

北美西部古新世-始新世极热事件 (PETM) 期间的哺乳动物群序列

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摘要: 跟随一队研究哺乳动物群在古新世-始新世变化的生物地层学和古地理学的学者, 已故周明镇教授开始了他的古脊椎动物学事业。这是化石记录中偶蹄类、奇蹄类和灵长类 (APP 类群) 首次出现的时期。随着北美西部 Polecat Bench 新的最晚古新世 Clarkforkian 哺乳动物群的发现, 古新世作为一个独立于始新世的分期从 1911 年开始被接受。后来, 研究证明古新世-始新世界线包括了一段时间, 这期间发育了矮小型哺乳动物支系。古新世-始新世碳同位素漂移 (CIE) 与哺乳动物矮小化以及 APP 类群的首次出现是同时的。据此可以对 CIE 进行全球性总结, 结果表明它与古新世-始新世极热事件 (PETM) 相关。PETM 这一全球温室变暖事件不仅对地球气候和生物群有短暂的影响, 而且对生物群同样具有深远持续的影响。我们所知的哺乳动物与 CIE 和 PETM 之间关系的大部分内容是通过对 Polecat Bench 周边剖面独特地层记录的高分辨率研究得到的。周教授早年曾在那里工作过, 如今他的骨灰也撒在那里。

关键词: 怀俄明州, 古新世, 始新世, 哺乳动物, 碳同位素漂移, 古新世-始新世极热事件
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MAMMALIAN FAUNAL SUCCESSION THROUGH THE PALEOCENE-EOCENE THERMAL MAXIMUM (PETM) IN WESTERN NORTH AMERICA

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Abstract The late Professor Minchen Chow started his career in vertebrate paleontology with a team of scholars working to clarify the biostratigraphy and paleogeography of Paleocene-Eocene change in mammalian faunas. The Paleocene-Eocene transition is the time of first appearance of artiodactyls, perissodactyls, and primates (APP taxa) in the fossil record. Recognition of the Paleocene as an epoch separate from the Eocene started to be accepted in 1911 following discovery of a new Clarkforkian latest-Paleocene mammalian fauna at Polecat Bench in western North America. Later the Paleocene-Eocene boundary was shown to include an interval with dwarfed mammalian lineages. A Paleocene-Eocene carbon isotope excursion (CIE) was discovered coincident with both mammalian dwarfing and the first appearance of APP taxa. This enabled global generalization of the CIE, which was linked in turn to the Paleocene-Eocene thermal maximum (PETM). The PETM is a global greenhouse warming event that had transient effects on the earth's climate and biota, but also profound lasting effects on the biota.

Much of what we know about mammals in relation to the CIE and PETM we have learned through high-resolution study of the exceptional stratigraphic record flanking Polecat Bench, where Professor Chow worked early in his career and where his ashes now lie.

Key words Wyoming, Paleocene, Eocene, mammals, CIE, PETM

1 Introduction

The late Professor Minchen Chow (Zhou Mingzhen) received his B. Sc. degree at Chongqing University in 1943. In 1947 he traveled to the United States, where he earned an M. A. degree at Miami University (Ohio) in 1948, and a Ph. D. at Lehigh University (Pennsylvania) in 1950. Dr. Chow spent the summer of 1949 working at the American Museum of Natural History in New York, and the years from 1949 to 1951 at Princeton University, first finishing his doctoral dissertation and then working as a postdoctoral scholar with Professor Glenn Jepsen. Dr. Chow spent the summer of 1950 working in Wyoming, at Princeton Quarry near Polecat Bench in the northern Bighorn Basin, and at other sites of late Paleocene through early Eocene age. Dr. Chow returned to China in 1951. His Princeton experience gave him a special interest and experience in Paleogene vertebrate paleontology that blossomed into expertise when he found Paleocene and Eocene mammals at numerous sites in many depositional basins in China.

This review is written to honor Professor Chow by placing his early field work in Wyoming in the context of what field studies there were in the process of becoming. The area bordering Polecat Bench in the Bighorn Basin, where Professor Chow worked in 1950, has subsequently become the most thoroughly documented record known anywhere of mammalian faunal change across the Paleocene–Eocene epoch boundary. Polecat Bench has an exceptional record of mammalian faunal succession through the Paleocene–Eocene thermal maximum (PETM), during the formative Paleocene–Eocene global greenhouse warming event that was possibly responsible for the origin and certainly responsible for the dispersal of many of the dominant modern orders of mammals. This is a review of the Paleocene–Eocene transition in western North America focusing on change in the northern Bighorn Basin. We all benefit from seeing fossils and stratigraphic sections on site, and hands-on experience in the Bighorn Basin undoubtedly contributed to Professor Chow's interest in developing a parallel Paleocene–Eocene record in China.

2 Background

The Eocene 'period' (now epoch) was named by Charles Lyell in Volume III of his *Principles of Geology* (Lyell, 1833:55). It was the first and oldest of four Lyellian subdivisions of 'Tertiary' strata, thought to follow immediately on the 'Secondary' chalk or Cretaceous in Britain. Schimper (1874) inserted a Paleocene 'period' between the Cretaceous and Eocene, based on localities in western Europe with a distinctive flora. This was echoed by Gervais (1877), who distinguished the lower Eocene in France as 'Orthocene,' based on localities with a distinctive vertebrate fauna including the champsosaur *Simoedosaurus* and primate *Plesiadapis*. However, there was no convincing evidence for recognition of a distinct Paleocene epoch of the Cenozoic until William Sinclair and Walter Granger discovered the mammalian fauna of the 'Ralston' or Clark Fork beds (now Clarkforkian land-mammal age) near Polecat Bench in the northern Bighorn Basin of Wyoming (Fig. 1). Sinclair was a geology professor at Princeton University, and Granger was a geologist and paleontologist at the American Museum of Natural History.

The 'Ralston' or Clarkforkian fauna was first found on August 12 and 13, 1911, and reported by Sinclair and Granger (1912; see also Sinclair, 1912; Scott, 1913; Granger, 1914; Sinclair and Granger, 1914). The fauna was called Ralston and then Clarkforkian because the

first discoveries were made at the base of the bluff (Polecat Bench) north of the village of Ralston and at the head of Big Sand Coulee. The latter is a tributary of the Clarks Fork River (Fig. 1). After finding the 'Ralston' fauna, Sinclair and Granger continued their collecting survey on the south side of the Shoshone River, where they found a small fauna thought to be from the same 'Ralston' faunal interval.

