

Mammalian responses to climate change at the Paleocene-Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming

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ABSTRACT

The Paleocene-Eocene transition in North American land-mammal faunas is well documented on the south side of Polecat Bench and in surrounding badlands of northwestern Wyoming. Here a rich fossil record is known from a stratigraphic section with an established geomagnetic polarity time scale and medium- to high-resolution carbon and oxygen isotope records. The Paleocene-Eocene carbon isotope excursion (CIE) and temperature maximum (PETM) associated with greenhouse warming are both represented, starting at ca. 55 Ma and lasting ~86 k.y., during the transition from Paleocene to Eocene epochs and from Clarkforkian to Wasatchian land-mammal ages. Attention is focused on transient dwarfing of earliest Wasatchian (Wa-0) mammals during the CIE-PETM interval and on more lasting changes in generic composition and diversity. Faunal changes lagged initiation of the CIE by some 13 and 22 k.y., consistent with the idea of a stepped and pulsed response to climate change. Body size dwarfing in Wa-0 mammals cannot be explained as a response to temperature alone, and elevated atmospheric CO₂ probably played an important role.

INTRODUCTION

Evolution is an expected response to environmental change, and, similarly, climatic change and other environmental shifts are widely acknowledged to be important mechanisms driving evolution. Why then is it so difficult to show correlations in time between mammalian evolution and changing climates?

For every study claiming to see some correlation of mammalian evolution with climate change, there is another questioning such an interpretation. Sloan (1970), Gingerich (1976, 1985), and Rose (1981b) studied late Paleocene and early Eocene mammals in North America and regarded mammalian faunal change through this interval as a consequence of climatic cooling followed by warming, a pattern questioned by Krause and Maas (1990). Stucky (1990), Janis (1993), and Webb and Opdike (1995) studied broad changes in Cenozoic mammalian

faunas and related these to climate change, but subsequent studies of the North American record by Prothero (1999) and Alroy et al. (2000) failed to find relationships to climate and instead emphasized intrinsic biotic controls on faunal change. Vrba (1985) studied mammalian faunal change through the Plio-Pleistocene record in southern Africa and developed a 'turnover pulse' hypothesis of climatically driven rapid speciation and faunal evolution, but evidence for the principal pulse was queried by Behrensmeyer et al. (1997).

The Paleocene-Eocene boundary is one case where the correlation of a turnover pulse of mammalian faunal change with climate change appears unequivocal. Here I summarize what is known of the North American Paleocene-Eocene transition based on the stratigraphic record of mammals and climate in the vicinity of Polecat Bench in the northern Bighorn Basin of northwestern Wyoming.

HISTORY OF STUDY

The Thanetian stage/age of the Paleocene and the Ypresian stage/age of the Eocene in Europe have long been known to contain different mammalian faunas. Similarly, the Tiffanian and Clarkforkian land-mammal ages of the Paleocene and the Wasatchian land-mammal age of the Eocene in North America have long been known to differ faunally. The Thanetian and Tiffanian-Clarkforkian on both continents are dominated by archaic mammalian orders such as Multituberculata, plesiadapiform Proprimates, and Condylarthra, while the younger Ypresian and Wasatchian on both continents are dominated by modern orders such as Artiodactyla, Perissodactyla, and true Primates (see, for example, Gervais, 1877; Lemoine, 1891; Russell, 1964; Cope, 1888; Granger, 1914; Jepsen, 1930; Rose, 1981a). From the 1870s and 1880s, these differences were understood to indicate a profound reorganization of early Cenozoic mammalian faunas. Sometime between 1910 and 1912, vertebrate paleontologists accepted the Paleocene as representing a distinct epoch of mammalian evolution. First appearances of Artiodactyla, Perissodactyla, and true Primates were taken to mark the beginning of the succeeding Eocene epoch. Sinclair (1912) and Scott (1913) were at the forefront of modern acceptance of the Paleocene as a distinct epoch.

What does the transition from Paleocene to Eocene mammalian faunas look like? This is a more difficult question that requires high-resolution biostratigraphy. It is a question best studied in a sharply eroding badland setting like the Bighorn Basin of Wyoming, and the contiguous Clarks Fork Basin of Wyoming and Montana (Fig. 1), where accumulation of Paleocene-Eocene sediments was virtually continuous and the resulting strata are thick, well exposed, and richly fossiliferous. This area has special interest as the type area of the Clarkforkian land-mammal age.

Granger (1914), Jepsen (1930), Wood et al. (1941), and others, considered Clarkforkian and Wasatchian faunas to be distinct. However, in the 1960s, two studies cast doubt on this, and indeed on our whole understanding of the Paleocene-Eocene transition in North America. Wood (1967) studied published evidence of the Clarkforkian land-mammal age fauna and concluded that it resulted from an intermixture of late Paleocene Tiffanian land-mammal age faunal elements and early Eocene Wasatchian elements. This meant, at best, that the Paleocene-Eocene transition was slow and gradual, and, at worst, that very little was known about the transition. Jepsen and Woodburne (1969) published a record of the "dawn horse" perissodactyl *Hyracotherium* that was said to come from the Paleocene of the Clarks Fork Basin. This extension of temporal range reinforced the idea of a phased faunal transition, and led to temporary confusion of intercontinental faunal correlation.

GENERAL RESULTS

With this background, resolution could only come from new, larger, stratigraphically controlled collections of mammals

from the Clarks Fork and northern Bighorn Basins. I initiated a project of new collections in 1975, which has since gone through several phases with substantial studies completed on the Clarkforkian land-mammal age (Rose, 1979, 1980, 1981a, 1981b), paleomagnetic stratigraphy (Butler et al., 1981, 1987; Clyde et al., 1994), mammalian biostratigraphy (Gingerich, 1983, 1991, 2001a), the Clarkforkian-to-Wasatchian faunal transition (Gingerich, 1989; Clyde and Gingerich, 1998; Gunnell, 1998; Gingerich and Clyde, 2001), carbon and oxygen isotope stratigraphy (Koch et al., 1992, 1995; Fricke et al., 1998; Bowen et al., 2001), and the Wasatchian land-mammal age (Badgley and Gingerich, 1988; Clyde, 1997, 2001). A dissertation on the Tiffanian land-mammal age is in progress by R. Secord. Parallel studies of sedimentology, paleobotany, and mollusks have been carried out by Kraus (1980, 1987, 1996, 2001), Hickey (1980), Wing (1998), Hartman and Roth (1998), Wing et al. (2000), and Wing and Harrington (2001).

There is no longer any doubt that the Clarkforkian land-mammal fauna in the type area is distinct from both the preceding Tiffanian-age fauna and the succeeding Wasatchian-age fauna (Fig. 2). The Clarkforkian fauna contains Rodentia, Tillodontia, the condylarth *Haplomyilus*, and the pantodont *Coryphodon* not found in the preceding Tiffanian, and lacks Artiodactyla, Perissodactyla, Primates, and hyaenodontid Creodonta that first appear in the succeeding Wasatchian fauna. The beginning of the Clarkforkian land-mammal age in the type area is defined by the first appearance of Rodentia, which is constrained within about ± 50 m stratigraphically and within about ± 100 k.y. temporally. The end of the Clarkforkian land-mammal age coincides with the beginning of the Wasatchian land-mammal age defined by the first appearance of Perissodactyla, and this is even more tightly constrained stratigraphically and temporally (Fig. 2). Note that the Wa-0 faunal interval at the beginning of the Wasatchian, of particular interest here, coincides with the carbon isotope excursion (CIE) and Paleocene-Eocene Thermal Maximum (PETM) at the beginning of the Eocene (see below).

