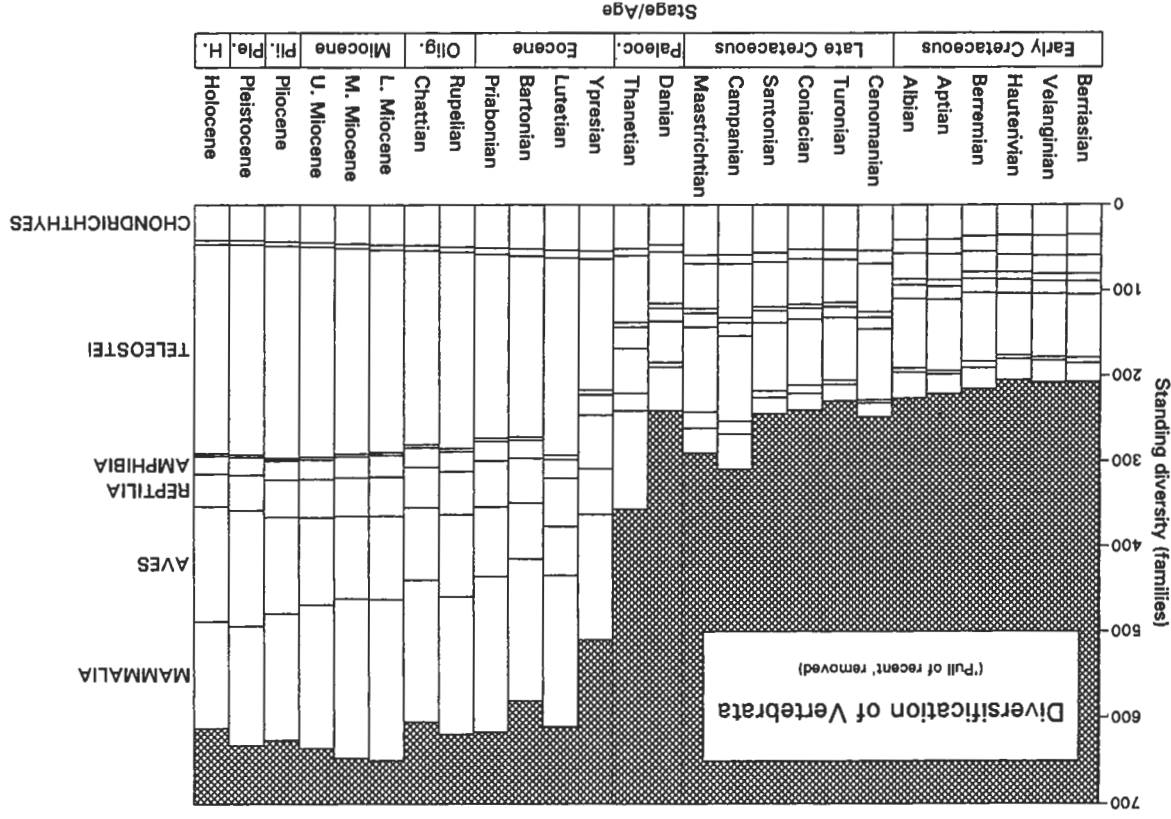
lichsten aus der abrupten Reaktion und nachfolgenden Stabilität der Säugetiere in einem Zeitbereich von zehn- bis hunderttausend Jahren während und unmittelbar nach dem Paläozän-Eozän-Wärme-Maximum ausgeprägt. Das Paleogen ist wichtig für das Verständnis der frühen Geschichte der Wirbeltiere und für ihre Entwicklung bis zur Gegenwart.

## 1. Introduction

The Cenozoic Era is commonly called the 'Age of Mammals' but it could equally well be called the 'Age of Birds' or the 'Age of Bony Fishes.' All three classes, Mammalia, Aves, and Teleostei, diversified rapidly and greatly at the beginning of Cenozoic time. The Paleogene period of the early Cenozoic captures much of this change. The classes Chondrichthyes, Amphibia and Reptilia, in contrast, are surviving representatives of essentially Paleozoic and Mesozoic vertebrate groups.

One of the most fundamental and important questions about evolution in any group of organisms is the degree to which it responds to environmental change. This is important in a 'forward' sense because the theory of natural selection by which we explain evolution involves, fundamentally, a response of species to the environment around them. A species steps forward in time, generation by generation, shaped by its environment at some level. This environment external to a species can be conceived in a near sense as comprising the surrounding biota, and more generally in a far sense as comprising the surrounding biota and its greater physical environmental context.

Fig. 1. Diversification of vertebrate groups considered together as a phylum. Histogram shows change in the family-level standing diversity of vertebrates, stage by stage, through the Early and Late Cretaceous periods of the Mesozoic Era and through the Paleogene and Neogene periods of the Cenozoic Era, a total of about 145 million years. Note that Mesozoic diversity characteristically comprised about 200-300 families, while Cenozoic diversity comprised about 600 families. The change from Mesozoic to Cenozoic diversity happened rapidly during the Paleocene-Eocene transition. Graphs for each class are shown separately in Fig. 2. Data are from BENTON (1993; <http://palaeo.gly.bris.ac.uk/frwhole/FR2.html>); compiled class by class by CAPPETTA et al. 1993; GARDNER 1993; PATTERSON 1993; SCHULTZE 1993; MILNER 1993; BENTON 1993b; UNWIN 1993; and STUCKY & MCKENNA 1993, respectively). The 'pull of the recent' has been removed by correcting the declining proportional representation of sedimentary rocks of successively older ages (BLATT & JONES 1975).