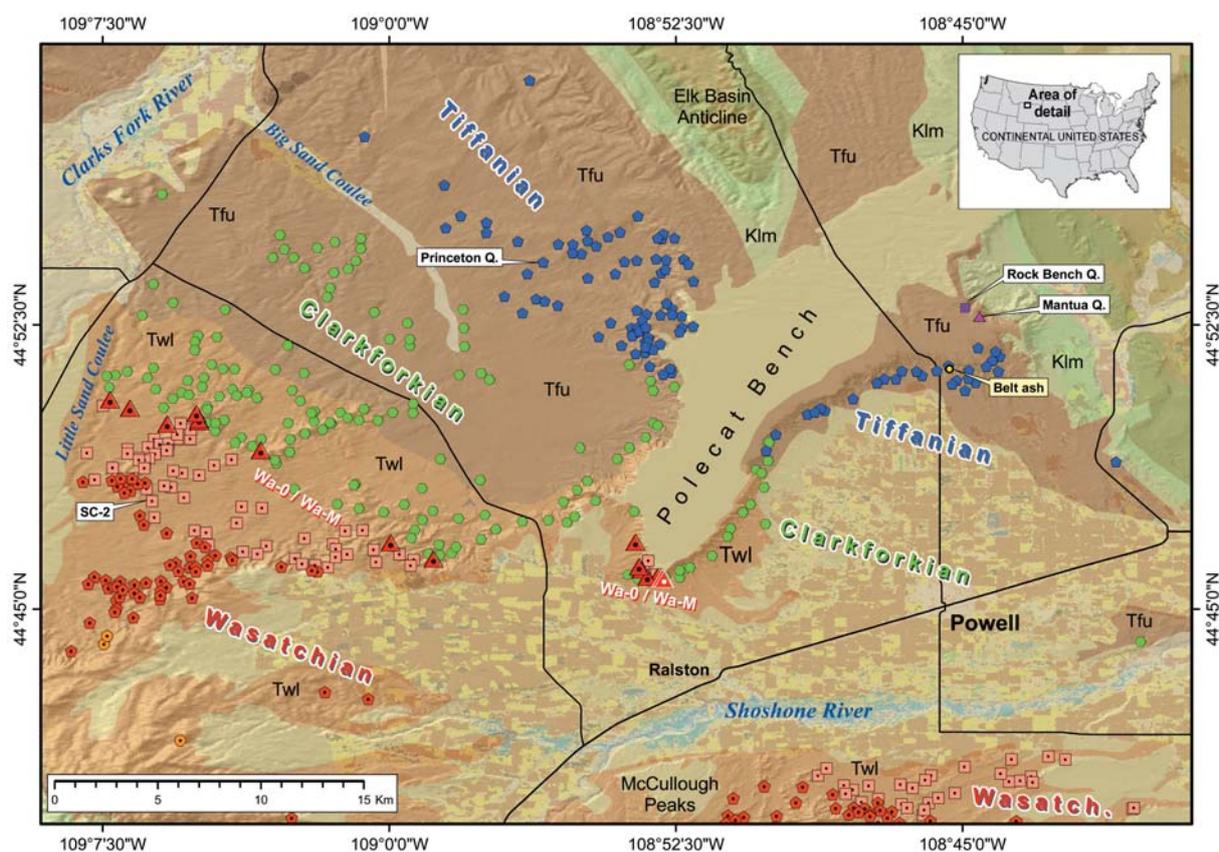


Fig. 1 Geological map of the northern Bighorn Basin in northwestern Wyoming showing University of Michigan localities yielding fossil mammals

Localities are color coded: blue pentagons are Tiffanian, green hexagons are Clarkforkian; red triangles are Wa-M and Wa-0 localities; red squares and pentagons are Wa-1 to 2 and Wa-3 to 4, respectively, and orange circles are Wa-5. Fossiliferous beds of all three formations dip gently to the southwest. Mantua Quarry, Princeton Quarry, Rock Bench Quarry, and SC-2 are localities worked by Jepsen. Belt ash was dated by Secord et al. (2006). Polecat Bench is a Pleistocene river terrace forming a divide between the Clarks Fork River flowing to the north and the Shoshone River flowing to the east (where it joins the Bighorn River). This bench has fossiliferous stratigraphic sections of the Cretaceous Lance and Meeteetse formations (Klm); the drab, carbon-rich, predominantly-Paleocene Fort Union Formation (Tfu); and the overlying, red-banded, predominantly-Eocene Willwood Formation (Twl) on both sides. The Polecat Bench-Sand Coulee (PCB-SC) stratigraphic section shown in Fig. 2 was measured continuously from the Cretaceous-Paleogene boundary at a point near Mantua Quarry, along the southeast side of Polecat Bench, through the head of Big Sand Coulee, and into the head of Little Sand Coulee near the southwest corner of the map. Geology is from Love and Christiansen (1985)

Granger spent September of 1912 with a local farmer, William Stein, working in the Clarks Fork drainage basin investigating the Clarkforkian fauna of late Paleocene age and also the immediately overlying 'Sand Coulee' fauna (Sandcouleean subage of the early Wasatchian land-mammal age, early Eocene). The former was characterized by the absence of perissodactyls and abundance of phenacodontid condylarths, and the latter by the presence of perissodactyls but absence of '*Systemodon*' (now *Homogalax*). Investigation of the south side of Polecat Bench was halted by an early October snow storm, or Granger and Stein might have discovered older

Paleocene faunas as well. Stein worked at the head of Big Sand Coulee again alone for a few days in 1913, when the famous ‘notoungulate’ *Arctostylops steini* was found (recent study indicates affinity with Asia rather than South America; Missiaen et al., 2006).

The next phase of study of the Clarks Fork Basin started in 1928. Princeton graduate student Glenn Jepsen led a small team of students that first camped and worked in lower Wasatchian strata on the divide between Big Sand Coulee and Little Sand Coulee. Jepsen’s camp was in what is now University of Michigan locality SC-2 (Fig. 1). Jepsen’s team then moved to Clarkforkian strata on the west side of Polecat Bench, and ultimately Tiffanian strata on the southeast side of Polecat Bench. Bigger discoveries were made in 1929, when William Sinclair revisited Wyoming as Jepsen’s professor. Princeton Quarry of late Tiffanian age (late Paleocene) was found on July 11. The holotype of Clarkforkian *Plesiadapis cookei* was found on July 29. Rock Bench Quarry of Torrejonian age (middle Paleocene) was found on August 6, and Mantua Quarry of Puercan age (early Paleocene) was found on August 14 (Fig. 1). This extraordinary series of discoveries meant that fossil mammals from five successive ages, Puercan early Paleocene, Torrejonian middle Paleocene, Tiffanian and Clarkforkian late Paleocene, and Wasatchian early Eocene, were all known from the Polecat Bench stratigraphic section. Jepsen wrote his Ph. D. dissertation on this material, publishing first a general faunal study (Jepsen, 1930b). This was followed by more detailed study of the multituberculate mammals (Jepsen, 1940).

Jepsen continued collecting at Polecat Bench and vicinity through the 1950s and 1960s. During the summer of 1950 Minchen Chow worked for Jepsen at Princeton Quarry. Later one of Jepsen’s undergraduate students, Roger Wood (son of fossil rodent expert Albert Wood), wrote a Princeton senior thesis arguing that the Clarkforkian land-mammal age was an artifact resulting from inadvertent mixing of Tiffanian late Paleocene and Wasatchian early Eocene fossil collections (Wood, 1967). The summer of 1967 was my first summer working for Jepsen as a student assistant, and Bighorn Basin field work was largely devoted to testing Wood’s conjecture about the Clarkforkian being a mixed collection. We had little success finding *Plesiadapis cookei*, considered the principal guide fossil for the Clarkforkian, which was frustrating. It turned out that the difficulty was caused by Jepsen’s interpretation of red-banded strata as Eocene in age, and hence of no interest, while the Paleocene-age Clarkforkian mammals he sought, like *Plesiadapis cookei*, later proved to be most abundant in the lower red-banded strata. Such rigidity on Jepsen’s part is surprising because he himself once wrote that “red strata occur well down in the Clark Fork beds” (Jepsen, 1930b:237).