The Tiffanian, Clarkforkian, and Wasatchian land-mammal ages of the Clarks Fork and northern Bighorn basins can be further subdivided, respectively, into six, three, and seven zones and their corresponding biochrons (Fig. 2). Stratigraphic levels and interpolated ages and durations of the biochrons are shown and explained in Table 1. Briefly, age and duration were calculated by interpolation, using a cubic spline to describe the fit of stratigraphic thickness to radiometric age. The spline was calibrated using the stratigraphic positions and accepted ages of paleomagnetic anomalies. Accumulation of Paleocene and lower Eocene strata on Polecat Bench was not linear with time (although through much of the Clarkforkian and Wasatchian was this approximately linear), and a spline provides a model-free description of the pattern. Faunal samples are generally aggregated from 10 to 20 m of section in any particular locality, with the position of each locality in the master section rounded to the closest 5 m level (meaning that precision and accuracy are both

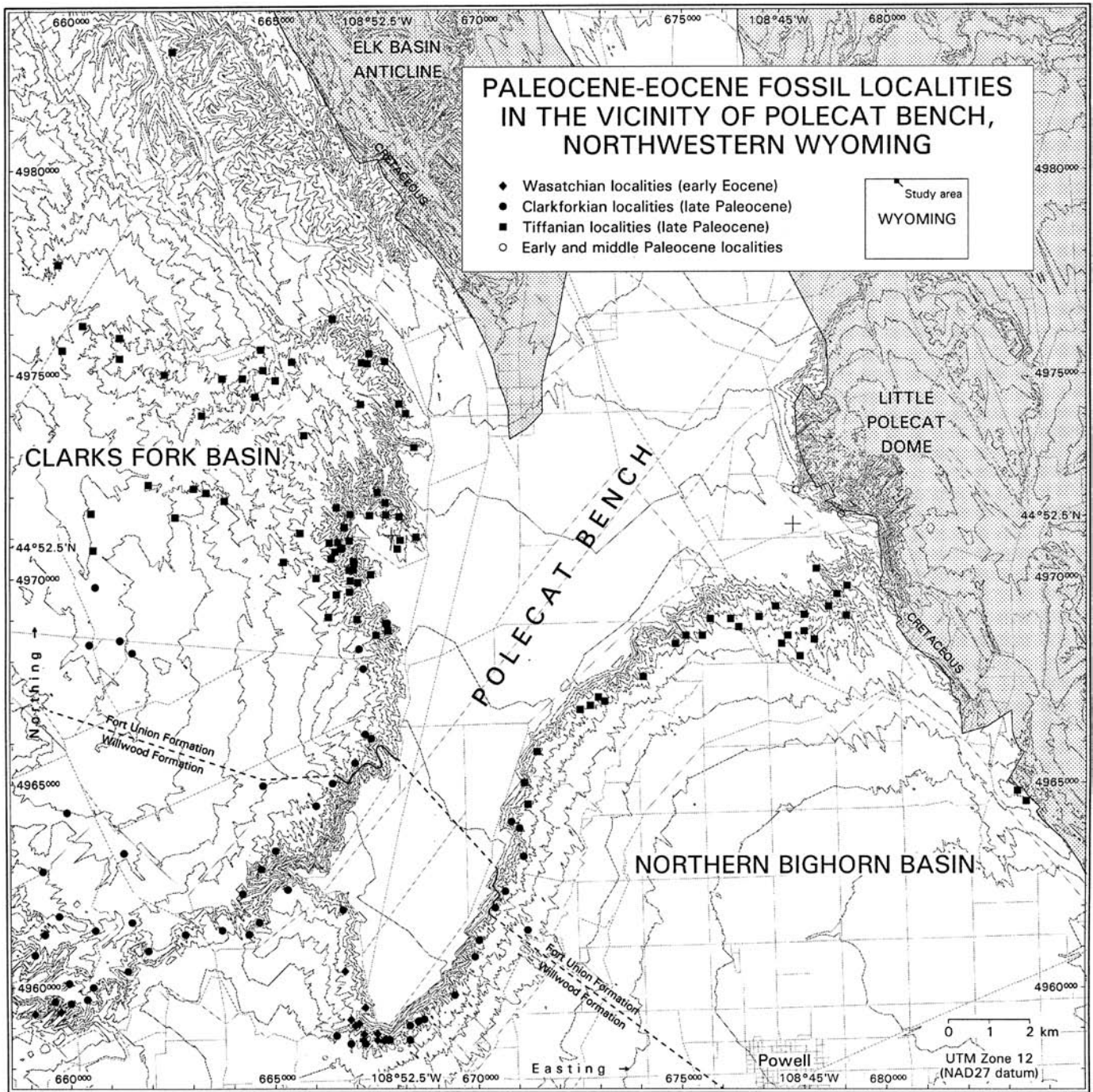


Figure 1. Map of vertebrate fossil localities in the vicinity of Polecat Bench in the Clarks Fork and northern Bighorn basins of northwestern Wyoming. This 20 × 20 km area includes Cretaceous and older strata in the northeast (stippled) overlain by Paleogene strata that dip shallowly to the southwest. Polecat Bench is a Pleistocene river terrace surrounded by sharply weathering badlands exposing Paleocene and lower Eocene strata and making them accessible for fossil collecting. The Clarks Fork Basin is the type area of Clarkforkian land-mammal age (Granger, 1914; Wood et al., 1941). The area immediately west of Polecat Bench is called Sand Coulee, which includes the type area of the overlying Sandcouleean land-mammal subage (Granger, 1914). The town of Powell is located in the lower right at the bottom of the map. Most localities shown here are Tiffanian late Paleocene (solid squares) and Clarkforkian late Paleocene (solid circles). Wasatchian localities (solid diamonds) are exposed at the southwestern tip of Polecat Bench and in the head of Big Sand Coulee. Vertebrate-bearing Paleocene and lower Eocene strata extend some 20 km farther to the west across the Clarks Fork Basin, and some 120 km farther to the southeast through the entire length of the Bighorn Basin.

TABLE 1. AGE AND DURATION ESTIMATES FOR BIOSTRATIGRAPHIC ZONES ABOVE AND BELOW THE PALEOCENE-EOCENE BOUNDARY ON POLECAT BENCH

Zone name	Zone bottom (m)	Zone top (m)	Zone bottom (ma)	Zone top (ma)	Zone duration (k.y.)
Wa-5	2200	—	−53.48	—	—
Wa-4	2020	2200	−53.87	−53.48	393.2
Wa-3b	1780	2020	−54.40	−53.87	530.4
Wa-3a	1750	1780	−54.47	−54.40	66.2
Wa-2	1645	1750	−54.70	−54.47	230.8
Wa-1	1543	1645	−54.92	−54.70	221.9
Wa-0	1506	1543	−55.00	−54.92	79.8
Cf-3	1335	1506	−55.36	−55.00	362.3
Cf-2	1180	1335	−55.68	−55.36	317.8
Cf-1	885	1180	−56.27	−55.68	587.6
Ti-6	820	885	−56.41	−56.27	145.0
Ti-5b	655	820	−56.89	−56.41	478.5
Ti-5a	530	655	−57.39	−56.89	492.9
Ti-4	415	530	−57.85	−57.39	463.4
Ti-3	215	415	−58.93	−57.85	1079.7
Ti-2	155	215	−59.48	−58.93	551.7

Note: These are calculated by interpolation, using a cubic spline describing the fit of stratigraphic thickness to radiometric age. Spline calibration points are the bottoms and tops of magnetic anomalies 26R, 26N, 25R, 25N, and 24R in the Polecat Bench–Sand Coulee stratigraphic section (Fig. 2). See Table 2 for more detailed interpolation in the vicinity of Wa-0.

on the order of 20 k.y.). Faunal samples analyzed here include all specimens from all localities recorded at a particular 5 m stratigraphic level.

The Clarkforkian-Wasatchian boundary is of special interest because it coincides closely with the Paleocene-Eocene epoch boundary, and both boundaries lie within paleomagnetic anomaly 24R (Fig. 2). The average long-term sediment accumulation rate through this interval is ~467 m/m.y. Spline and linear interpolations yield ages for the Clarkforkian-Wasatchian boundary of 55.00 and 54.97 Ma respectively (base of Wa-0?), or 54.99 and 54.96 Ma respectively (base of Wa-0), and ages for the Paleocene-Eocene boundary of 55.01 and 54.98 Ma respectively (Table 2). Note that both interpolations yield a Clarkforkian-Wasatchian boundary recognized by the first appearance of perissodactyls that is at most 21.5 k.y. younger than the Paleocene-Eocene boundary at the base of the carbon isotope excursion (CIE; see below).