The response of organisms to environmental change is also important in a 'backward' sense because, correctly or incorrectly over the years, much of what we know about physical environmental change has been inferred from change observed in organisms. Hence patterns of change observed in organisms have been used to infer or 'back out' environmental change through earth history.

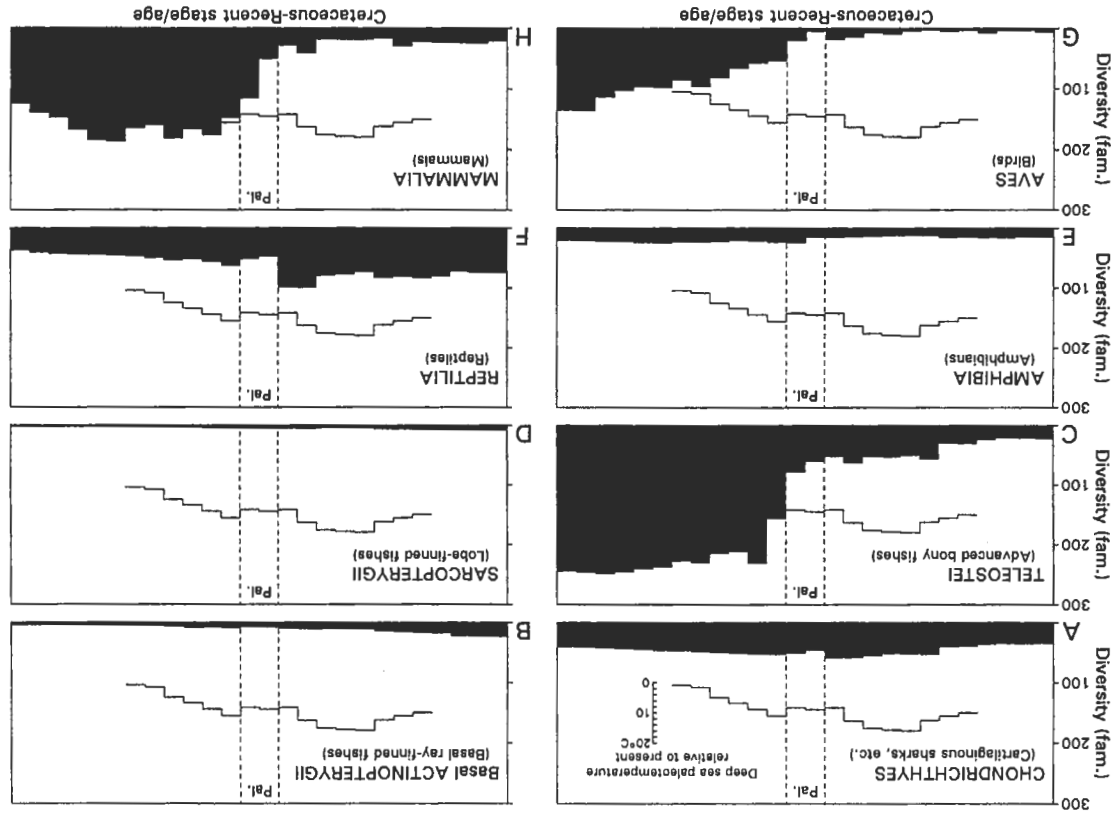
It is a question of much interest and debate whether life evolves continuously in response to biotic interactions ('Red Queen' hypothesis of VAN VALEN 1973), or episodically in response to changes in the more-distant physical environment ('Stationary' hypothesis of STENSETH & SMITH 1984). These are not necessarily exclusive alternatives, and it is not always easy to devise tests that will distinguish them.

Here I consider the relationship of biotic change in vertebrates to change in the physical environment through the Cretaceous and Paleogene, with emphasis on mammals because of their familiarity and exceptionally good fossil record.

## 2. Paleogene vertebrates

The pattern of diversification of vertebrates as a phylum is shown in Figure 1, which illustrates global family-level diversity, and spans the Cretaceous, Paleogene (Paleocene through Oligocene epochs), and Neogene periods (Miocene through Holocene epochs) of the past 145 million years. Figure 1 and the following Figures 2 and 3 have been corrected for the 'pull of the recent' – an artifact of some diversity profiles reflecting the greater accessibility of more-recently formed strata, and the generally better pre-

Fig. 2. Diversification of vertebrate groups considered individually class by class. Solid histograms show change in the family-level standing diversity of each class, stage by stage, through the Cretaceous, Paleogene, and Neogene, a total of about 145 million years. Note that the diversity of Chondrichthyes (A), basal Actinopterygii (B), Sarcopterygii (D), and Amphibia (E) changed little from Cretaceous through Recent times, while the diversity of Reptilia (F) decreased substantially. Three groups, Teleostei (C), Aves (G), and Mammalia (H), are responsible for the rapid increase in diversity of Vertebrata as a phylum shown in Fig. 1. Here too the changes from Mesozoic to Cenozoic diversity happened rapidly during the Paleocene-Eocene transition (during and immediately following the Paleocene [Pal.] interval enclosed by dashed lines). Sources and treatment of faunal data are explained in the caption for Fig. 1. Stepped paleotemperature curves are derived from oxygen isotopes in benthic Foraminifera (calibration is in °C relative to present-day bottom water temperatures; see ZACHOS et al. 2001; BRALOWER et al. 2002).



servation of fossils in these rocks (RAUP 1979). This artifact has been removed by dividing sampled diversity in each stratigraphic stage/age by the corresponding area of exposure of sedimentary rock of that age (an exponential curve declining with increasing geological age; BLATT & JONES 1975).