3 Paleocene–Eocene biostratigraphy

3.1 Plesiadapid biostratigraphy

My interest in Paleocene mammals started in 1967 and 1968 when I worked for Jepsen as a student. During the summer we collected many specimens of plesiadapid primates at Rock Bench Quarry and Cedar Point Quarry. I was surprised then to learn how little Jepsen and others seemed to know about the evolution of this common group. When I asked for information about the evolutionary history of Plesiadapidae, Jepsen showed me the bubble-diagram of plesiadapid phylogeny published by Russell (1964). When I asked about the relative ages of Paleocene fossil localities, Jepsen pointed me to a diagram in Van Valen and Sloan (1966), where known fossil localities were seemingly scattered haphazardly on a Paleocene time chart. As a student, I made the common mistake of expecting more to be known. I thought reports on biostratigraphy and phylogeny would be more explicit about ages and relationships.

My undergraduate thesis was a study of Paleocene pollen stratigraphy on Polecat Bench. The most important part of this research was possibly measurement of the thickness of the ‘Polecat Bench Formation’ of Jepsen (1940; now regarded as Fort Union Formation). Topographic

maps were not yet available. My brother assisted me, and together we used a plane table and alidade to survey a 15 km series of stations on the south side of Polecat Bench. We also measured three-point coordinate sets on bed traces. I then wrote Fortran programs to calculate strikes and dips for the beds, and to integrate these with the station locations and calculate the cumulative stratigraphic thicknesses for each station location. This is the basis for the Paleocene part of the Polecat Bench-Sand Coulee (PCB-SC) stratigraphic section shown in Fig. 2. In the end, the total thickness I computed for the formation was surprisingly close to the estimate Jepsen published in 1940 (surprising because Jepsen admitted that the length of the section he used to calculate its thickness was measured with the odometer of his car while driving along the edge of Polecat Bench).

I had experience collecting plesiadapids from different localities and was able to relate some of these to the stratigraphic section I had measured on Polecat Bench. Seeing the potential, I arranged with Jepsen to study the biostratigraphy and phylogeny of Plesiadapidae for my Ph. D. research. My dissertation, completed in 1974, followed the classic stratigraphic principles of superposition and faunal succession, ordering localities in time where they could be superposed in stratigraphic sections, and then correlating the sections whenever possible by matching the species present in each. This led to subdivision of the land-mammal ages, with two plesiadapid zones in the North American Torrejonian, five plesiadapid zones in the Tiffanian, and a distinct zone with *Plesiadapis cookei* marking the Clarkforkian (Gingerich, 1975, 1976).

3.2 Clarkforkian land-mammal age

I moved to the University of Michigan in the summer of 1974, and Jepsen died later that year. I then organized a field and museum project to continue research on Paleocene–Eocene mammals in the northern Bighorn Basin. My initial priorities were: 1) collection of additional *Plesiadapis cookei* specimens and associated mammals to better define the Clarkforkian land-mammal age; and 2) collection of additional perissodactyl specimens to clarify possible differences between the Sandcouleean and Graybullian subages within the Wasatchian. At the time there were several reports of *Hyracotherium* in Paleocene faunas of North America.

Kenneth Rose was my first Ph. D. student. Rose started graduate study at Michigan in 1975 and undertook a comprehensive review and revision of the North American Clarkforkian land-mammal age as his dissertation research. This was based on older American Museum and Princeton University specimens, but primarily on large new stratigraphically-controlled University of Michigan collections from the band of Clarkforkian localities (green circles) shown in Fig. 1. Integrating all that was known, Rose produced a definitive monograph on Clarkforkian faunas (Rose, 1981). Rose's study redefined the Clarkforkian land-mammal age and put to rest Wood's (1967) idea that the Clarkforkian is an artifact resulting from mixing of Tiffanian late Paleocene and Wasatchian early Eocene fossil collections.

3.3 Perissodactyl biostratigraphy

My research interests in the 1970s were focused on the stratigraphic distribution of *Hyracotherium* and other perissodactyls, characterization of the Sandcouleean subage of the early Wasatchian land-mammal age, and clarification of the Paleocene–Eocene boundary in the northern Bighorn Basin. Perissodactyla, when present, are usually common, and the absence of perissodactyls has long been a hallmark of Paleocene time for paleomammalogists (Sinclair and Granger, 1912; Granger, 1914). Exceptions, putatively Paleocene-age *Hyracotherium*, were reported by Morris (1966, 1968), Jepsen and Woodburne (1969), and Schiebout (1974). Thus at an early stage in our study of the North American Clarkforkian it seemed that the Clarkforkian might be correlative with the European Sparnacian, and hence Eocene on a continental time scale (Gingerich, 1975, 1976; Gingerich and Rose, 1977).

One key to resolving this was intensive collecting at Jepsen's 'horse pasture' locality near Princeton Quarry (University of Michigan locality SC-144), which failed to corroborate the presence of *Hyracotherium*, and demonstrated the fauna there to be Tiffanian and not Clarkforkian (thus making a record of *Hyracotherium* even less likely). By 1980 we were forced to conclude that locality information for the Jepsen and Woodburne *Hyracotherium* was erroneous (Gingerich et al., 1980; Gingerich 1989:62). The Morris record of 'Paleocene' *Hyracotherium* was corrected by Flynn and Novacek (1984) and Novacek et al. (1991), who showed that it came from a Wasatchian fauna. Finally, Schiebout et al. (1987) reidentified a "barylambdid" as *Coryphodon*, and reassigned the Schiebout (1974) *Hyracotherium* to the Wasatchian land mammal age (Eocene). Thus there are no remaining records of *Hyracotherium* in the Paleocene of North America.

Jepsen (1930a:119) reported a single specimen of *Homogalax* from the Sand Coulee beds of Granger (1914), and argued that this meant Granger's Sandcouleean was synonymous with his lower Graybullian. Simpson (1937) disputed Jepsen's proposed synonymy of the Sandcouleean and Graybullian, emphasizing the less advanced character of Sandcouleean mammals compared to those of the Graybullian. No museum number was published for Jepsen's *Homogalax*, and it is almost certain that this was a specimen of *Cardiolphus* (Gingerich, 1991). Our research has shown, as Granger reported, that Sandcouleean faunas differ from those of the early, middle, and late Graybullian in lacking *Homogalax*.

3.4 Biostratigraphic zonation and magnetostratigraphy

Biostratigraphic zonation of the northern Bighorn Basin was summarized in 1983, building on studies by Granger (1914), Jepsen (1930b, 1940), Gingerich (1976), Schankler (1980), Rose (1981), and others. The Tiffanian was divided into five zones (Ti-1 to Ti-5), the Clarkforkian into three zones (Cf-1 to Cf-3), and the Wasatchian into seven zones (Wa-1 to Wa-7; Gingerich, 1983). These were demonstrated to be mappable units and are hence legitimately called zones as well as biochrons. Their purpose, like that of land-mammal ages (Walsh, 2005), was to summarize evolving knowledge of the sequence of more important faunal events documented by fossil mammals in the Bighorn Basin. In favorable settings, this can now be done on time scales more finely divided than land-mammal ages.

