

Mammalian community response to the latest Paleocene thermal maximum: An isotaphonomic study in the northern Bighorn Basin, Wyoming

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ABSTRACT

New stratigraphic and paleontological information from the McCullough Peaks, northern Bighorn Basin, Wyoming, is incorporated into an isotaphonomic faunal database and used to investigate the impact of the latest Paleocene thermal maximum and coincident earliest Wasatchian immigration event on local mammalian community structure. Surface collections from Willwood Formation overbank deposits provide taphonomically consistent and stratigraphically resolved samples of the medium- to large-sized components of underlying mammalian communities. Rarefaction shows that the immigration event caused an abrupt and dramatic increase in species richness and evenness. After this initial increase, diversity tapered off to more typical Wasatchian levels that were still higher than those in the preceding Clarkforkian. Wasatchian immigrants were rapidly incorporated into the new community organization, representing ~20% of the taxa and ~50% of the individuals. Immigrant taxa generally had larger body sizes and more herbivorous and frugivorous dietary habits compared to endemic taxa, causing significant turnover in body-size structure and trophic structure. There was a significant short-term body-size decrease in many lineages that may have been prompted by the elevated temperatures and/or decreased latitudinal thermal gradients during the latest Paleocene thermal maximum. Rapid short-term climatic change (transient climates) and associated biotic dispersal can have abrupt and long-lasting effects on mammalian community evolution.

INTRODUCTION

The Paleocene-Eocene boundary has been recognized as an important period in mammalian evolution for more than a century (Gervais, 1877). Eocene mammalian faunas in North America and Europe differ from those of the Paleocene in having artiodactyls, perissodactyls, and primates, new orders that dominate holarctic mammalian faunas from the beginning of the Eocene to the present. Not a single well-documented occurrence of any of these important modern orders of mammals has been recorded in deposits of Paleocene age, despite intense collecting effort.

Recent paleoclimatological studies have indicated the existence of a rapid short-term warming event near the Paleocene-Eocene boundary that significantly reduced latitudinal temperature gradients (latest Paleocene thermal maximum [LPTM]; Zachos et al., 1993). Isotopic studies of paleosol carbonates, mammalian tooth enamel, and fish scales (Koch et al., 1992, 1995; Fricke et al., 1998) have established that this climatic anomaly correlates precisely with the long-documented mammalian turnover near the Paleocene-Eocene boundary in North America (Clarkforkian-Wasatchian land-mammal age boundary). These results strongly support earlier suggestions that increased equability opened high-latitude mammalian migration corridors, allowing members of the modern orders to disperse across the entire holarctic region and possibly farther (McKenna, 1983; Krause and Maas, 1990). The geographic origin of these Eocene orders, however, remains a mystery.

Here we combine new information from the McCullough Peaks region with similarly detailed records from elsewhere in the Bighorn Basin (Fig. 1) to evaluate the effect of the LPTM and coincident earliest Wasatchian immigration event on local mammalian diversity, body size structure, and trophic structure. Our study differs from previous studies on Bighorn Basin mammalian turnover (Rose, 1981; Gingerich, 1989; Gunnell et al., 1993; Maas et al., 1995; Gunnell et al., 1995; Morgan et al., 1995; Wing et al., 1995) in

two important ways: (1) We focus on the ecological impact of the LPTM and coincident immigration event, and (2) we use a database that includes all material (including previously unidentified elements labeled "miscellaneous") collected from a single taphonomic mode (surface-collected overbank assemblages). This isotaphonomic approach (Behrensmeyer et al., 1992) is especially important in studies like this because catalogued collections often represent a composite of several taphonomic settings that are not distributed uniformly through time.