Family-level diversity was relatively stable at about 200-300 families of vertebrates through much of the Cretaceous and early Paleocene, and it has been relatively stable at about 600 families of vertebrates from the middle Eocene to the present. The biggest change in vertebrate diversity during this interval of history came between the early Paleocene and the middle Eocene, when the number of families approximately doubled. The Cretaceous-Paleocene boundary (K-T or K-P boundary) receives much attention because of the bolide impact thought to be responsible for a mass extinction of vertebrates at this time (ALVAREZ 1987; see also CLEMENS 2002), but it is really the Paleocene-Eocene transition that is most interesting from the point of view of vertebrate diversification. Extinction at the Cretaceous-Paleocene boundary is inferred to have involved loss of about 50 families of vertebrates (comparing Maastrichtian diversity to that in the Danian), while origination across the Paleocene-Eocene transition is inferred to have added about five times this many families (about 110 comparing Danian diversity to that in the Thanetian, and a further 150 comparing Thanetian diversity to that in the Ypresian; based on tables in BENTON 1993). This is what makes study of vertebrate evolution across the Paleocene-Eocene boundary so interesting.

Patterns of change in diversity differ in different classes. This can be seen in the changing proportions of classes in Figure 1, but it is best shown by considering each separately as illustrated in Figure 2. The diversity of Chondrichthyes, basal Actinopterygii, Sarcopterygii, and Amphibia changed little in the 145 million-year Cretaceous through Recent interval analyzed here, while the diversity of Reptilia decreased substantially at the Cretaceous-Paleocene boundary (from about 100 families in the Maastrichtian to 50 in the Danian, constituting virtually all of the loss of vertebrate diversity at this boundary). Three groups, Teleostei, Aves, and Mammalia, are responsible for the rapid increase in diversity by about 70, 30, and 30 families, and these each increased in diversity by about 70, 30, and 30 families, respectively, across the K-P boundary (comparing inferred Thanetian and Ypresian numbers).

If we look at Mammalia in more detail (Figure 3), we see for the whole Cretaceous to Recent interval studied that the highest numbers of inferred first appearances of new family groups (removing the 'pull of the recent') are in the Thanetian and Ypresian stages (about 70 and 60 families, respectively. Addition of 60 new families in the Ypresian, when net diversity goes up by only 30 (previous paragraph), means that some 30 families disappeared at this boundary.

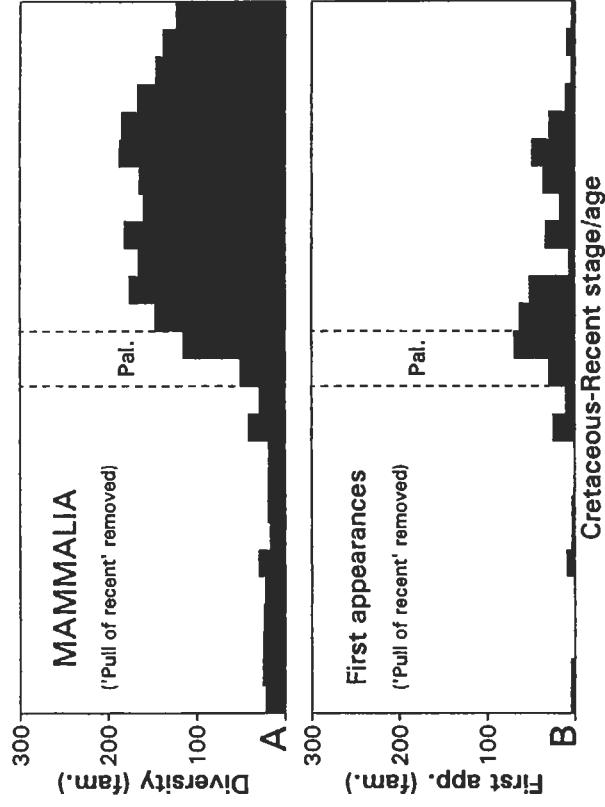


Fig. 3. Diversification of Mammalia as a class (A) compared to the number of first appearances of new mammalian families in each stage (B). The greatest numbers of new appearances for the entire 145 million-year Cretaceous to Recent interval are in the late Paleocene (50) and early Eocene (47), contributing to the rapid increase in diversity of Mammalia as a class at this time. Sources and treatment of data are explained in the caption for Fig. 1. Mammal ranges analyzed here are documented in detail in STUCKY & MCKENNA (1993).

All of these numbers are estimates, based on an extensive collection of stratigraphic range data compiled at the level of stages. The 26 stages analyzed here span 145 million years, meaning that a stage averages about 5-6 million years in duration. The numbers are not reliable at any finer scale of study, but indicate clearly that the Paleocene and the Paleocene-Eocene transition are important times in vertebrate history.

### 3. Environmental change

We can now compare change in Cretaceous-Paleocene vertebrate diversity to change in the environment through the same interval. Temperature is an important environmental indicator, and paleotemperatures inferred from

**Table 1.** Test of the expected correlation of family-level standing diversity with global average temperature for classes illustrated in Figure 2 ( $n = 16$ ;  $*p < 0.05$ ,  $**p < 0.01$ ).