Correlation of land mammal stratigraphy to a global geological time scale requires identification of dated synchronous global events like magnetochron boundaries. Magnetochrons 27N, 26N, and 25N were identified in the PCB-SC stratigraphic section of the northern Bighorn Basin by Butler et al. (1981, 1987). University of Michigan graduate student William Clyde extended this magnetostratigraphy to include chron 24N in Foster Gulch and McCullough Peaks south of the Shoshone River (Clyde et al., 1994). Clyde and others were later able to recognize chron 26N on the west side of Polecat Bench, clarifying the age of Princeton Quarry (Secord et al., 2006), and to correlate chrons 26N, 25N, and 24N to other parts of the Bighorn Basin, clarifying the ages of other key localities such as Cedar Point Quarry and Divide Quarry (Clyde et al., 2007). Magnetostratigraphy for the PCB-SC stratigraphic section is shown in Fig. 2, with an age model derived for the entire sequence.

In recent years the biostratigraphy of Tiffanian faunas in the Clarks Fork Basin and northern Bighorn Basin have been studied by University of Michigan graduate student Ross Secord (Secord et al., 2006; Secord, 2008). The use of plesiadapid species-level biostratigraphy to subdivide the Tiffanian and Clarkforkian land-mammal ages has been complemented and superseded to some extent by recognition that the first appearances of the distinctive primate *Phenacolemur*, dinoceratan *Probathyopsis*, Rodentia, and condylarth *Copecion* can be recognized more objectively than species boundaries. Secord's synthesis is the basis for current subdivision of the Tiffanian and Clarkforkian shown in Fig. 2.

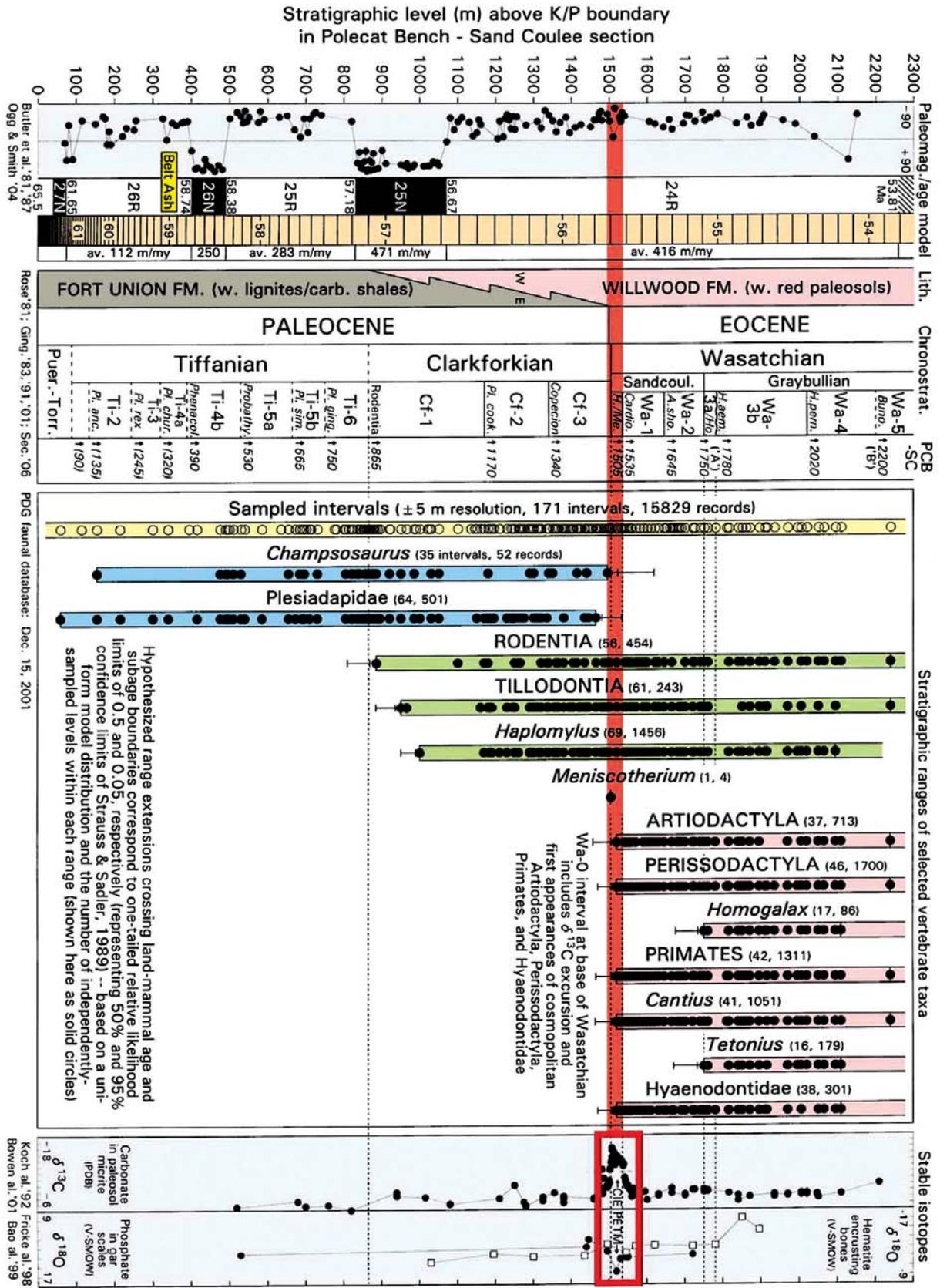


Fig. 2 Stratigraphic context of faunal change in the Polecat Bench-Sand Coulee (PCB-SC) stratigraphic section spanning the Paleocene–Eocene boundary in the Bighorn and Clarks Fork basins of northwestern Wyoming

3.5 Wa-0 faunal zone

Recognition of the distinctive character of mammalian faunas at and even within the Paleocene–Eocene boundary started in 1976 with collection of several specimens of *Ectocion parvus* at the then new University of Michigan locality SC-67 at the south end of Polecat Bench. This distinctively small species of *Ectocion* was named by Granger, 1915, who described a single specimen (AMNH 16080) and reported that it was collected in 1911 from “Clark Fork beds, head of Big Sand Coulee, Clarks Fork Basin, Wyoming” (Granger, 1915:353). The AMNH field catalog for 1911 indicates that this was collected by W. J. Sinclair on August 12-13. Our 1976 specimens were the first added to the species in the 65 years since the type was collected. Further, *E. parvus* proved to be the most common mammalian species at SC-67, indicating that the fauna from this interval was unusual. Another new species named by Granger (1915), *Meniscotherium priscum*, was found by Sinclair on August 12-13 in the same area with similar documentation. More will be said about this later.

The original *Ectocion parvus* specimen was attributed to the new ‘Ralston’ or ‘Clark Fork’ fauna mentioned above. Another specimen of interest was found on August 12 when W. J. Sinclair collected AMNH 15857, the type specimen of *Dipsalidictis platypus* Matthew, 1915. This was collected from “Clark Fork beds, 3 miles north of Ralston, Bighorn Basin, Wyoming” (AMNH field catalogue for 1911; Matthew, 1915:65). By chance, miscellaneous teeth collected by our team in 1986 included the trigonid fitting onto m2 of the holotype of *Dipsalidictis platypus*. These miscellaneous teeth were found at University of Michigan locality SC-67 at the south end of Polecat Bench, proving that Sinclair’s specimen came from SC-67 as well (Gingerich, 1989:32). The type specimen of *Ectocion parvus* was found within a day of Matthew’s discovery of *D. platypus* at SC-67 (it may have been collected the same day), which supports the idea that the type of *E. parvus* came from SC-67.