SAMPLING AND TAPHONOMY

Faunal abundance data from the McCullough Peaks southeast composite section (Clyde, 1997) were combined with similarly detailed information from Rose (1981) and Gingerich (1989) to form a database composed of 9723 records, 243 localities, and 134 different stratigraphic levels. Almost all localities are in the northern Bighorn Basin (north of the Greybull River; Fig. 1). Many important middle and late Wasatchian localities are known from the southern part of the Bighorn Basin as well (e.g., Bown et al., 1994), but these were not included in this study due to uncertain stratigraphic correlation. Localities had to satisfy several taphonomic criteria to be included in this database. To limit changes in preservation bias through time, only localities that sample Willwood overbank paleosol (mudstone) facies were

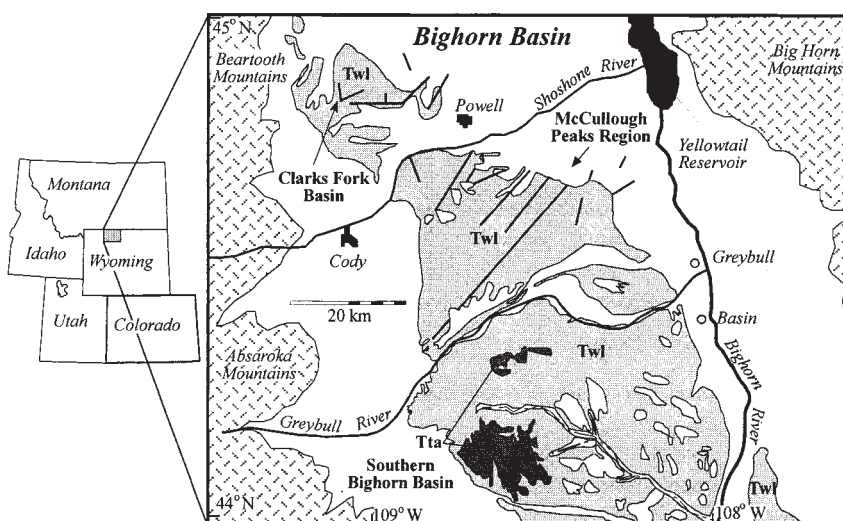


Figure 1. Map of Bighorn Basin showing location of stratigraphic sections used to develop database employed in this paper. Shaded area represents lower Eocene deposits and white areas represent Paleocene and earlier sedimentary strata. Twl (light gray)—lower Eocene Willwood Formation, Tta (dark gray)—lower Eocene Tatman Formation.

included. To minimize the impact of changing collection technique, only surface collections were used. Localities that sample other facies (e.g., channel lag, fresh-water limestone) or were collected using other techniques (e.g., quarrying, screen-washing) were excluded since these are not yet sampled uniformly enough to incorporate in this type of high resolution study. An isotaphonomic sampling strategy limits the part of the underlying community that is sampled (in this case causing small mammals that are fragile and difficult to find to be under represented), but provides an important control on the potentially confounding effects of depositional environment and collection technique (Behrensmeier et al., 1992). As long as there is no systematic change in the facies being sampled or in the collection procedure, sampling should be consistent and unbiased for all samples compared. Changes that are seen cannot be due to taphonomic differences.

Faunal data were grouped into 13 sampling intervals for analysis. Species composition and relative abundance data were combined for all localities within a sampling interval, allowing each interval to be evaluated for both individual- and species-level ecological attributes. Age estimates for sampling intervals were derived from the age model in Clyde (1997). This uses linear interpolation between calibration points, both magnetostratigraphic (C25N/C24R, C24R/C24N.3n, C24N.3n/C24N.2r, and C24N.2n/C24N.1r; Butler et al. 1981, Clyde et al., 1994, see also Tauxe et al., 1994) and chemostratigraphic (carbon isotope excursion; Koch et al., 1995 and Clyde, 1997). Ages for paleomagnetic calibration points

are taken from the most recent geomagnetic polarity time scale (Cande and Kent, 1995) and an estimated age of 55.5 million years was used for the carbon isotope excursion (Berggren et al., 1995). An age model that excludes the carbon isotope event as a calibration point does not significantly differ from the one used here. Estimated durations of the sampling intervals used here range from 0.03–0.31 m.y.; the average is 0.21 m.y. Individual abundances of species were tallied in terms of the minimum number of individuals although results do not differ significantly when abundances are calculated using total number of specimens.

RESULTS

First and Last Appearances

First and last appearances were calculated for genera using 10 m intervals in our new northern Bighorn Basin database. If taxa were identified in the study area from deposits older (younger) than those studied here, they were not counted as first (last) appearances. First and last appearances were recorded at the generic level because many of the recorded species belong to single lineages (chronospecies) and thus would not afford reliable first or last appearance information.