Vertebrate class	Correlation
Mammalia	-0.75
Aves	-0.82
Reptilia	0.61*
Amphibia	-0.75
Sarcopterygii	0.50
Teleostei	-0.74
Actinopterygii	0.62**
Chondrichthyes	0.26

oxygen isotopes in deep-sea benthic Foraminifera are shown in Figure 2 (based on data in ZACHOS et al. 2001, and BRALOWER et al. 2002). The floating stepped line in Figure 2 shows paleotemperatures for 16 successive stratigraphic stages, from the Aptian in the mid-Cretaceous to the Chattian in the Oligocene. In an ice-free world,  $\delta^{18}\text{O}$  in benthic forams is a proxy for temperature in oceanic bottom water, which in turn represents an averaged record of high-latitude sea surface temperatures. In this Aptian to Chattian record, temperatures rose five times and fell 10 times, from one stage to the next, and the prevailing trend is one of decreasing temperature. The highest temperature, in the Turonian, was about  $16^\circ\text{C}$  warmer than present, and the lowest temperature at the end, in the Chattian, was only about  $1^\circ\text{C}$  warmer than present.

In the living world today there is a strong correlation of vertebrate biodiversity with temperature (and environmental energy; CURRIE 1991). Equatorial tropical climates include the most vertebrate species and higher taxa, and there are many fewer vertebrate species living in polar climates. Hence we would expect to find diversity and temperature to be positively correlated in the geological past if temperature was an important factor controlling diversification. The results, however, are surprising (Table 1). Diversity is positively correlated with temperature in only four class-level vertebrate groups, and within these, only two, basal Actinopterygii and Reptilia, are significantly positively correlated. The other six groups have diversity-temperature correlations that are either positive but not significant, or negative. Evidently temperature was not a very important determinant of family-level diversity in vertebrates observed through the course of Cretaceous-Paleogene time.

It is tempting to conclude from this lack of correlation with temperature that biotic interactions were more important than the physical environment

in determining vertebrate diversity. However, there are other environmental factors, such as continental positions and intercontinental connections, bolide impacts, and short-term climate change, that are not tested here. The most abrupt change in reptilian diversity happened at the end of the Cretaceous, when a high level of reptilian diversity of about 100 families in the Campanian and Maastrichtian stages dropped to about 50 families in the Danian and Thanetian. The cause of this change is thought to have been environmental in the most distant sense: impact of an extraterrestrial bolide, probably an asteroid (ALVAREZ 1987; ROBERTSON et al. 2004). All three of the vertebrate groups that diversified so dramatically in the Cretaceous-Paleogene interval, teleosts, birds, and mammals, did so immediately following the K-P mass extinction during the initial Danian, Thanetian, and Ypresian stages of the early Paleogene. This is not a 'Red Queen' pattern of long-term constancy of diversity and rate but a 'Stationary' pattern of dramatic change and then stability following an environmental event.

#### 4. Paleocene-Eocene transition

Within the vertebrates, mammals appear to have the best fossil record in the sense of its completeness, and hence mammals are commonly studied to learn about evolution as a process and about evolutionary history in relation to environmental change. Mammals have relatively simple skeletons that are compact and dense, with information enabling identification and ecological interpretation recorded unequivocally in teeth, supplemented by foot bones, all of which preserve well as fossils. In contrast, bony fishes have complex skeletons that are easily disarticulated in all but the quietest depositional environments, while birds, due to flight, have relatively simple and fragile skeletons. Consequently, the fossil histories of bony fishes and birds are less completely known as a proportion of their diversity than is the fossil history of mammals.

Extinction of the great terrestrial and marine reptiles at the end of the Cretaceous left a void that was filled in two waves, first in the Paleocene by archaic and relatively generalized mammals (e.g., Multituberculata, Condylarthra, Proprimates, etc.), and then in the Eocene by more specialized mammals that we recognize and classify in the orders familiar today (e.g., Perissodactyla, Artiodactyla, Primates, etc.). For vertebrate paleontologists of the twentieth century, the Paleocene Epoch was, literally, the time between the extinction of dinosaurs and the appearance of perissodactyls in the form of dawn horses.

Change from the Mesozoic to the Cenozoic was rapid, possibly as instantaneous geologically as a single catastrophic asteroid impact. It has taken a long time, but in recent years we have come to appreciate that the



A new transitional earliest Wasatchian 'Wa-0' mammalian fauna was discovered, and surprisingly this included taxa that were dwarfed in comparison to congeneric species that preceded and succeeded them (Figure 5).

In the 1990s a distinctive 'late Paleocene' carbon isotope excursion (CIE) was found in deep-sea sediments coincident with an oxygen isotope event reflecting abrupt warming (KENNETT & STOTT 1991), and the CIE was then found on land in the Wa-0 faunal interval (KOCH et al. 1992). Discovery of the CIE led to a revised concept of the marine Paleocene-Eocene boundary making it correlative in time with the Clarkforkian-Wasatchian boundary on land (a revision now ratified by the International Commission on Paleogeography in 2002 and the International Commission on Stratigraphy in 2003). The CIE enables precise correlation of marine strata with terrestrial deposits in North America and Europe (KOCH et al. 1995; STEURBAUT et al. 1999; BAINS et al. 2003; MAGIONCALDA et al. 2004; Figures 4 and 6), and work is in progress extending this to continental Asia (BOWEN et al. 2002). The warming peak coincident with the CIE, the Paleocene-Eocene thermal maximum or PETM, is now known to be global as well (ZACHOS et al. 2003). The CIE and PETM are tied in different ways to mobilization of marine methane clathrates responsible for a 100 kyr natural greenhouse climate event (DICKENS et al. 1995; SCHMIDT & SCHINDELL 2003), explaining both the holarctic cosmopolitanism of vertebrate faunas and the dwarfing of Wa-0 mammals (GINGERICH 2003).