A third specimen of interest is AMNH 16145, the type specimen of *Meniscotherium priscum* Granger, 1915, which was collected on August 12-13, 1911, again from “Clark Fork beds, head of Big Sand Coulee, Clarks Fork Basin, Wyoming” (AMNH field catalogue for 1911; Granger, 1915:360). The appearance and circumstances of discovery of this specimen are so similar to those of *Ectocion parvus* that initially it seemed reasonable to interpret AMNH 16145 as coming from the SC-67 stratigraphic interval as well. The first report on the SC-67 mammalian fauna included the hyaenodontid creodont *Arfia*, *Ectocion parvus*, *Hyracotherium*, and by implication *Meniscotherium priscum*. The fauna was interpreted as early Wasatchian and early Eocene in age (Gingerich, 1982).

Ordinate is stratigraphic level in meters above the Cretaceous–Paleogene (K-P) boundary. Polecat Bench is exceptional in combining such a rich faunal record in the same stratigraphic section with magnetostratigraphy (left columns) and isotope chemostratigraphy (right columns). Geological age model (orange column) is based on spline interpolation using published ages for magnetochrons. This yields a long-term sediment accumulation rate across the Paleocene–Eocene boundary averaging 416 meters per million years, meaning a meter of sediment represents about 2400 years. Density of faunal sampling is shown by open circles (yellow column). Tiffanian, Clarkforkian, and Wasatchian are North American land-mammal ages. Stratigraphic ranges for selected taxa are shown with solid circles for holdover Tiffanian taxa (blue), Clarkforkian taxa (green), and first appearances of Wasatchian taxa (red). The pronounced negative carbon isotope excursion (CIE) related to the Paleocene–Eocene warming event (PETM) is enclosed in the red box on the right. Note near synchronicity of 1) last appearances of champsosaurs and plesiadapids; 2) first appearances of the modern mammalian orders Artiodactyla, Perissodactyla, and Primates; and 3) the CIE are shown by the red line. Paleomagnetism is from Butler et al. (1981, 1987; calibrated from Ogg and Smith, 2004). Biostratigraphy is from Gingerich (1976, 1983, 1991, 2001a), Rose (1981), Secord et al. (2006), and Secord (2008). Isotope stratigraphy is from Koch et al. (1992), Fricke et al. (1998), Bao et al. (1999), and Bowen et al. (2001). Confidence limits on taxon ranges are calculated following Strauss and Sandler (1989) to emphasize the quality of the record. One-tailed limits are employed in each case because they are larger and hence more conservative. Chart here is updated from Gingerich (2003, 2006)

Focused collecting of fossil mammals from the SC-67 interval indicated that a distinct zone older than Wa-1 is represented, for which I proposed the name Wa-0 (Gingerich, 1989). Twenty Wa-0 localities were identified around the Bighorn Basin, and these yielded a mammalian fauna of 35 genera and 41 species. The Wa-0 fauna included the earliest North American representatives of Artiodactyla, hyaenodontid Creodonta, Perissodactyla, and true Primates, interpreted to represent the beginning of the Eocene. However, the Wa-0 fauna was dominated by hyopsodontid and phenacodontid Condylarthra, and was compositionally intermediate between earlier Clarkforkian and later Wasatchian faunas. Cenogram depiction suggested a forest-dwelling fauna inhabiting a humid environment. Surprisingly, some genera present before and after were represented by dwarfed species in the Wa-0 interval. The best sampled are *Ectocion parvus*, *Copecion davisii*, *Thryptacodon barae*, and *Chriacus badgleyi*. The Wa-0 artiodactyl, *Diacodexis ilicis*, Wa-0 perissodactyl *Hyracotherium sandrae*, and Wa-0 primate *Cantius torresi* are also notably smaller than Wa-1 congeners. *Haplomylys*, present before and after, is conspicuously absent in the Wa-0 interval.

3.6 Wa-M faunal zone

A surprise came in 2000 when UM 108645, a specimen of *Meniscotherium priscum*, was found in a 4 ~ 5 meter thick interval of distinctively-colored brown paleosols. These beds were known to yield *Celtis* endocarps (Gingerich, 1989), at the top of a sequence of strata previously considered to be Cf-3 in age. *Meniscotherium* has been considered to be a Wasatchian immigrant to North America (Gingerich, 1982). The new specimen was only the third specimen of *Meniscotherium* to be found in the Bighorn Basin, and it was the first found in situ in stratigraphic context. It was found in a saddle where contamination from overlying Wa-0 strata is impossible (Gingerich, 2001a; Fig. 3). Further study of the Wa-M interval at Polecat Bench, overlying Cf-3 and underlying Wa-0, yielded additional specimens of *Meniscotherium*, the oldest record of *Macrocranium* in North America, a new leptictid *Amphigyion straitae*, and abundant remains of a distinctively small species of the condylarth *Haplomylys* (*H. zalmouti*; Gingerich and Smith, 2006). The type specimen of *Meniscotherium priscum* described by Granger (1915) almost certainly came from this Wa-M interval at Polecat Bench.

Meniscotherium has been found in strata overlying Cf-3 mammals in the western Bighorn Basin (Gingerich, 2001a) and in strata underlying Wa-0 mammals in the southern Bighorn Basin (Strait, 2001). Both of these records are consistent with restriction of Bighorn Basin *Meniscotherium* to a narrow Wa-M faunal biochron and biozone at the beginning of the Wasatchian land-mammal age. However, *Meniscotherium* ranges through much of the Wasatchian in more southern faunas of New Mexico, Colorado, and southern Wyoming (Gazin, 1965; Williamson and Lucas, 1992).

4 Paleocene-Eocene Thermal Maximum

Distinctive characteristics of the Wa-0 mammalian fauna were initially interpreted to be related to sampling a high-floodplain environment (Gingerich, 1989), building on an idea of lateral variation of mammals in paleosols related to environmental gradients on a floodplain (Bown and Beard, 1990; but see Clyde et al., 2005). A more satisfactory explanation is now available. This developed from study of stable isotopes of carbon and oxygen in marine and continental settings (reviewed in Gingerich, 2006).

The initial study in a marine setting was in the Southern Ocean at ODP site 690. Here, in a high-resolution stratigraphic study, carbon and oxygen isotope anomalies were found (Stott et al., 1990; Kennett and Stott, 1991) in association with a benthic foraminiferal extinction (Thomas, 1989, 2003). An abrupt decrease in $\delta^{18}\text{O}$ in carbonate tests of deep-living forams

was interpreted to indicate rapid warming of southern ocean bottom water by some 4°C, with, by inference, elevation of global temperatures (Stott et al., 1990; Kennett and Stott, 1991). Association with a foraminiferal extinction event was important because it is difficult to recognize an anomaly as in interpretable excursion if there is no associated effect. At site 690, a brief and similarly abrupt carbon isotope excursion (CIE) involving decrease of $\delta^{13}\text{C}$ by some -2.5% was found to coincide with the $\delta^{18}\text{O}$ excursion. This was originally interpreted to indicate loss of a previously-existing isotopic gradient between surface and deep ocean waters, but its significance went much farther.