The Wasatchian immigration event is characterized by 15 first appearances during Wa-0 (the earliest faunal zone in the Wasatchian) and this is the largest first appearance event in the record (Fig. 2). Last appearances show only a slight increase across the Paleocene/Eocene boundary interval suggesting that the immigration event did not precipitate (or require) significant extinction

or emigration. At their initial appearance in Wa-0, species of immigrant genera represent 18% of the total fauna, a figure that changes very little throughout the rest of the Wasatchian (Fig. 2). At an individual level, immigrant species represent 21% of all Wa-0 individuals but increase to 40% in the next sampling interval, where their abundance remains more or less constant for the rest of the record (Fig. 2). The establishment of numerical dominance by one or a few introduced species is a common pattern observed over relatively short time scales today but has only rarely been resolved in fossil studies. The existence of an observable temporal lag between the immigration of Wasatchian species and the establishment of their numerical dominance suggests that the intervening period (Wa-0) was a transient interval of competition between Clarkforkian endemic holdovers and Wasatchian immigrants.

Diversity

Rarefaction compensates for the strong relationship between diversity and sample size by standardizing to the smallest sample being compared (Raupe, 1975). Clarkforkian samples show relatively low species richness for a given sample size, whereas Wasatchian samples show relatively high species richness for a given sample size (Figs. 2 and 3). The Wa-0 sample shows anomalously high species richness values. These results support earlier conclusions (Rose, 1981, Gingerich, 1989) that Clarkforkian faunas generally have fewer species than overlying Wasatchian faunas, and rule out differences in sampling as the cause. Species evenness, which tracks the distribution of