Stable isotopes in soil nodules, gar scales, and hematite encrusting bones document: (1) a profound 4–5 per mil (‰) negative excursion in $\delta^{13}\text{C}$ at the time of the Clarkforkian-Wasatchian transition (Koch et al., 1992; Bowen et al., 2001; Bains et al., this volume), reflecting the global carbon isotope excursion, or CIE, first recognized in the deep sea (the base of the CIE is now taken to mark the Paleocene-Eocene boundary here and elsewhere; Luterbacher et al., 2000; Fig. 2); (2) a substantial ~2‰ positive excursion in $\delta^{18}\text{O}$ at the time of the Clarkforkian-Wasatchian transition (Fricke et al., 1998), reflecting a brief interval of warm climate during the Paleocene-Eocene

Thermal Maximum (PETM) associated with the CIE (Fig. 2); and (3) a longer-term 4‰ negative trend in $\delta^{18}\text{O}$ through much of Clarkforkian and early Wasatchian time (Bao et al., 1999), consistent with a background pattern of slight climatic cooling across the Paleocene-Eocene boundary (Fig. 2).

HIGH-RESOLUTION STRATIGRAPHY

High-resolution carbon isotope stratigraphy shows the CIE to span the 1500 through 1540 m interval in the Polecat Bench section, with an interpolated duration of ~86,000 yr (Fig. 3; Table 2). Stratigraphically, the Wa-0 mammalian fauna at the beginning of the Wasatchian land-mammal age falls entirely within the CIE. Clarkforkian mammals are found as high as 1505 m, and the onset of the CIE evidently happened during latest Clarkforkian time.

The interval from 1506 to 1511 m contains unusual brown paleosols, abundant *Celtis* (hackberry) endocarps, and the only specimens of the rare condylarth *Meniscotherium* from the Bighorn Basin for which precise stratigraphic information is available. *Meniscotherium* is unusual for a condylarth in being a highly specialized selenodont herbivore. It is common in later Wasatchian faunas in more southern localities (e.g., New Mexico). The *Meniscotherium*-bearing interval in the Polecat Bench section coincides with maximum excursion values of the CIE. The remainder of the CIE, from 1512 through ~1540 m, contains numerous bright red and purple paleosols and yields the classic Wa-0 mammalian fauna (Gingerich, 1989).

TABLE 2. AGE AND DURATION ESTIMATES FOR STRATIGRAPHIC EVENTS AND INTERVALS IN THE PALEOCENE-EOCENE AND CLARKFORKIAN (CF)-WASATCHIAN (WA) TRANSITIONS ON POLECAT BENCH

Stratigraphic level (m)	Position in 24R	Spline interpolation			Linear interpolation		
		Estimated age (Ma)	Time in 24R (m.y.)	CIE duration (k.y.)	Estimated age (ma)	Time in 24R (m.y.)	CIE duration (k.y.)
2260	1190	-53.35	2.55	—	-53.35	2.55	—
1543	473	-54.92	0.98	—	-54.89	1.01	—
1540	470	-54.93	0.97	86.2	-54.89	1.01	85.7
1510	440	-54.99	0.91	21.5	-54.96	0.94	21.4
1506	436	-55.00	0.90	12.9	-54.97	0.93	12.9
1500	430	-55.01	0.89	0.0	-54.98	0.92	0.0
1070	0	-55.90	0.00	—	-55.90	0.00	—

Note: The stratigraphic interval from 1500 to 1540 m (in bold) is the interval of the carbon isotope excursion (CIE) marking the beginning of the Eocene. The earliest Eocene interval from 1500 to 1506 m has a Cf-3 mammalian fauna. The interval from 1506 to 1510 m is the *Meniscotherium priscum* zone (Wa-0?), and the interval from 1510 to 1540 m is in the *Hyracotherium sandrae* zone (Wa-0). Ages and durations were calculated using cubic spline interpolation (columns 3–5) and, for comparison, linear interpolation (columns 6–8). Spline calibration points are the bottoms and tops of magnetic anomalies 26R, 26N, 25R, 25N, and 24R in the Polecat Bench–Sand Coulee stratigraphic section (Fig. 2). Linear interpolation is calibrated using the bottom and top of anomaly 24R at 1070 and 2260 m, respectively.

Discovery that there are three successive, distinctly different, mammalian faunas, a late Clarkforkian fauna, a *Meniscotherium* zone fauna, and the classic Wa-0 fauna, all within an 86-k.y. interval of the CIE, means that the Paleocene-Eocene boundary interval on Polecat Bench requires more intensive study. As the vertebrate record improves it should be possible to study mammalian body size changes through the Wa-0 interval at higher resolution. It should also be possible to develop an enhanced paleotemperature record for the Wa-0 interval using $\delta^{18}\text{O}$ in the phosphate of gar scales and mammalian teeth. There is a high-resolution $\delta^{18}\text{O}$ record in paleosol carbonate showing a $\sim 1\%$ positive excursion consistent with warming, but interpretation is confounded by effects of temperature, precipitation, evaporation, and large-scale atmospheric circulation (Bowen et al., 2001).

MAMMALIAN BODY SIZE ACROSS THE PALEOCENE-EOCENE BOUNDARY

The earliest Wasatchian or Wa-0 mammalian fauna known from University of Michigan locality SC-67 at the south end of Polecat Bench was first recognized to be unusual because of the abundance of small and otherwise-rare specimens identified as *Ectocion parvus* Granger, 1915 (see Gingerich, 1982). Granger (1915) stated that the type and only previously known specimen of *Ectocion parvus* had come from 'Clark Fork' beds at the head of Big Sand Coulee, just north and west of Polecat Bench, but it now appears more likely that the specimen came from the Wa-0 stratigraphic interval at the south end of Polecat Bench (Gingerich, 1989, p. 51). Specimens initially identified as *Ectocion parvus* were later found to belong to two different species, one being *Ectocion parvus* and the other being *Copecion davisi*.

Ectocion is one of the more common genera of mammals in strata of Clarkforkian and early Wasatchian age. It is represented by a long lineage, stationary or unchanging through time, comprising a single species *Ectocion osbornianus*, and a contemporary sample or very short parallel lineage of smaller *E. parvus*. This pattern is shown in Figure 4, where the tooth size of individual specimens is plotted against their geological age. *Ectocion parvus* was first distinguished from *E. osbornianus* by its smaller size (Granger, 1915), and no further differences have been discovered subsequently. The body weight of *E. osbornianus*, estimated from molar size, averaged $\sim 8\text{--}10$ kg in life, while the body weight of *E. parvus* with smaller molars was only $\sim 4\text{--}5$ kg (Fig. 4).

Differences in mean values of samples of *Ectocion osbornianus* from successive stratigraphic levels are all small (circles in the range of 0–4 standard deviations plotted in Figure 4A), and these differences fall within a $1 - \alpha = 99.9\%$ confidence band (open area) for samples of a given size drawn at random from a population with the previous mean (calculated as $\pm t_{\alpha[n-1]} / \sqrt{n}$; Sokal and Rohlf, 1981, p. 148). In contrast, differences involving Wa-0 *Ectocion parvus* are larger (diamonds in stippled area of Figure 4A).

Ectocion parvus appears to be a distinctly smaller congeneric species that replaced *E. osbornianus* ecologically for a brief interval at the beginning of Wasatchian time, but it could conceivably be an evolutionarily dwarfed member of the *E. osbornianus* lineage (current taxonomy implies but does not demonstrate ecological replacement; the taxonomy may well need to be changed when the evidence is clear). The phrase of 'evolutionary dwarfing' is used to indicate that the observed case is unusual, that it involves small size, and to suggest inherited adaptive change (as opposed to temporary ecological stunting).