While the marine studies were underway, University of Michigan graduate student Paul Koch conceived an isotope study to see if he could find a five-million-year Paleocene–Eocene marine trend toward isotopically lighter carbon in the Polecat Bench PCB-SC continental section. Koch studied mammalian dental apatite and soil nodule carbonate. He found the long-term trend, but also a short-term CIE. Here again, this CIE coincided with a faunal event, the Wa-0 first appearance of perissodactyls and other modern orders of mammals in a fauna of dwarfed species (Koch et al., 1992), and here again it was at or near the Paleocene–Eocene boundary. Finding evidence of the CIE in both marine and continental sections meant that it was global, involving the atmosphere as well as the oceans. The CIE soon became so important for precise correlation of marine and continental strata that the Paleocene–Eocene boundary was redefined to be the onset of the CIE (Aubry et al., 2007).

Several attempts have been made to study change in $\delta^{18}\text{O}$ and temperature in a continental PETM setting. Fricke et al. (1998) compared carbonate and phosphate components of hydroxyapatite in mammalian tooth enamel and fish scales from the PCB-SC section, and found an isotopic shift equivalent to a several-degree increase in PETM surface temperatures. Bao et al. (1999) studied a series of sites through the late Paleocene and early Eocene in the PCB-SC section, but lacked samples from the PETM.

The magnitude of the CIE is in the range of -2.5% to -4.5% in the deep sea (Kennett and Stott, 1991; Zachos et al., 1993) or as much as -4.5% to -7% or -8% on land (Koch et al., 1992; Bowen et al., 2001; Smith et al., 2007). Great changes like those seen in continental records would require that massive amounts of very light carbon be added to the atmosphere, and the only known reservoirs that might supply a great enough mass of sufficiently light carbon are seabed methane clathrates or methane ice deposits generated by anaerobic bacteria (Dickens et al., 1995). Methane ices are pressure and temperature sensitive, and it is easy to envision that decreasing pressure or increasing temperature (or both) might initiate methane release leading to positive feedback and runaway global warming. On the other hand, some of the CIE shift recorded in continental carbon isotope values may be enhanced by an increase in available moisture on land (Bowen et al., 2004), or by changing floral composition on land involving replacement of mixed angiosperm and conifer floras by more purely angiosperm floras (Smith et al., 2007). Either would exaggerate the magnitude of change in carbon isotope values in the proxy records being studied, relative to the true isotopic composition of the atmosphere.

If the magnitude of the CIE is less in the atmosphere than in the continental soil carbonate and organic carbon records studied, then release of massive amounts of seabed methane may not be required to explain the CIE and PETM. Nevertheless, there is general agreement that CO_2 was elevated during the PETM, possibly increasing by a factor of only 0.7 (Zeebe et al., 2009) or by a factor of 3 or 4 (Zachos et al., 2003; Curran et al., 2008). Plants respond to elevated CO_2 by producing less RuBisCO, a metabolic enzyme that is the primary protein in leaf tissues and by producing more secondary compounds inhibiting digestibility for herbivores. As a consequence, mammalian herbivores can be expected to grow more slowly and evolve to reproduce at smaller body size, which may explain dwarfing of Wa-0 mammals (Gingerich, 2003).

5 Mammalian faunal succession through the PETM

Our first understanding of mammalian faunal succession across the Paleocene–Eocene boundary came when the Clarkforkian fauna was distinguished from that of the Wasatchian in the northern Bighorn Basin (Sinclair and Granger, 1912; Granger, 1914). The breakthrough came when a fauna with a key guide fossil, the dawn horse *Hyracotherium*, was found superposed above a fauna that lacked perissodactyls — both in a single stratigraphic section. This empirical discovery at Polecat Bench was the demonstration that catalyzed recognition of a Paleocene epoch of geological time separate from the Eocene, first by vertebrate paleontologists and then by others. The stratigraphic range of *Hyracotherium* and other perissodactyls, as presently known, is shown in the Perissodactyla column of Fig. 2.

A second stage of understanding mammalian faunal succession across the Paleocene–Eocene boundary came when Jepsen and Sinclair found faunas representing all four of North American Paleocene land-mammal ages, Puercan, Torrejonian, Tiffanian, and Clarkforkian, and the first Eocene land-mammal age, Wasatchian, in stratigraphic superposition, again in the Polecat Bench PCB-SC section of the northern Bighorn Basin (Jepsen, 1930b; Wood et al., 1941). Further, as the faunas of each land-mammal age were studied in more detail, again in stratigraphic context, it proved possible to subdivide the Tiffanian, Clarkforkian, and Wasatchian ages into multiple local biochrons and biozones (Gingerich, 1975, 1976; Rose, 1981; Secord et al., 2006; Secord, 2008). These were numbered in the now familiar sequences Ti-1 to Ti-6, Cf-1 to Cf-3, and Wa-1 to Wa-7 (Gingerich, 1983, 2001a; Secord et al., 2006; Fig. 2).

A third stage of understanding the Paleocene–Eocene transition came when Butler et al. (1981, 1987) identified magnetochrons 27N, 26N, and 25N in the PCB-SC stratigraphic section. This magnetochronology and correlation to the North American land-mammal ages and Tiffanian–Clarkforkian biochrons was extended by Clyde et al. (1994), who added magnetochron 24N in relation to Wasatchian biochrons in a correlative McCullough Peaks stratigraphic section across the Shoshone River south of Polecat Bench. The importance of magnetostratigraphy is that it ties the mammalian biostratigraphy to the global geological timescale and permits development of a reliable age calibration for the North American middle Paleocene to early Eocene land-mammal ages and biochrons. The Polecat Bench record of paleomagnetism and the age model resulting from a spline fit to ages of magnetochron boundaries are shown in adjacent columns in Fig. 2 (where each rectangle in the age model encompasses 100 ky). This temporal calibration was tested and corroborated by recent dating of sanidine in the Belt ash of the Polecat Bench section, which yielded an age of 59.00 ± 0.30 Ma (Secord et al., 2006).

Now we are working in a fourth stage of high-resolution faunal succession across the Paleocene–Eocene boundary in a context permitting global correlation. This started, in some sense, with discovery that Artiodactyla, Perissodactyla, and Primates (‘APP taxa’) appear simultaneously in the Polecat Bench PCB-SC stratigraphic section, implying immigration from elsewhere. However, it is not just the immigrant taxa that make the fauna interesting at the time of their appearance. The initial immigrants are part of a distinct mammalian fauna, the Wa-0 fauna, that has conspicuously dwarfed forms (e. g., *Ectocion parvus*) in lineages of congeners that are present and larger before and after, lower and higher stratigraphically (Gingerich, 1989). Discovery of the Paleocene–Eocene CIE in the PCB-SC section (Koch et al., 1992) and its correlation with the PETM (Kennett and Stott, 1991), described above, is a finding that explains the immigration event and possibly the dwarfing. However, discovery of the CIE had global importance in relating Paleocene–Eocene faunal change in the North American continental interior to biotic change elsewhere in North America, change on other continents, and change in the world’s oceans.

The stratigraphic record at Polecat Bench is thick and exceptionally well exposed (Fig. 3),

making it possible to undertake a range of studies through the PETM interval. The first high-resolution studies of the Paleocene–Eocene CIE were carried out at Polecat Bench utilizing carbonate in soil nodules (Bowen et al., 2001; Bains et al., 2003). The fidelity of organic carbon as a carrier for the CIE was tested here (Magioncalda et al., 2004). Precession-scale wet and dry climate cycles have been documented, superimposed on a longer term decrease and then increase in precipitation (Kraus and Riggins, 2007; Abdul Aziz et al., 2008; Smith et al., 2008a,b). Trace fossils indicate that burrowing insects and earthworms were dwarfed like some of the mammals during the PETM interval (Smith et al., 2009). Polecat Bench has also proven to be a good location for quantifying downslope contamination of fossils from mammal-bearing conglomerates (Wood et al., 2008).