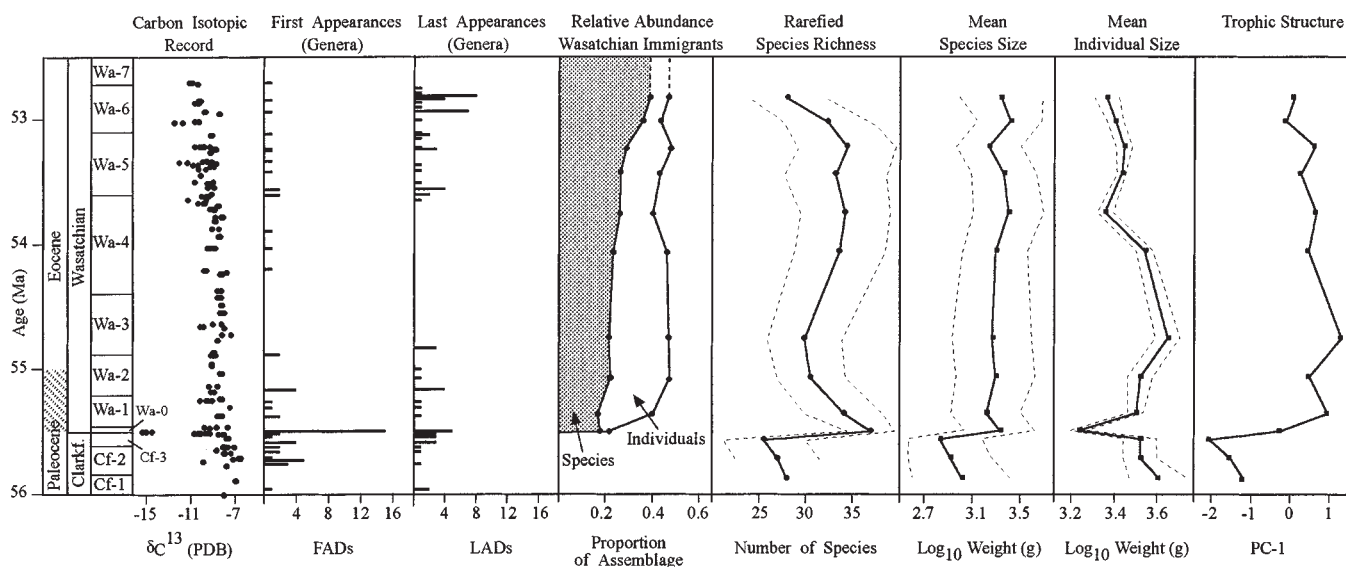


Figure 2. Graph showing changes in Bighorn Basin mammalian community structure coincident with latest Paleocene thermal maximum (LPTM). Carbon isotopic record (Koch et al., 1995) shows characteristic negative excursion at LPTM (PDB—Pedee belemnite standard). Coincident with isotopic excursion is a peak in first appearances (FAD—first appearance datum) representing influx of Wasatchian immigrants but few last appearances (LAD—last appearance datum). At species level, immigrant taxa represent ~20% of entire fauna (shaded area) upon immigration yet come to represent ~50% of all individuals (white area) soon after first appearance. Rarefied species richness rises dramatically in response to immigration event and then tapers to levels in Wasatchian that are still higher than during preceding Clarkforkian (Clarkf.) time. Mean species size increases dramatically at LPTM due to influx of larger bodied immigrants. Mean individual size decreases temporarily during brief warming of LPTM. Trophic structure also undergoes significant turnover across LPTM; herbivores and frugivores become more important in new Wasatchian community structure (PC-1—score on first principal component). Shaded area on time scale represents uncertainty pending designation of a new global stratotype for Paleocene-Eocene boundary. Dashed lines represent 95% confidence intervals.

individuals within species, follows almost an identical pattern with Wasatchian faunas being more evenly distributed than Clarkforkian faunas, and Wa-0 being more evenly distributed than both. Three taxa (*Hyopsodus loomisi*, *Copecion davisi*, *Ectocion parvus*) represent 36% of the individuals in the Wa-0 sample, whereas a single taxon (*Ectocion osbornianus*) represents almost the same percentage of a typical Clarkforkian sample. The relatively high diversity of Wa-0 has been noted before (Gingerich, 1989), but it is even more extreme when its relatively poor sampling (compared to other sampling intervals) is taken into account. The Wa-0 interval is also estimated to represent the shortest amount of time among the sampling intervals studied here. Less temporal averaging would be expected to lower diversity, making the relatively high Wa-0 diversity even more significant at this scale of sampling resolution. One simple explanation for this pattern would be if Wa-0 represented a mixed sample of Clarkforkian and Wasatchian assemblages. However, given the compositional differences between Wa-0 and typical Clarkforkian and Wasatchian assemblages (e.g., 12 of the 39 species at Wa-0 are known only from this level, and there is only one Clarkforkian species present in the Wa-0 fauna), faunal mixing cannot be an important cause for the abrupt rise in diversity at the beginning of the Wasatchian.

Body Size Structure

To investigate changes in body-size structure across the LPTM, body-weight estimates were calculated for taxa in each of the 13 sampling intervals using regressions of body size on tooth size (Legendre, 1989). Where more than one M_1 was measured for a given species, the mean was used to estimate body weight. Measurements

were taken from published sources when no M_1 measurements were available from the specimens used here. Ten species lacking known M_1 s were excluded from body-size analyses. Because the absolute accuracy of these distributions is highly skewed by the taphonomic filters mentioned earlier, we focus on relative changes in body-weight distributions. All body-weight estimates were calculated based on the same tooth (M_1), and errors introduced by regression should not affect relative body weight.

There is a clear long-term increase in the mean species size in the fauna at Wa-0, but a clear short-term decrease in the mean individual size (Fig. 2). The long-term pattern of mean species size reflects the disappearance of several small Clarkforkian species at Wa-0, and the immigration of new comparatively large-bodied Wasatchian immigrants (Fig. 4). The temporary Wa-0 decrease in mean individual size, which is superimposed on the increase in mean species size, is more complicated.

Mean individual size represents the relative numerical importance of the different-sized species in a sample. Many of the species (~50%) at Wa-0, both immigrant and endemic, are unusually small when compared to other members of their genus that occur elsewhere in the record (Gingerich, 1989: Figs. 14, 36, 26, 28, 33, and 41). In Wa-0, these relatively small taxa (small for their genus) are especially abundant and represent ~60% of the individuals. Whereas the smallest Clarkforkian lineages (i.e., genera) are no longer recorded at Wa-0 and afterward (partly causing the shift to higher mean species body size in the Wasatchian), about half of the lineages that are recorded in Wa-0 are represented by relatively small species, with some being abundant. Given (1) that this short-term size change affects both immigrant (e.g., *Hyacotherium*) and endemic (e.g., *Ectocion*) taxa, (2) that it coincides