South Polecat Bench section

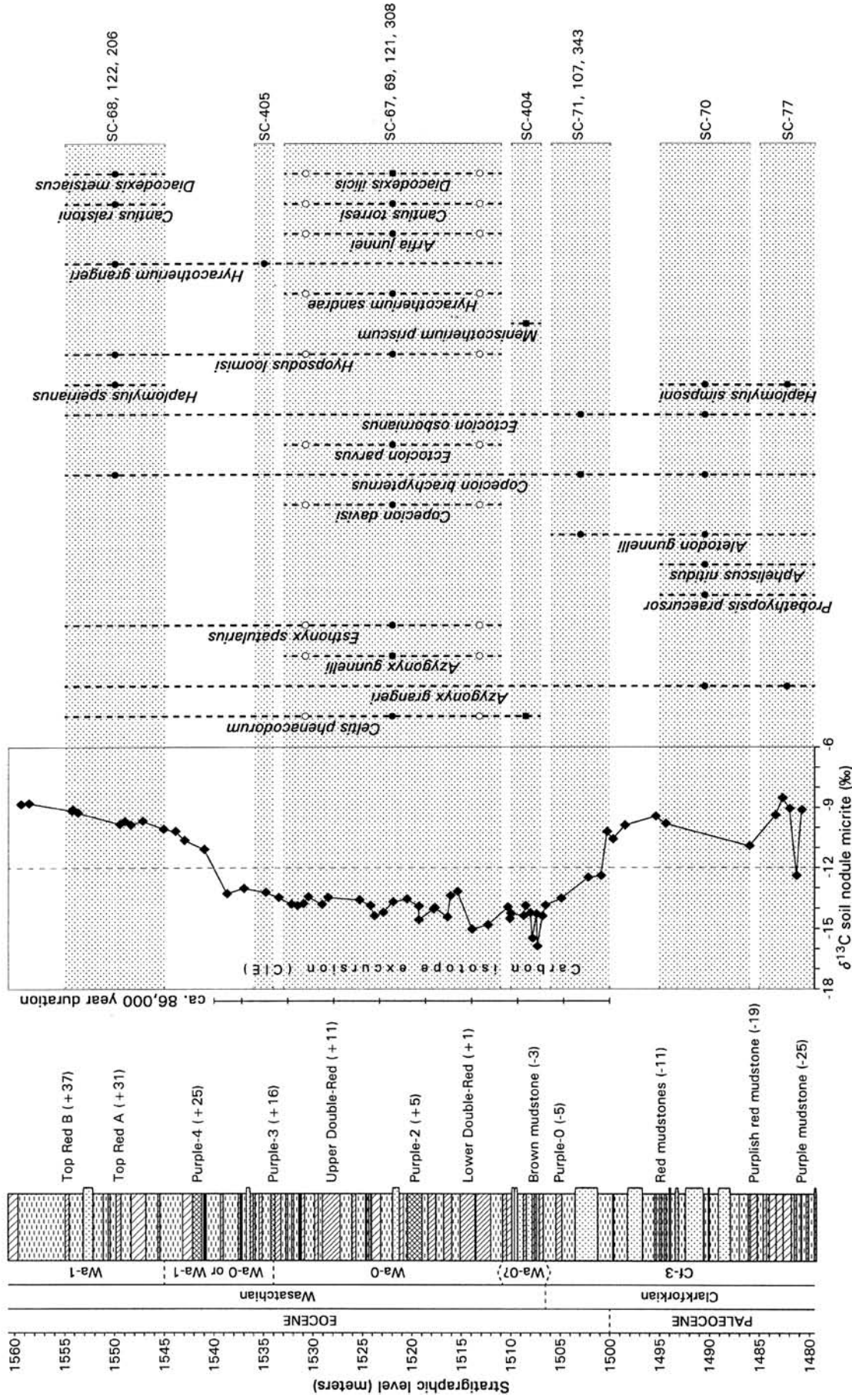


Figure 3. High-resolution carbon isotope stratigraphy and biotic change at the south end of Polecat Bench. Lithostratigraphy and stratigraphic ranges of the elm-related dicot *Celtis* (hackberry) and important mammalian taxa crossing the Paleocene-Eocene boundary are from Gingerich (2001a). Fourteen mammal-bearing localities are known (SC-77, etc.), representing seven distinct stratigraphic intervals (shaded). These can be grouped into four time-successive associations based on their biota (Cf-3, Wa-0?, Wa-0, and Wa-1 on the ordinate). The interval labeled “Wa-0 or Wa-1” on the ordinate is poorly sampled and could be either Wa-0 or Wa-1 in age. The 86,000-year time scale shown here is consistent with age interpolations in Table 2. Note that the beginning of the carbon isotope excursion is in the late Clarkforkian, overlapping the stratigraphic interval of localities SC-71, etc. The most negative $\delta^{13}\text{C}$ values ($\sim 15\text{‰}$) are in the earliest zone of the Wasatchian (Wa-0?), represented by SC-404 with the first hackberry *Celtis* and rare condylarth *Meniscotherium*. The remainder of the carbon isotope excursion spans the interval of the classic Wa-0 fauna with small *Ectocion* and *Copecion* from localities SC-67, etc. *Ectocion* and *Copecion* of standard size are known from localities SC-68, etc., in zone Wa-1 after carbon isotope values returned to normal (here $\sim 9\text{‰}$). Reproduced with modifications from Figure 6 in Bowen et al. (2001).