Fig. 3 Photograph of the south end of Polecat Bench showing the quality of stratigraphic exposure documenting the Paleocene–Eocene transition here

Stratigraphic sequence includes, in order of superposition: 1) Clarkforkian Cf-3-age locality SC-343 with Purple-0 paleosol marking the onset of the CIE; 2) site of the latest Clarkforkian SC-404 Shell Bed wash site; 3) site of the earliest Wasatchian Wa-M-age *Meniscotherium*-bearing locality SC-404 (SC-434 Gar Scale Channel and Brown Mudstone wash sites are at this level farther east); 4) base of early Wasatchian red beds yielding the Wa-0 fauna, including the lower double red (LDR), and Purple-2 beds that can be traced farther west into locality SC-67; and 5) base of early Wasatchian Wa-1 beds filling a scour cut into the upper part of Wa-0 locally. Stratigraphic separation of Purple-0 and the base of LDR is six meters (Gingerich, 2001a). Wash site faunas from SC-404 and SC-434 were studied by Gingerich and Smith (2006)

Maas et al. (1995), Clyde and Gingerich (1998), Gunnell (1998), and Gingerich and Clyde (2001) reviewed faunal change through the PETM interval in the Bighorn Basin. Subsequently, high-resolution study of the CIE at Polecat Bench has enabled a more precise understanding of its relation to faunal change locally (Bowen et al., 2001; Bains et al., 2003; Gingerich, 2003) and more globally (Smith et al., 2006). One motivation for study of the Polecat Bench section at the temporal resolution required to resolve transient environmental change is illustrated in Fig. 4. This illustrates the detail at which it is possible to study evolutionary lineages in the fossil record, with an analysis of the transitions of successive means and the evolutionary rates required (redrawn from Gingerich and Smith, 2006). Here the ranges of tooth size variation (shaded trends) have ‘cusps’ spaced at roughly 400 ky intervals, and it would not

be surprising if these are influenced by 400 ky planetary orbital eccentricity cycles. Spectral analysis of evolutionary time series like those in Fig. 4 may enable finer-scale orbital cycles to be identified as well.

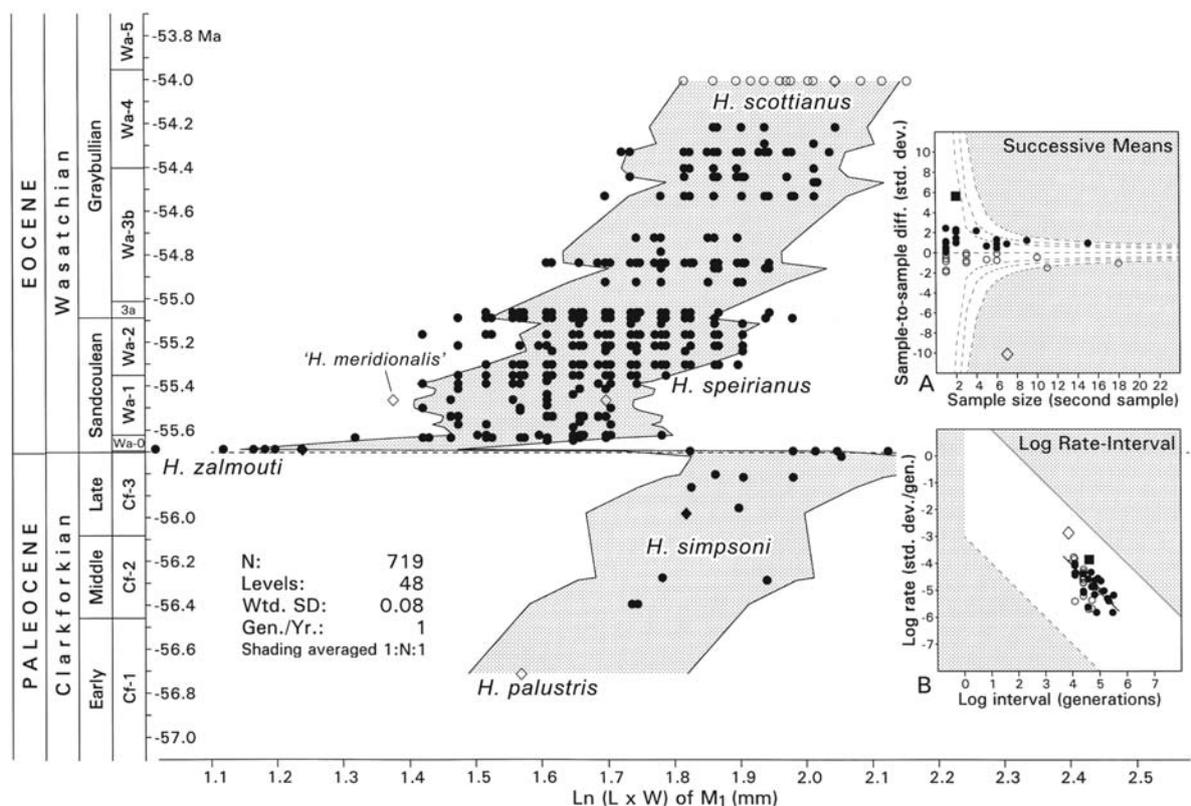


Fig. 4 Stratigraphic plot showing evolution of tooth size, and by inference body size, in the small mammalian condylarth *Haplomylys* through the late Paleocene and early Eocene of the PCB-SC section in the northern Bighorn and Clarks Fork basins

Abscissa is the natural logarithm of crown area for the first lower molar (m_1). Ordinate shows the spacing of samples in geological time, following the age model of Fig. 2. Bighorn Basin species, possibly representing a single evolutionary lineage, are *H. palustris* Gingerich (1994), *H. simpsoni* Rose (1981), *H. zalmouti* Gingerich and Smith (2006), *H. speirianus* (Cope, 1880), and *H. scottianus* Gingerich (1994). Solid symbols represent specimens collected from localities tied to the Polecat Bench-Sand Coulee section. Diamonds represent type specimens. Type of *H. meridionalis* (Beard and Dawson, 2009), if distinct, is an m_1 closer in size to Wa-1 *H. speirianus* than it is to Wa-M *H. zalmouti*. Inset figure A shows that the difference between adjacent samples of *H. simpsoni* and *H. zalmouti* (open diamond in lower left quadrant) is greater than expected by chance resampling of a normal distribution with the mean and standard deviation of the former sample (0.95, 0.99, and 0.999 confidence regions are shown). Inset figure B shows that the rate of change from *H. simpsoni* to *H. zalmouti* is high (ca. 10^{-3} standard deviations per generation averaged over ca. 10^4 generations; open diamond in center of inset B), but this is still feasible as a response to natural selection (Gingerich, 2001b). Insets A and B have positive and negative change represented by solid and open symbols; diamonds show change from Cf-3 to Wa-M, and squares show change from Wa-M to Wa-0