precisely with a ~4 °C warming event in mean annual temperatures (Fricke et al., 1998), and (3) that modern mammalian individual (and population) body size is known to correlate negatively with temperature (Searcy, 1980), there is substantial circumstantial evidence that the LPTM had a direct short-term impact on the body-size structure of local mammalian communities. Whether this short-term body-size phenomenon was the result of in situ evolution or cline migration is difficult to ascertain, but in either case, smaller individual body sizes are consistent with warmer average temperatures (Koch, 1986).

Trophic Structure

Trophic structure, like body-size structure, is another important taxon-free ecological parameter that can be evaluated for ancient mammalian communities. It is evidence of one of the sets of interactions that make up the complex ecological web we term a community, and ultimately determines, in large part, the transfer of energy from one community member to another. Dietary determinations for Clarkforkian and Wasatchian species were made on the basis of visual inspection of tooth morphology, body size, postcranial elements, and masticatory muscle reconstruction. Given the uncertainty of this subjective coding system, only five trophic categories are considered here: herbivore, carnivore, omnivore, insectivore, and frugivore. For each sampling interval, each trophic category is represented by a certain fraction of the total number of species and a certain fraction of the total number of individuals.

Results of a principal components analysis performed on the combined species and individual data show a noticeable trend across the Clarkforkian-Wasatchian boundary (Fig. 2). Clarkforkian assemblages have relatively low scores on Principal Component 1, and Wasatchian assemblages have relatively high scores on Principal Component 1, with Wa-0 falling out as intermediate. The high Wasatchian scores are associated with relatively high species abundances of herbivores, frugivores, and carnivores, as well as high individual abundances of herbivores and frugivores. The low Clarkforkian scores, on the other hand, are associated with relatively high species abundances and individual abundances of both omnivores and insectivores. This trophic turnover is largely driven by the influx of Wasatchian immigrants which are characterized by a higher fraction of herbivores, carnivores and frugivores and a lower fraction of omnivores and insectivores, compared to endemics (χ^2 test $p < 0.001$ for both species and individuals). Hence the trophic shift at Wa-0 is due to the influx of immigrants rather than a direct in situ response of the community to the LPTM climatic perturbation.

DISCUSSION AND CONCLUSIONS

These paleoecological observations show that the LPTM and coincident earliest Wasatchian immigration event had significant short-term and

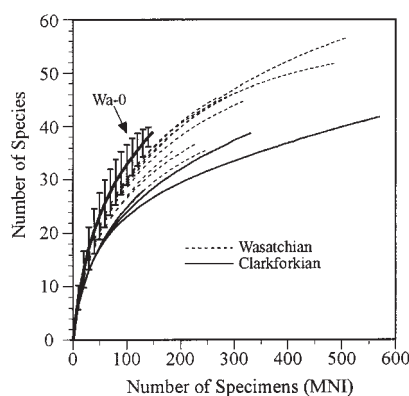


Figure 3. Rarefaction curves for Wasatchian and Clarkforkian assemblages. Wasatchian assemblages (dashed lines) are characterized by higher species richness for given sample size than Clarkforkian assemblages (solid lines). Wasatchian-0 (Wa-0, heavy solid line) is characterized by especially high species richness values. MNI—minimum number of individuals. Error bars on the Wa-0 line represent 95% confidence intervals.

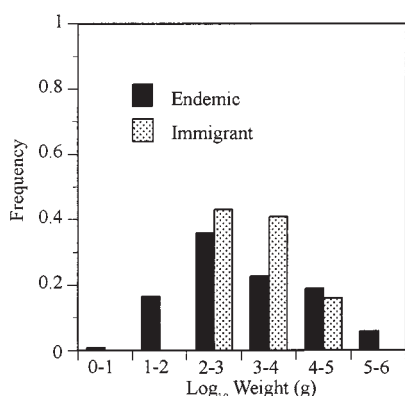


Figure 4. Distribution of estimated body sizes for Wasatchian immigrant taxa (stippled) and Clarkforkian endemic taxa (black). Wasatchian immigrant taxa are generally larger in body size than endemic taxa (χ^2 test $p < 0.02$), supporting idea that their immigration caused observed change in mean species size shown in Figure 2.