The distinctive Eocene vertebrate fauna with modern mammalian orders Artiodactyla, Perissodactyla, and Primates dispersed across high latitude land bridges connecting Asia, Europe, and North America within the first 10 kyr or so of Eocene time. PETM climatic warming had a transient effect

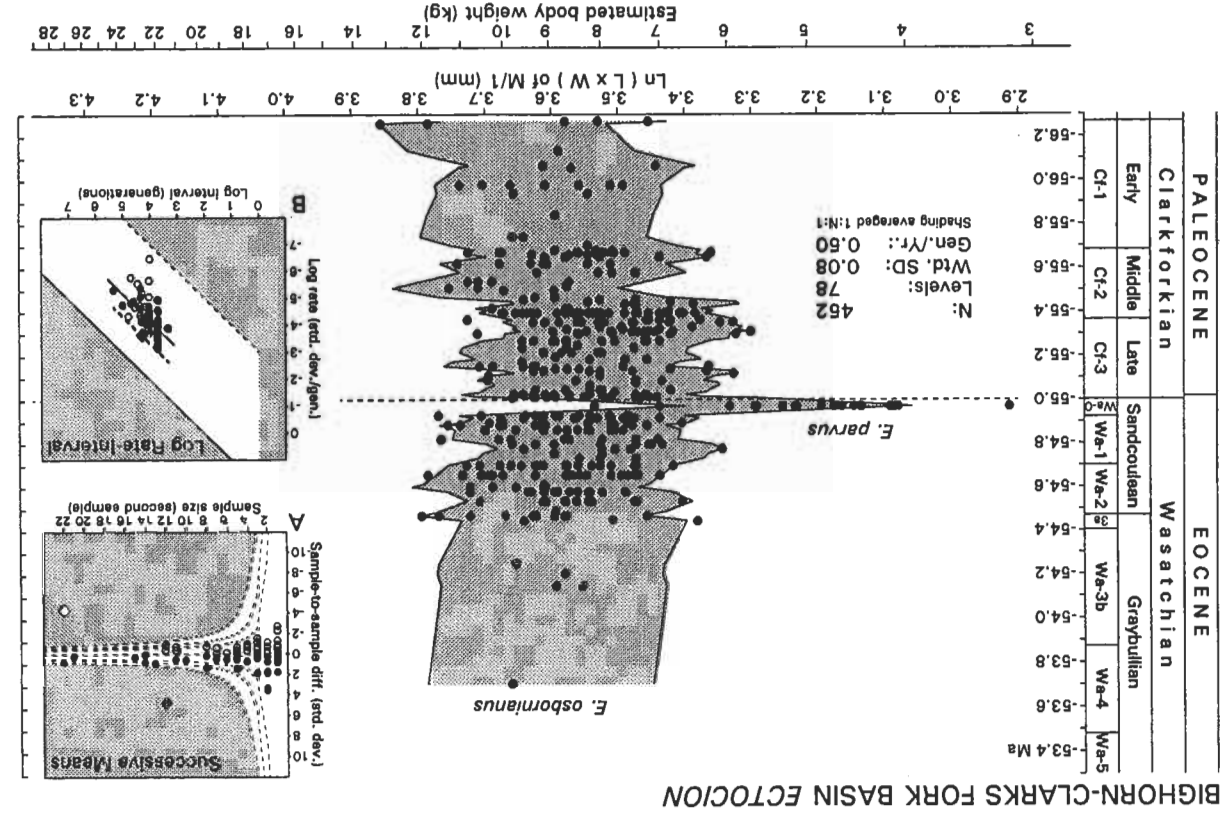


Fig. 5. Dwarving in common North American Paleocene-Eocene condylarth mammalian *Ectocion* associated with the carbon isotope excursion (CIE) and Paleocene-Eocene thermal maximum (PETM), based on Clarkforkian and early Wasatchian specimens of known stratigraphic level in the northern Bighorn and Clarks Fork basins, Wyoming, U.S.A.. Most specimens represent the common species *Ectocion osbornianus* of about 8-10 kg body weight, but smaller specimens of *Ectocion parvus* of about 4-5 kg body weight predominate in the Wa0 stratigraphic interval coinciding with the CIE and PETM (cf. Fig. 4). Vertical axis is time, based on cubic spline interpolation of Figure 4. Figure is reproduced from GINGERICH (2003); references and explanation of details are given therein). Note rapid replacement of *E. osbornianus* by dwarfed *Ectocion parvus* in the Wa-0 CIE-PETM interval, and rapid return to *E. osbornianus* in overlying strata following the PETM. It is not yet certain that dwarfed *E. parvus* evolved from earlier *E. osbornianus*, but this is plausible from an evolutionary rate point of view.



on mammalian body size during Wa-0 time, but a profound and lasting effect on the composition of terrestrial vertebrate faunas on all three northern continents (CLYDE & GINGERICH 1998). Change across the Paleocene-Eocene boundary studied on a time scale of 10s of thousands of years is not the same as change across the Cretaceous-Paleogene boundary studied on a time scale of millions of years, but here again a seemingly 'Stationary' pattern emerges of dramatic change and then relative stability following an environmental event.