Initiation of the CIE happened at the end of Clarkforkian time (near the very end of Clarkforkian biochron Cf-3). More precisely, faunal change lagged the onset of the CIE by several meters of accumulated sediment and hence possibly 5 ~ 10 thousand years. Maximum excursion of the CIE happened during the brief Wa-M interval at the beginning of Wasatchian time (comprising the remainder of a precession cycle or 10 ~ 15 thousand years; Abdul Aziz et al., 2008). Thus the Wa-M fauna can be viewed as the fauna of maximum excursion of the CIE

and, possibly, of most elevated temperatures of the PETM. Brown paleosols are the sedimentological expression of this maximum excursion. The rest of the main body of the CIE, spanning all of Wa-0 time, occupied about 4.5 precession cycles or about 95 ky (Abdul Aziz et al., 2008). The Wa-0 fauna is the fauna typical of the CIE and PETM. Red paleosols are the sedimentological expression of the main body of the CIE. Finally, the recovery tail of the CIE seemingly extended about two precession cycles into Wa-1 time. This means that a Wa-1 fauna with normally-sized *Ectocion*, *Copecion*, and other taxa dwarfed during the PETM replaced the Wa-0 fauna early in the recovery tail of the CIE.

The importance of the CIE as a global stratigraphic event lies not only in the correlation potential of a Paleocene–Eocene boundary defined by its onset, but also in the accuracy and precision of correlation that is possible when a 100 ky event has a resolvable pattern of change within it. It is this pattern of change in the CIE that enabled Smith et al. (2006) to infer that the primate *Teilhardina asiatica* from the Hengyang Basin of China is slightly older than European *Teilhardina belgica* from Dormaal, which is in turn slightly older than the North American Wa-0 species *Teilhardina brandti* and later *Teilhardina americana*. Analysis of morphological characteristics of all four species supports an Asian origin and a westward Asia-to-Europe-to-North America dispersal for *Teilhardina* (Smith et al., 2006). Further, the high-resolution CIE stratigraphic context indicates that this dispersal happened in an interval possibly as short as one precession cycle, or only 19 ~ 23 ky. Recognition of precession-scale climatic control of paleosol development within the PETM (Abdul Aziz et al., 2008) provides hope that this will become the scale of study and comparison of faunas and faunal succession in the future.

Transient climate and biotic change receive the most attention, but it is important to remember that transient dwarfing was not the only biotic response to PETM warming. The appearance of APP taxa, Artiodactyla, Perissodactyla, and Primates, at the beginning of the Eocene in Asia, Europe, and North America signal profound changes in mammalian composition that had lasting biotic effects (Clyde and Gingerich, 1998)

6 Other settings

Polecat Bench and Sand Coulee have an exceptionally rich fossil record, in a stratigraphic setting that is well exposed and accessible. This is not the only section yielding information about the Paleocene–Eocene transition in North America. Suzanne Strait discovered and developed a richly productive Wa-0 wash site in the southern Bighorn Basin, in a sequence of fossil mammal localities with Wa-M and Wa-0 faunas and with the CIE (Strait, 2001; Yans et al., 2006).

Scott Wing and his team have found additional sites in the southern Bighorn Basin yielding Wa-0 mammalian faunas, again tied to the CIE, and the only good leaf floras known from the PETM (Wing et al., 2005). The idea of Wing and Harrington (2001) and Wing et al. (2003) of a moderate floral response to PETM warming, dependent mainly on interactions between immigrant and native taxa rather than climate change, has been revised by discovery of profound floral change (Wing et al., 2005).

Wa-0 mammals have been reported from the Powder River Basin in Wyoming, east of the Bighorn Basin (Robinson and Williams, 1997; Wing et al., 2003), but these have not been studied in detail.

Beard and Dawson (2009) described a large number of new mammalian genera and species based on isolated teeth from a wash site in the marine T4 sand at Red Hot Truck Stop near Meridian, Mississippi. Their interpretation of the mammals, principally the species *Haplomylus meridionalis* based on an isolated m1 (not m2), suggested correlation with the Wa-M fauna at Polecat Bench (Beard and Dawson, 2009:239). However, the Red Hot Truck Stop locality is

considered to be reliably dated to the first 1.6 my of the early Eocene (Danehy et al., 2007), or possibly the first 0.8 my (Gingerich et al., 2008). Correlation of the T4 sand and its mammalian fauna with Wa-M and the first 25 ky of the early Eocene is improbable. The chance of falling in any 25 ky part of an 800 ky interval is $25/800$, or for the longer interval $25/1600$, reducing to one chance in 32 or 64, respectively, or 0.031 or 0.016 as probabilities, much less likely than correlation of the Red Hot Truck Stop locality to later Wa-1 or Wa-2. Correlation from marine to continental environments with the necessary precision will require that the CIE be found in a stratigraphic section with the T4 sand.

7 Conclusions

I doubt that William Sinclair, Walter Granger, Glenn Jepsen, or Minchen Chow, laboring in the summer sun at Polecat Bench, ever imagined that we could know so much about mammalian faunal succession through the Paleocene–Eocene transition. Their efforts led us to understand that there is a Paleocene epoch distinctly different from the Eocene, and each can be divided faunally into land-mammal ages and subages. We now know that there are faunal changes within the ages and subages that define zones and biochrons on a finer temporal scale. The Paleocene–Eocene transition is represented by a series of faunas, Cf-3, Wa-M, Wa-0, and Wa-1, that can be related to the global Paleocene–Eocene carbon isotope excursion (CIE) and Paleocene–Eocene thermal maximum (PETM), and there is potential for orbital tuning of the whole record of climatic and biotic change on even finer scales of time.

There has been a revolution in understanding earth history and climate change in recent years, and Paleocene–Eocene mammals have played a substantial role in this. The PETM was a global greenhouse warming event with transient effects on the earth's climate and biota, but it also had lasting effects on the biota. These include the rapid rise to dominance of Artiodactyla, Perissodactyla, and Primates that continues today. Much of what we know so far about change in mammalian faunas in relation to the CIE and PETM we have learned through high-resolution study of the exceptional Polecat Bench stratigraphic record in Wyoming. But one continent will never tell us everything. Happily the seed carried from western North America to Asia by Professor Chow, sown with an active generation of students in China, is now bearing the fruit required to illuminate the Paleocene–Eocene biotas of both continents.

Acknowledgments Results summarized here represent a century of effort initiated by William Sinclair and Walter Granger, carried forward by Glenn Jepsen and his students and colleagues, including Minchen Chow, and then developed with my own students and colleagues. PhD dissertations by Kenneth Rose, William Clyde, and Ross Secord are three key studies advancing our understanding of Paleocene–Eocene biostratigraphy, chronology, and faunal succession. David Krause, Gregg Gunnell, Jon Bloch, Iyad Zalmout, and Aaron Wood made major contributions to field surveys yielding the collections on which this research is based. Many additional scientific collaborators and co-authors are listed in the references. The Winston Churchill family in Powell, Wyoming, has aided and encouraged field work on Polecat Bench for three generations, before and after the summer Minchen Chow spent with them. William Sanders prepared many of the fossils forming the basis of this project, and Bonnie Miljour has enhanced the illustrations. I thank William Clyde, Gregg Gunnell, and Pieter Missiaen for reading and improving the manuscript. This research has been supported by grants from the U. S. National Science Foundation including EAR-8918023 and 0125502, and grants from the American Chemical Society including PRF 36318-AC8 and 46858-AC8.

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