long-term effects on diversity, body-size structure, and trophic structure in Bighorn Basin mammalian communities. Short-term effects are apparent in the high species-level diversity and small size of individuals of the Wa-0 assemblage. Long-term effects, which continued through the entire Wasatchian record studied here, include higher diversity, larger average species size, and more herbivory and frugivory in Wasatchian assemblages compared to preceding Clarkforkian assemblages. Most changes are the result of the earliest Wasatchian immigration event, with the Wasatchian immigrants rapidly imposing their distinct ecological attributes on the existing Clarkforkian endemic community. The one change that does not seem to relate directly to the immigration event is the short-term, within-lineage decrease in body size exhibited by a number of immigrant and endemic lineages at Wa-0. This short-term phenomenon likely represents a direct effect (via *in situ* evolution or cline migration) of the LPTM.

Zachos et al. (1993) coined the term *transient climate* to describe the short-term climatic response to crossing a critical physical or chemical threshold during longer periods of climatic change. Transient climates represent aberrant, unstable climatic conditions that rapidly return to background levels after geologically short durations. The latest Paleocene thermal maximum seems to represent a classic example of this phenomenon. The biological impact of these transient climates, however, can be profound and irreversible. In the case of the latest Paleocene, the transient climate was characterized by especially low latitudinal temperature gradients that permitted holarctic dispersal of mammalian taxa. Immigrant taxa permanently changed the ecological framework of local holarctic mammalian communities. In the Bighorn Basin, the climatic shift and coincident dispersal resulted in transient ecological conditions (Wa-0), quickly followed by a new, stable, ecological framework quite different from that known before. The latest Paleocene transient climate rapidly returned to normal, but its impact on biological communities continues to be felt today.