BIGHORN-CLARKS FORK BASIN ECTOCION

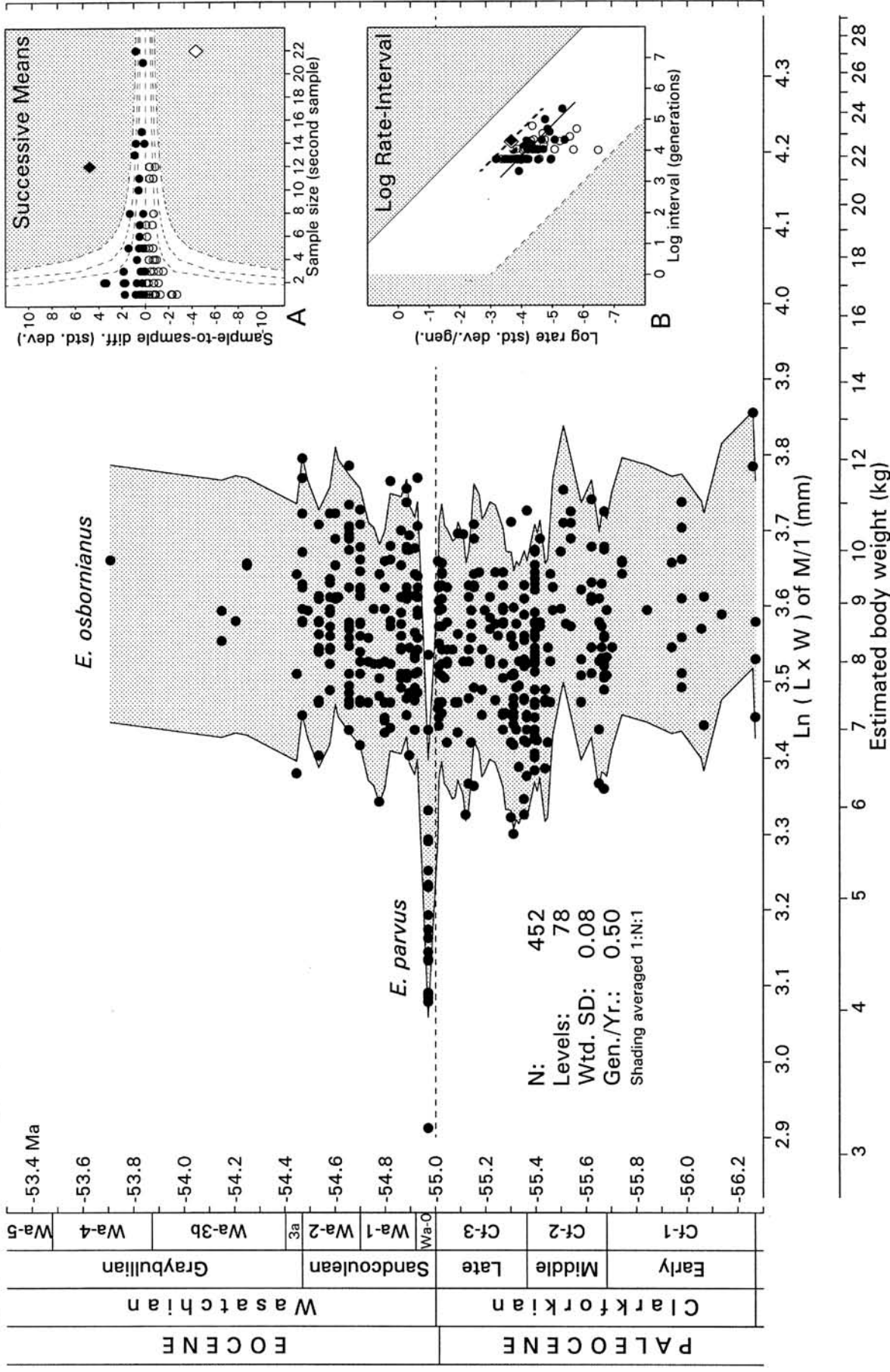


Figure 4. Stratigraphic record of tooth size and body size for the mammalian genus *Ectocion* through Clarkforkian and early Wasatchian time in the northern Bighorn and Clarks Fork basins. Most specimens represent the common species *Ectocion osbornianus* of ~8–10 kg body weight, but smaller specimens of *Ectocion parvus* of ~4–5 kg body weight predominate in the Wa-0 stratigraphic interval coinciding with the CIE and PETM (cf. Figure 2). Vertical axis is time, based on cubic spline interpolation of Figure 2 and Table 1. Inset A shows that the Wa-0 sample (diamonds) differs from adjacent samples more than expected by chance (symbols are open or closed reflecting negative and positive changes in tooth size, respectively). Dashed lines in A are confidence limits for $\alpha = 0.05, 0.01, \text{ and } 0.001$. Inset B shows rates for Wa-0 samples to be higher than all other rates calculated on the same time scale (dashed lines of slope 1 are fit to diamond rates involving Wa-0). Body weight is estimated from tooth size following ungulate regression of Legendre (1989, Table 1), and generation time is estimated from body weight (Eisenberg, 1981). *Ectocion osbornianus* in the Bighorn and Clarks Fork basins was chosen by Simpson (1943) as the featured example when he introduced the concept of an evolving chronocline, but improved sampling and stratigraphic control shown here indicates that *E. osbornianus* changed little through its known evolutionary history.

Rates required for dwarfing and recovery, plotted as diamonds in inset Figure 4B, are high but at the margin of rates calculated for the rest of the time series (and again within the range expected for evolutionary change, including island dwarfing, on these time scales; Gingerich, 2001b). There are two Wa-0 specimens the size of ordinary *E. osbornianus* in the Wa-0 fauna, which supports the idea of replacement rather than dwarfing, but these could be contaminants (this idea can be tested isotopically). Whether *E. parvus* represents a parallel lineage or a brief evolutionary dwarfing event in the longer *E. osbornianus* lineage, it is a conspicuous outlier with a body weight estimated to have been only ~50% the weight of its more common and longer-ranging congener.

Copecion too is represented by a long stationary lineage comprising a single species *Copecion brachypternus*, and a contemporary sample or very short parallel lineage of *C. davisi*. This pattern is shown in Figure 5. *Copecion davisi* was first distinguished from *C. brachypternus* by its smaller size (Gingerich, 1989), and no further differences have been discovered subsequently. The body weight of *C. brachypternus* estimated from molar size, like that of *E. osbornianus*, averaged ~8–10 kg in life, while the body weight of *C. davisi* with smaller molars was only ~5–6 kg.

Here again, differences in mean values of successive samples of *Copecion brachypternus* are all small (circles in the range of 0–4 standard deviations plotted in Figure 5A), and these differences again fall within a $1 - \alpha = 99.9\%$ confidence band (open area) for samples of a given size drawn at random from a population with the previous mean. In contrast, differences involving Wa-0 *Copecion davisi* are larger (diamonds in Figure 5A).

C. davisi appears to be a distinctly smaller congeneric species that replaced *C. brachypternus* ecologically for a brief interval at the beginning of Wasatchian time, but it could conceivably be an evolutionarily dwarfed member of the *C. brachypternus* lineage (again, current taxonomy implies but does not demonstrate ecological replacement).

Rates required for dwarfing and recovery, plotted as diamonds in inset Figure 5B, are high but again at the margin of rates calculated for the rest of the time series (and again within the range expected for evolutionary change on these time scales; Gingerich, 2001b). There are no Wa-0 specimens the size of ordinary *C. brachypternus*. Whether *C. davisi* represents a parallel lineage or a transient evolutionary dwarfing event in the longer *C. brachypternus* lineage, it is a conspicuous outlier with a body weight estimated to have been only ~60% the weight of its more common and longer-ranging congener.

Perissodactyls make their first appearance in the North American fossil record in the Wasatchian land-mammal age. The only common perissodactyl from Wa-0 is the small 5–6 kg, short-lived species *Hyracotherium sandrae* (Fig. 6). There is limited evidence that the larger 8–10 kg *Hyracotherium grangeri* comes from the Wa-0 interval too, but it is much rarer than *H. sandrae*, at least in northern Bighorn Basin localities (*H. grangeri* is the only species reported from the Castle Gardens

Wa-0 fauna in the southeastern Bighorn Basin; Strait, 2001). Thus, the body size pattern for *Hyracotherium* through the Wa-0 to Wa-2 part of the record is similar to that for *Ectocion* and *Copecion*, with *H. sandrae* being a conspicuous outlier in having a body weight estimated to have been only some 60% the weight of its more common and longer-ranging congener *H. grangeri*. There are no differences known to distinguish *H. sandrae* from *H. grangeri* except size.

More examples could be shown (see Gingerich, 1989), but Figures 4–6 convey the idea that unusually small body size is a salient characteristic of Wa-0 species from the CIE and PETM interval of the earliest Wasatchian. Some species, such as *Hypopsodus loomisi*, seem to have made the transition from Wa-0 to Wa-1 with no substantial change in body size. No species are known to exhibit larger body size in response to the elevated mean annual temperatures in the Wa-0 interval.

EXPLANATION FOR EVOLUTIONARY DWARFING

How can we explain the rapid replacement or evolution of a common, successful Paleocene species by a congener only 50%–60% of its body weight? Requisite rates of change lie within the range of evolutionary rates observed on 10^4 – 10^5 generation time scales in other settings, so the replacement is not rate limited. The problem is rather to identify the selective forcing factor or factors. We know that the CIE-PETM interval on land is unusual for its isotopically light carbon, its isotopically heavy oxygen, its ambient temperature elevated by up to 8 °C, and its elevated levels of greenhouse gases such as CO₂ in the atmosphere (Koch et al., 1992; Fricke et al., 1998; Dickens, 2000; Royer et al., 2001; Zachos et al., 2001). Elevated temperature and elevated CO₂ are both possible forcing factors.

Bergmann's rule is one of the best documented and widely known ecological and biogeographic generalizations (Bergmann, 1847; Rensch, 1929; Ashton et al., 2000): As a rule, the body size of a species increases in cooler climates and decreases in warm climates. Koch (1986) studied geographic clines in extant North American mammals and showed that today 0.02 ln units of tooth crown area are approximately equivalent to 1.0 °C of temperature change. The difference in tooth crown area distinguishing, for example, *Ectocion parvus* in the earliest Wasatchian from *E. parvus* in the Clarkforkian is about –0.3 ln units, which would require a temperature rise of some 15 °C (compared to ~4 °C reported by Fricke et al., 1998). Thus, a simple Bergmann response to temperature elevation cannot be the whole explanation for the dwarfing observed Wa-0 mammals.