### 5. Evolution from a rate perspective

The problem in both the Cretaceous-Paleogene (K-P) and the Paleocene-Eocene (P-E) transitions is not so much to explain how older dinosaurs and then condylarth-grade mammals became extinct as it is to explain first how condylarth-grade mammals replaced dinosaurs, and then how modern orders of mammals so rapidly replaced the mammals that preceded them. As the far corners of the earth are explored and more or less the same kinds and grades of fossils are found, it is beginning to seem that new and more

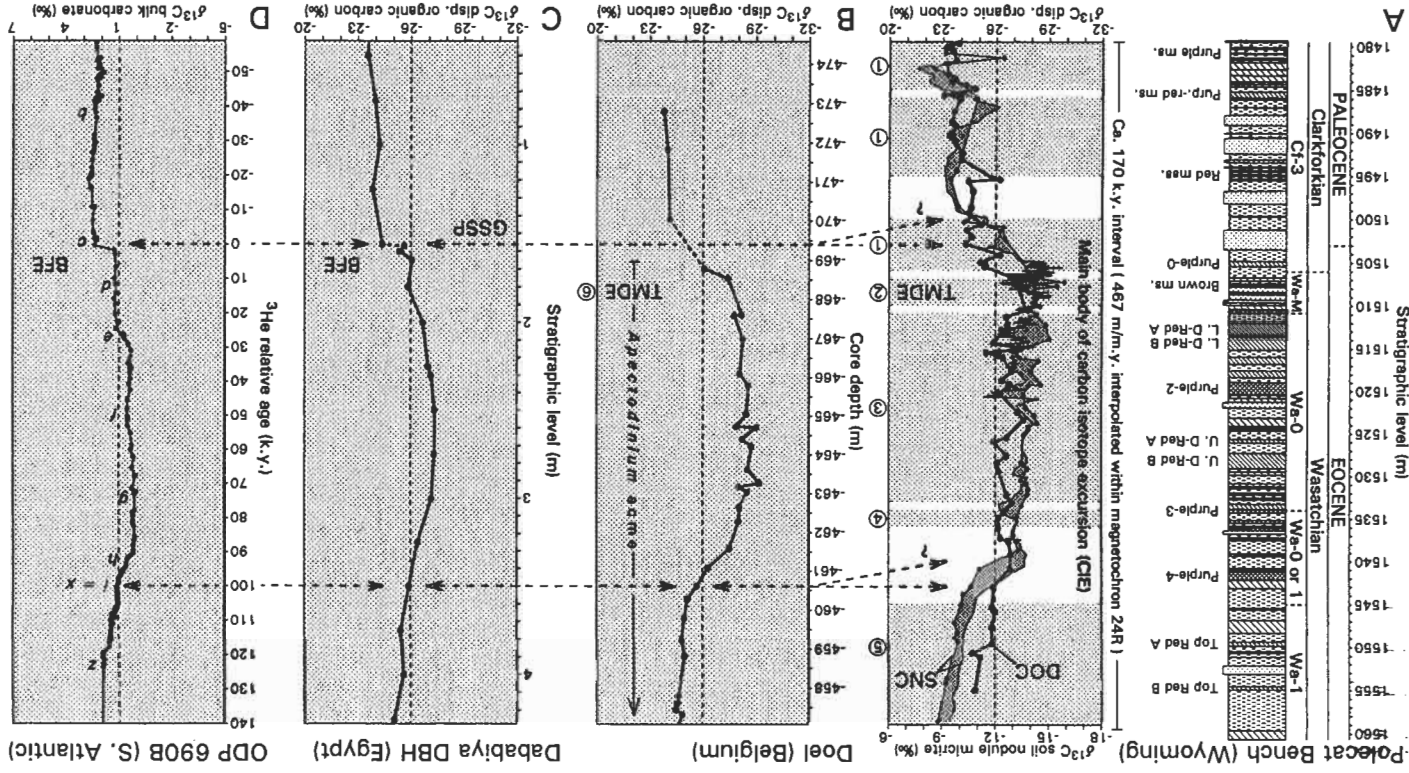


Fig. 6. High resolution stratigraphy of the carbon isotope excursion (CIE) in the Polecat Bench, Wyoming, U.S.A., continental section compared to marine CIE sections studied elsewhere. Dispersed organic carbon (DOC) is shown by heavy black lines. Soil-nodule carbonate (SNC) is shown by light black lines, and marine carbonate is shown by a light black line. Dashed correlation lines show points being matched: sediment accumulation is not necessarily linear with time within or following correlated intervals. Paleocene-Eocene epoch boundary is drawn at the onset of the CIE, and the Clarkforkian-Wasatchian land-mammal age boundary is drawn at the first appearance of characteristically Wasatchian land mammals including here *Meniscotherium*. Figure is reproduced from MAGIONCALDA et al. (2004; references and explanation of details are given therein). The calibration of ODP 690B section is from FARLEY & ELTGROTH (2003), showing that the main body of the CIE lasted 100 thousand years. Late Clarkforkian Cf-3 zone Paleocene mammals are found in the Polecat Bench shaded zones numbered (1), a new basal Wasatchian faunal zone Wa-M with *Meniscotherium* occupies the initial 10 thousand years of the CIE-PETM interval in shaded zone (2), and the better known Wa-0 fauna with *Ectocion parvus* and other dwarfed taxa are found through most of the remaining 90 thousand years of the CIE-PETM interval in shaded zone (3). Shaded zone (4) may be part of faunal zone Wa-0 or succeeding Wa-1. Wasatchian Wa-1 mammals of normal size are found in shaded zone (5). Note that while the Clarkforkian-Wasatchian land-mammal age boundary and the CIE are very close in time, there is a definite lag (inferred to represent 5-10 thousand years) between the onset of the CIE and the faunal shift from Clarkforkian to Wasatchian mammals.