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REFERENCES CITED

- Behrensmeyer, A. K., Damuth, J. D., DiMichele, W. A., Potts, R., Sues, H.-D., and Wing, S. L., 1992, Terrestrial ecosystems through time: Evolutionary paleoecology of terrestrial plants and animals: Chicago, Illinois, University of Chicago Press, 568 p.
- Berggren, W. A., Kent, D. V., Swisher, C. C., and Aubry, M.-P., 1995, A revised Cenozoic geochronology and chronostratigraphy, in Berggren, W. A., Kent, D. V., Aubry, M.-P., and Hardenbol, J., eds., Geochronology, time scales and global stratigraphic correlation: SEPM (Society for Sedimentary Geology) Special Publication no. 54, p. 129–212.
- Bown, T. M., Rose, K. D., Simons, E. L., and Wing, S. L., 1994, Distribution and stratigraphic correlation of upper Paleocene and lower Eocene fossil mammal and plant localities of the Fort Union, Willwood, and Tatman formations, southern Bighorn Basin, Wyoming: U.S. Geological Survey Professional Paper 1540, p. 1–103.
- Butler, R. F., Gingerich, P. D., and Lindsay, E. H., 1981, Magnetic polarity stratigraphy and biostratigraphy of Paleocene and lower Eocene continental deposits, Clarks Fork Basin, Wyoming: *Journal of Geology*, v. 89, p. 299–316.
- Cande, S. C., and Kent, D. V., 1995, Revised calibration of the geomagnetic polarity time scale for the Late Cretaceous and Cenozoic: *Journal of Geophysical Research*, v. 100, p. 6093–6095.
- Clyde, W. C., 1997, Stratigraphy and mammalian paleontology of the McCullough Peaks, northern Bighorn Basin, Wyoming: Implications for biochronology, basin development, and community reorganization across the Paleocene-Eocene boundary [Ph.D. Thesis]: Ann Arbor, Michigan, University of Michigan, 256 p.
- Clyde, W. C., Stamatakis, J., and Gingerich, P. D., 1994, Chronology of the Wasatchian Land-Mammal Age (early Eocene): Magnetostratigraphic results from the McCullough Peaks section, northern Bighorn Basin, Wyoming: *Journal of Geology*, v. 102, p. 367–377.
- Fricke, H. C., Clyde, W. C., O'Neil, J. R., and Gingerich, P. D., 1998, Evidence for rapid climate change in North America during the latest Paleocene thermal maximum: Oxygen isotope compositions of biogenic phosphate from the Bighorn Basin (WY): *Palaeogeography, Palaeoclimatology, Palaeoecology* (in press).
- Gervais, P., 1877, Énumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine: Paris, *Journal de Zoologie*, v. 6, p. 74–79.
- Gingerich, P. D., 1989, New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely sampled high-floodplain assemblage: *University of Michigan Papers on Paleontology*, v. 28, p. 1–97.
- Gunnell, G. F., Bartels, W. S., and Gingerich, P. D., 1993, Paleocene-Eocene boundary in continental North America: Biostratigraphy and geochronology, northern Bighorn Basin, Wyoming, in Lucas, S. G., and Zidek, J., eds., *Vertebrate paleontology in New Mexico*: New Mexico Museum of Natural History and Science Bulletin 2, p. 137–144.
- Gunnell, G. F., Morgan, M. E., Maas, M. C., and Gingerich, P. D., 1995, Comparative paleoecology of Paleogene and Neogene mammalian faunas: Trophic structure and composition: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 265–286.
- Koch, P. L., 1986, Clinal geographic variation in mammals: Implications for the study of chronoclines: *Paleobiology*, v. 12, p. 269–281.
- Koch, P. L., Zachos, J. C., and Gingerich, P. D., 1992, Correlation between isotope records in marine and continental carbon reservoirs near the Paleocene/Eocene boundary: *Nature*, v. 358, p. 319–322.
- Koch, P. L., Zachos, J. C., and Dettman, D. L., 1995, Stable isotope stratigraphy and paleoclimatology of the Paleogene Bighorn Basin (Wyoming, USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 61–90.
- Krause, D. W., and Maas, M. C., 1990, The biogeographic origins of the late Paleocene–early Eocene mammalian immigrants to the western interior of North America, in Bown, T. M., and Rose, K. D., eds., *Dawn of the age of mammals in the northern part of the Rocky Mountain interior, North America*: Geological Society of America Special Paper 243, p. 71–105.
- Legendre, S., 1995, Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: Structures, milieux, et évolution: *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, v. 16, p. 1–110.
- Maas, M. C., Anthony, M. L., Gingerich, P. D., Gunnell, G. F., and Krause, D. W., 1995, Mammalian generic diversity and turnover in the late Paleocene and early Eocene of the Bighorn and Crazy Mountains Basins, Wyoming and Montana (USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 181–207.
- McKenna, M. C., 1983, Cenozoic paleogeography of North Atlantic land bridges, in Bott, M. H. P., Saxon, S., Talwani, M., and Thiede, J., eds., *Structure and development of the Greenland-Scotland ridge*: New York, Plenum Press, p. 351–399.
- Morgan, M. E., Badgley, C., Gunnell, G. F., Gingerich, P. D., Kappelman, J. W., and Maas, M. M., 1995, Comparative paleoecology of Paleogene and Neogene mammalian faunas: Body-size structure: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 287–317.
- Raup, D. M., 1975, Taxonomic diversity estimation using rarefaction: *Paleobiology*, v. 1, p. 333–342.
- Rose, K. D., 1981, The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary: *University of Michigan Papers on Paleontology*, v. 26, p. 1–196.
- Searcy, W. A., 1980, Optimum body sizes at different ambient temperatures: An energetics explanation of Bergmann's rule: *Journal of Theoretical Biology*, v. 83, p. 579–593.
- Tauxe, L., Gee, J., Gallet, Y., Pick, T., and Bown, T., 1994, Magnetostratigraphy of the Willwood Formation, Bighorn Basin, Wyoming: New constraints on the location of the Paleocene/Eocene boundary: *Earth and Planetary Science Letters*, v. 125, p. 159–172.
- Wing, S. L., Alroy, J., and Hickey, L. J., 1995, Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 115, p. 117–155.
- Zachos, J. C., Lohmann, K. C., Walker, J. C. G., and Wise, S. W., 1993, Abrupt climate change and transient climates during the Paleogene: A marine perspective: *Journal of Geology*, v. 101, p. 191–213.

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