Body size in mammals is also influenced by food quality (Case, 1979). Here new and ongoing experiments with herbivores fed on plants grown in CO₂-enriched atmospheres are particularly interesting (e.g., Fajer et al., 1989; Kinney et al., 1997; Tuchman et al., 2002). Experiments show that 'high' CO₂ partial pressures (~700 ppmv, compared to present-day pressures of ~350 ppmv) are sufficient to increase photosynthesis, and to increase carbon and decrease nitrogen in plant tissues. The ex-

BIGHORN-CLARKS FORK BASIN COPECEON

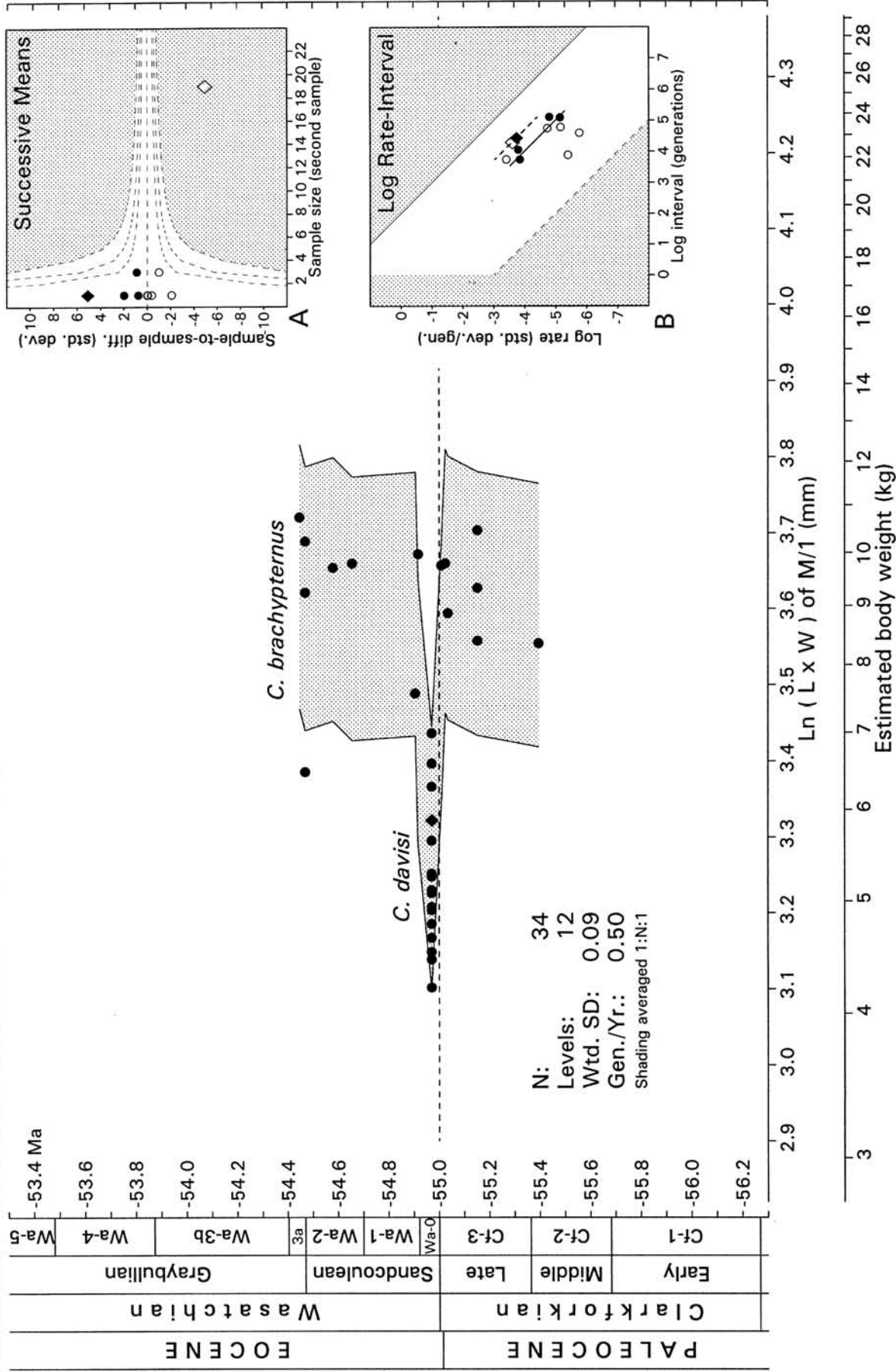


Figure 5. Stratigraphic record of tooth size and body size for the mammalian genus *Copeceon* through Clarkforkian and early Wasatchian time in the northern Bighorn and Clarks Fork basins. Most specimens represent the common species *Copeceon brachypternus* of ~8–10 kg body weight, but smaller specimens of *Copeceon davisii* of ~5–6 kg body weight predominate in the Wa-0 stratigraphic interval coinciding with the CIE and PETM (cf. Figure 2). Vertical axis is time based on cubic spline interpolation. Insets A and B show that the Wa-0 sample (diamonds) differs from adjacent samples more than expected by chance (symbols are open or closed reflecting negative and positive changes in tooth size, respectively). Dashed lines in A are confidence limits for $\alpha = 0.05, 0.01, \text{ and } 0.001$. Distribution in B shows rates for Wa-0 samples to be higher than all other rates calculated on the same time scale (dashed lines of slope 1 are fit to diamond rates involving Wa-0). Body weight is estimated from tooth size following ungulate regression of Legendre (1989, Table 1), and generation time is estimated from body weight (Eisenberg, 1981).