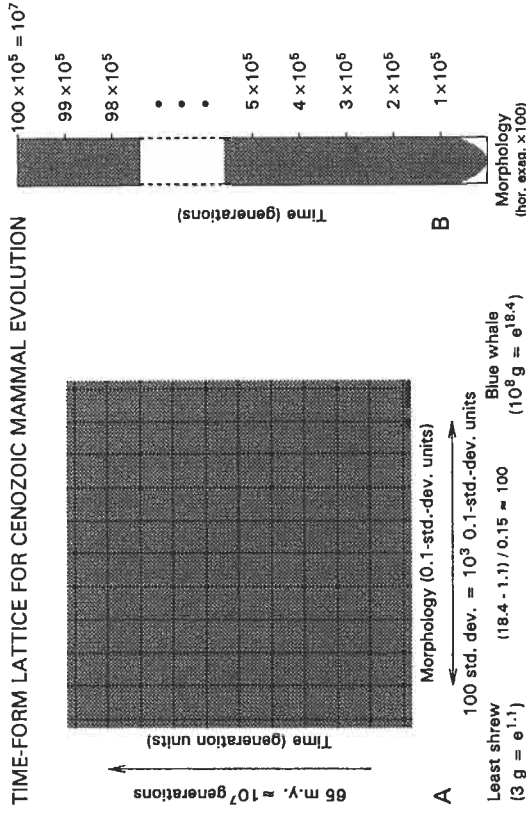


modern mammal groups are not just *appearing* rapidly but are in fact *evolving* rapidly in response to new environmental conditions. This is not inconsistent with what we know about rates of evolutionary change in the morphology of mammals and other organisms living today. Neither change nor rates of change are constant, but when change takes place it can be almost literally fast enough to see in a lifetime (GINGERICH 2001).

Rates are important too for comparing the Red Queen and Stationary hypotheses of evolutionary change (STENSETH & SMITH 1984). Geological time series of closely related animals yield low rates of morphological evolutionary change that suggest in turn that evolution is a very slow process. However, these rates are inversely proportional to the timescale over which they are calculated (GINGERICH 1983). The effect of this time-scale dependency can be removed by regression, with the result that geological time series generally indicate high rates of change, on the order of 0.1 standard deviations per generation on a time scale of one generation (the time scale of the evolutionary process; GINGERICH 1993, 2001). Such rates are consistent with short-term laboratory and field studies, which also typically show rates of evolution to be on the order of 0.1 standard deviations per generation on a time scale of one generation.

Comparing morphology and time, a 0.1-standard-deviation-per-generation rate means that a 0.1 standard deviation step or difference in morphology corresponds to a one-generation step or difference in evolutionary time. The smallest living mammal is the least shrew weighing about 3 or  $e^{1.1}$  g, and the largest living mammal is the blue whale weighing about 100 metric tonnes or  $e^{8.4}$  g. The standard deviation of body weight in mammals is about 0.15 units on a natural logarithmic scale. Hence the largest and smallest mammals living today differ by approximately 100 standard deviations or  $10^3$  0.1-standard-deviation units (Figure 7A). These are physiological limits, and mammals have never been much smaller than a least shrew or much larger than a blue whale: thus the time-form lattice for mammalian evolution is about  $10^3$  units wide. The generation time for an average living mammal is on the order of one year, and the Cenozoic history of the modern orders of mammals as we know them goes back 55–65 million years, which is, conservatively, about 10 million or  $10^7$  generations. Thus the time-form lattice for Cenozoic mammal evolution is about  $10^7$  units long temporally (Figure 7A).

The time-form lattice for mammalian evolution is not square, but some four orders of magnitude longer temporally than it is wide in form (Figure 7B). Mammals starting at some average size at the beginning of the Cenozoic can be expected to have diffused and filled the lattice in less than  $10^5$  generations – less than one percent of their subsequent Cenozoic history. If nothing else happened evolution would probably stabilize and rates slow down to some minimal more or less undetectable level within the lattice for



**Fig. 7.** Heuristic time-form lattice to explain how evolution can be so dynamic in the short term and so static over longer intervals. (A) Representative generation rates on the order of 0.1 standard deviations per generation (on a per-generation time scale) mean that a 0.1 standard deviation step or difference in morphology corresponds roughly to a one-generation step or difference in evolutionary time. The smallest living mammal is the least shrew weighing about 3 or  $e^{1.1}$  g, and the largest living mammal is the blue whale weighing about 100 metric tonnes or  $e^{8.4}$  g. The standard deviation of body weight in mammals is about 0.15 units on a natural logarithmic scale. Hence the largest and smallest mammals living today differ by approximately 100 standard deviations or  $10^3$  0.1-standard-deviation units. These are physiological limits and mammals have never been much smaller or much larger: thus the time-form lattice for mammalian evolution is about  $10^3$  units wide. The generation time for an average living mammal is on the order of one year, and the Cenozoic history of the modern orders of mammals as we know them goes back 55–65 million years, which is conservatively about 10 million or  $10^7$  generations. Thus the time-form lattice for Cenozoic mammal evolution is about  $10^7$  units long temporally. (B) The lattice is not square, but some four orders of magnitude longer temporally than it is wide in form. Mammals starting at some average size at the beginning of the Cenozoic can be expected to have diffused and filled the lattice in less than  $10^5$  generations [ $(500/1.96)^2$  (65000 generations)] less than one percent of their subsequent Cenozoic history. Then they were constrained to evolve within the lattice for the remaining 99 percent of their history. Rates of evolution *on the time scale of the process* are so high that lineages rapidly find and fill most niches within their physiological limits. Then they change little until the system is perturbed.

the remaining 99 percent of their history. Rates of evolution *on the time scale of the process* are so high that lineages rapidly find and fill most niches within their physiological limits. Then little change is possible until the system is perturbed. This is exactly the Stationary evolutionary model of STENSETH & SMITH (1984), rediscovered from a rate perspective, and the model can be expected to yield a 'punctuated equilibria' pattern of evolutionary change through geological time, while the underlying mechanism of evolution is both gradual and Darwinian.

DARWIN (1859) was concerned that the 'lapse' of geological time be long enough to permit the gradual evolutionary diversification he envisioned, and credited Lyell's *Principles of Geology* with supplying the long earth history required. Ironically, the problem is not whether geological time has been long enough, but rather that it has been so much longer than necessary. The evolutionary process is fast enough to have filled the world with diversity many times over, and the episodic changes we see in dominance and diversity through geological time probably reflect more a pattern of Stationary evolution perturbed by episodic environmental change than they do any Red Queen constancy of diversity or rates of speciation and phyletic evolution.

## 6. Discussion

We have considered Paleogene vertebrates and their response to environmental change on two scales of time: (1) the ca. 5-million-year time scale of stratigraphic stages spanning the Cretaceous-Paleogene (K-P) boundary; and (2) the 10 to 100-thousand-year time scale of the greenhouse thermal events spanning the Paleocene-Eocene (P-E) boundary. Not surprisingly, responses to environmental change look different on these different time scales. The simple correlation of vertebrate diversity with temperature that we might have expected to find across the K-P boundary was not born out, but on further reflection it has become clear that the asteroid impact marking the K-P boundary preceded diversification of all three vertebrate classes, Teleostei, Aves, and Mammalia, that make the Cenozoic so different from the Mesozoic, and all three subsequently reached more or less stable Cenozoic diversities. This is an expectation of the Stationary model of STENSETH & SMITH (1984) on a very broad temporal and taxonomic scale.

The case is more clear for rapid faunal change in response to environmental change on the finer temporal and taxonomic scale of the Paleocene-Eocene boundary because the appearance of the three mammalian orders, Artiodactyla, Perissodactyla, and Primates, that make this boundary so important appear on all three northern continents within 10 thousand years or so of the onset of a chemostratigraphic event, the carbon isotope excursion (CIE) that marks the important Paleocene-Eocene thermal maximum (PETM) representing a global greenhouse climate event and associated

environmental change. Documented high rates of evolutionary change in relation to an extremely long history of the earth further support the Stationary model of STENSETH & SMITH (1984).

There is of course a literature favoring the Red Queen hypothesis of continual origination and extinction independent of changes in the physical environment. VAN VALEN (1973) cited surprisingly constant rates of extinction in proposing the Red Queen hypothesis in the first place, but interpretation of this evidence was challenged by RAUP (1975) and MCCUNE (1982). More recently ALROY et al. (2000) studied the correlations of Cenozoic mammalian diversity, faunal turnover, and body size with climate, on a million-year time scale, and found only unpredictable effects of a few major events. Alroy et al. concluded that biotic factors like logistic diversity dynamics and within-lineage evolutionary trends are probably more important determinants of diversity. This is reminiscent of my initial interpretation of the non-significant or negative effect of temperature on diversity in Figure 2. However, Figure 4 shows how relationships that are invisible on million-year time scales can become more clear on finer scales of time, and I would expect the same to be true for the longer Cenozoic history of mammals when more of it is studied on finer time scales.

One challenge for paleontology today is to reconcile patterns of diversification observed in the fossil record with assumptions and inferences about the history of life generated by biologists with no experience studying earth history, who project living organisms and their interrelationships back through a geological time that is to them simply an empty and hypothetical void. Vertebrate paleontologists have worked intensively for two centuries to discover and compile information about the Mesozoic and Cenozoic like that shown in Figures 1 and 2 here. NOVACEK (1999) and ALROY (2001) have addressed this, and it is discussed by ROBERTSON et al. (2004) as well. Meeting the challenge of reconciling paleontological and biological approaches to life's history may depend more on explaining the details and generalities of global environmental change, at important times like the Cretaceous-Paleogene or Paleocene-Eocene transition, than it will on the fossil record alone or any other evidence studied in isolation. Here the Paleogene is of primary importance: both for understanding vertebrate history back to the deeper past, and for understanding vertebrate evolution forward to the present.

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#### Address of the author:

Prof. Philip D. Gingerich, Department of Geological Sciences and Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079 U.S.A., E-mail: gingeric@umich.edu