BIGHORN-CLARKS FORK BASIN HYRACOTHERIUM

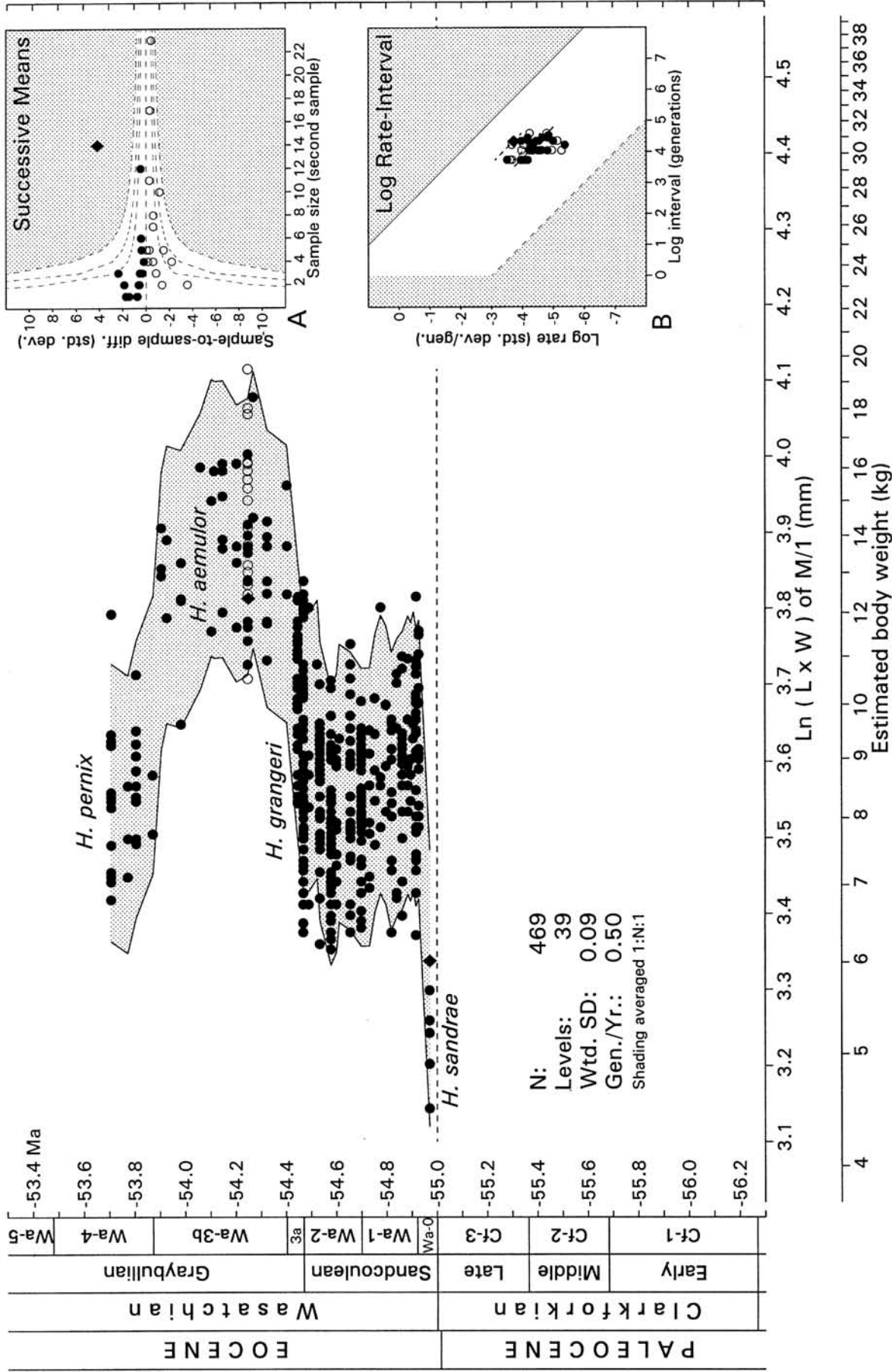


Figure 6. Stratigraphic record of tooth size and body size for the mammalian genus *Hyracotherium* through Clarkforkian and early Wasatchian time in the northern Bighorn and Clarks Fork basins. Most specimens represent the common species *Hyracotherium grangeri* of ~8–10 kg body weight, but smaller specimens of *Hyracotherium sandrae* of ~5–6 kg body weight predominate in the Wa-0 stratigraphic interval coinciding with the CIE and PETM (cf. Figure 2). Vertical axis is time based on cubic spline interpolation. Inset figures A and B show that the Wa-0 sample (diamonds) differs from adjacent samples more than expected by chance (symbols are open or closed reflecting negative and positive changes in tooth size, respectively). Dashed lines in A are confidence limits for $\alpha = 0.05, 0.01, \text{ and } 0.001$. Distribution in B shows rates for Wa-0 samples to be higher than all other rates calculated on the same time scale (dashed line of slope 1 is fit to diamond rate involving Wa-0). Body weight is estimated from tooth size following ungulate regression of Legendre (1989, Table 1), and generation time is estimated from body weight (Eisenberg, 1981).

tra carbon is used to enhance secondary compounds, inhibiting digestibility for herbivores. CO₂ enrichment also leads to reduction in rubisco enzyme concentrations in foliage, thus decreasing leaf protein and lowering nutritional value for herbivores. Experimentally, insect herbivores are observed to grow more slowly on high-CO₂ foliage. No experiments have been done with mammalian herbivores, but it is logical to expect that mammals too would experience slower growth. Slower growth, coupled with any of the usual seasonal temperature, rainfall, or day-length effects controlling reproductive cycles, would lead to reproduction at smaller body size rather than at the same or larger size. This would be, simply and directly, environmental selection favoring evolutionary dwarfing. Alternatively, under some conditions, we might expect 'normal'-sized species to be replaced by smaller congeners or other species.

We do not know very much about the partial pressure of CO₂ during the PETM or Wa-0 interval of dwarfing in mammals. Royer et al. (2001) published one estimate of 800 ppmv based on the stomatal index of *Ginkgo gardneri* from Ardtun Head on the Isle of Mull, which is correlated over some distance to an interval with CIE and PETM indicators. Further, we do not yet know anything experimentally about the effects that a diet of plants grown in CO₂-enhanced environments might have on the body size of mammalian herbivores. Nevertheless, the coincidental transience of both the elevated partial pressure of CO₂ postulated during the PETM and the transience of the dwarfed body size of mammals during this interval suggest a cause and effect relationship. The temperature rise during the PETM interval is not sufficient by itself to explain all of the dwarfing observed through any simple Bergmann response to warming, but temperature plus an elevated partial pressure of CO₂ might explain this.

OTHER RESPONSES TO CLIMATE CHANGE

Differences distinguishing the Wa-0 mammalian fauna of the CIE-PETM interval from faunas that preceded or followed in time can be divided into two categories: Transient differences and permanent differences. The size changes in *Ectocion* and *Copecion* illustrated here are transient in the sense that the sizes of species observed following the CIE-PETM event returned to the sizes observed before the event. Unusually small species appeared during the PETM interval, and smaller size is plausibly a response to elevated temperature and elevated CO₂. A second transient change concerns the proportion of digging mammals (palaeonodons and taeniodonts) in the Wa-0 fauna (Gingerich, 1989). Digging mammals typically constitute <1% of all specimens in a Clarkforkian or Wasatchian fauna, but rise to 6% during Wa-0 time (of which ~3% are palaeonodons and ~3% are taeniodonts). It is not clear that digging would be favored by a warmer climate, but a better-drained landscape promoting development of especially mature paleosols, like those in the Wa-0 interval, could plausibly favor digging mammals. Both of these transient faunal changes are so closely linked to the CIE-

PETM interval, occurring in precisely the same strata, that there can be little question that they are, directly or indirectly, responses to climate change.

A more permanent faunal change occurring at the time of the CIE-PETM event is evident in a range chart showing the relative timing of first and last appearances of mammalian genera from the northern Bighorn and Clarks Fork basins (Fig. 7). Integration of appearances and disappearances shows a plateau of diversity of ~45–50 genera in the middle and late Clarkforkian, which then rises to a higher plateau of ~55–60 genera in the early Wasatchian. This rise coincides with and results from a peak of 14 first appearances of new genera in the Wa-0 fauna. Lesser peaks of first and last appearances are scattered through Clarkforkian and Wasatchian time, but the most conspicuous one is the peak of first appearances coinciding with the CIE-PETM event.

Other lasting changes at the CIE-PETM event are an increase in mean species body size, and an increase in the relative importance of herbivores and frugivores (see Clyde and Gingerich, 1998). These equally rapid but more permanent changes almost certainly reflect immigration of new taxa. The cosmopolitanism of the new taxa (*Artiodactyla*, *Perissodactyla*, *Primates*, etc.) is itself evidence of adaptive advantages enabling the immigrants to invade and live side by side with endemic taxa.

DISCUSSION

Webb and Opdike (1995, Tables 11.1 and 11.2) listed 15 mammalian genera as North American immigrants at the beginning of Wasatchian time. Nine of the genera listed by Webb and Opdike not only make their first appearance in the Wasatchian land-mammal age, but also make their first appearance in the Wa-0 fauna (as do five genera not listed by Webb and Opdike as Wasatchian immigrants). The remaining six genera listed by Webb and Opdike appear at different times later in the

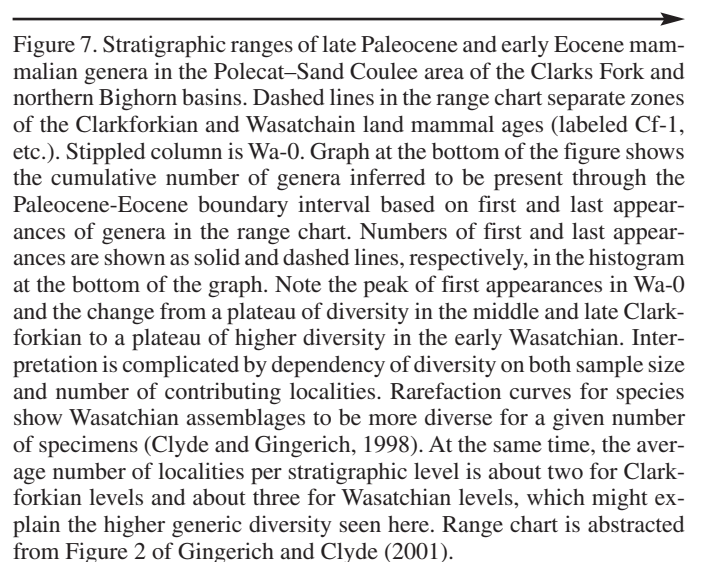
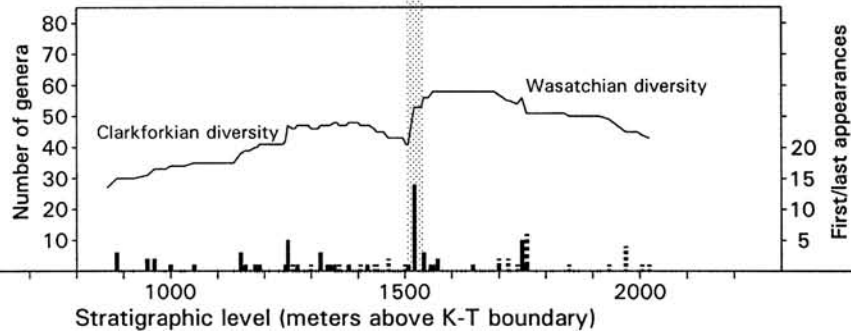
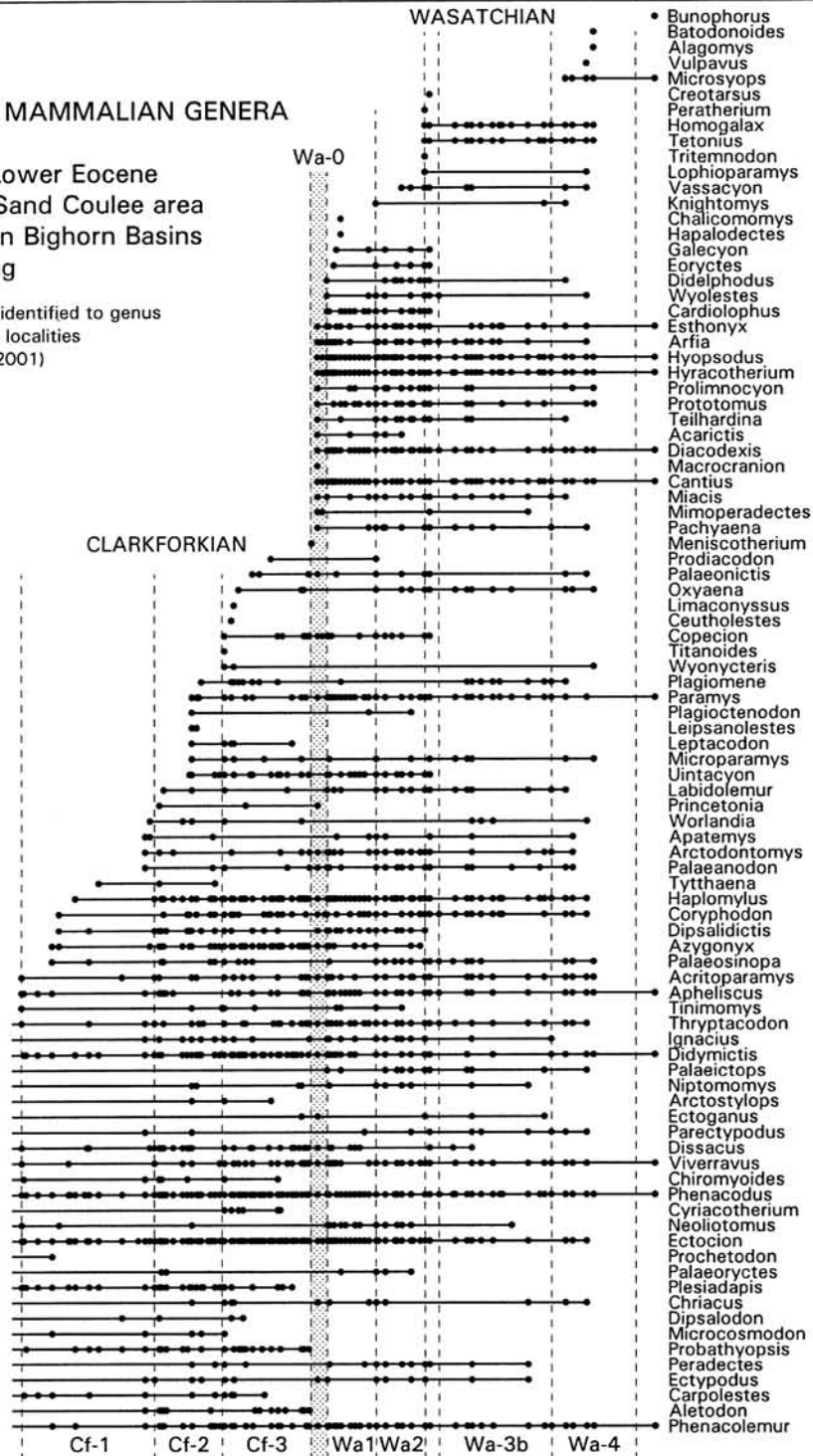


Figure 7. Stratigraphic ranges of late Paleocene and early Eocene mammalian genera in the Polecat-Sand Coulee area of the Clarks Fork and northern Bighorn basins. Dashed lines in the range chart separate zones of the Clarkforkian and Wasatchian land mammal ages (labeled Cf-1, etc.). Stippled column is Wa-0. Graph at the bottom of the figure shows the cumulative number of genera inferred to be present through the Paleocene-Eocene boundary interval based on first and last appearances of genera in the range chart. Numbers of first and last appearances are shown as solid and dashed lines, respectively, in the histogram at the bottom of the graph. Note the peak of first appearances in Wa-0 and the change from a plateau of diversity in the middle and late Clarkforkian to a plateau of higher diversity in the early Wasatchian. Interpretation is complicated by dependency of diversity on both sample size and number of contributing localities. Rarefaction curves for species show Wasatchian assemblages to be more diverse for a given number of specimens (Clyde and Gingerich, 1998). At the same time, the average number of localities per stratigraphic level is about two for Clarkforkian levels and about three for Wasatchian levels, which might explain the higher generic diversity seen here. Range chart is abstracted from Figure 2 of Gingerich and Clyde (2001).

STRATIGRAPHIC RANGES OF MAMMALIAN GENERA

Upper Paleocene - Lower Eocene
of the Polecat Bench - Sand Coulee area
Clarks Fork and northern Bighorn Basins
Wyoming

Based on 13592 specimens identified to genus
collected from 294 localities
(February 26, 2001)



Wasatchian. Appearance of so many mammals in such a restricted interval of time coinciding with the CIE-PETM event reinforces the arguments by Stucky (1990), Janis (1993), and Webb and Opdike (1995) that climate has an important effect on Cenozoic mammalian faunas. This is shown too by the transient changes mentioned above. Whether climate has any direct effect on speciation remains to be substantiated, but mammalian turnover is pulsed and the Wa-0 pulse discussed here clearly coincides with climate change (Vrba, 1985).

Prothero (1999) and Alroy et al. (2000) studied Cenozoic climate and mammals on million-year time scales and failed to find any substantial biotic response to climate change. Prothero (1999) excluded the Paleocene-Eocene transition from his study because it involved immigrant genera, while Alroy et al. (2000) included it and found evidence associating climate and biotic change in this brief transition. One reason the relationship of faunal change to climate is clear at the Paleocene-Eocene boundary is because the isotopic record being compared comes from the very same stratigraphic section, standardizing the spatial scale and removing uncertainties inherent in correlation of distant sections like those on land and in the deep sea. Another reason the relationship is clear here may be that important climatic events operate on short time scales, and any direct forcing of mammalian change will be blurred if mammals being compared are not sampled on comparably short time scales. Aggregation of mammalian records on million-year time scales may not be precise enough to reveal patterns on the time scale of climate change (just as study of evolutionary change on million-year time scales is inadequate to characterize rates on the time scale of the evolutionary process; Gingerich, 2001b).

Climate plays a large role in structuring living mammalian faunas both geographically and ecologically (Badgley and Fox, 2000). The links between Wa-0 faunal change and climate change demonstrated here cannot be generalized to the whole faunal history of Cenozoic mammals, but at the same time it is clear that climate plays an important role in faunal change and such relationships deserve careful investigation.

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