

Mammal faunal response to the Paleogene hyperthermals ETM2

A. E. Chew

Mammal faunal response to the Paleogene hyperthermals ETM2 and H2

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Received: 13 March 2015 – Accepted: 17 March 2015 – Published: 16 April 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Scientists are increasingly turning to deep-time fossil records to decipher the long-term consequences of climate change in the race to preserve modern biotas from anthropogenically driven global warming. “Hyperthermals” are past intervals of geologically rapid global warming that provide the opportunity to study the effects of climate change on existing faunas over thousands of years. A series hyperthermals is known from the early Eocene (~ 56–54 million years ago), including the Paleocene-Eocene Thermal Maximum (PETM) and two subsequent hyperthermals, Eocene Thermal Maximum 2 (ETM2) and H2. The later hyperthermals occurred following the onset of warming at the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic. The PETM has been comprehensively studied in marine and terrestrial settings, but the terrestrial biotic effects of ETM2 and H2 are unknown. Their geochemical signatures have been located in the northern part of the Bighorn Basin, WY, USA, and their levels can be extrapolated to an extraordinarily dense, well-studied terrestrial mammal fossil record in the south-central part of the basin. High-resolution, multi-parameter paleoecological analysis reveals significant peaks in species diversity and turnover and changes in abundance and relative body size at the levels of ETM2 and H2 in the south-central Bighorn Basin record. In contrast with the PETM, faunal change at the later hyperthermals is less extreme, does not include immigration and involves a proliferation of body sizes, although abundance shifts tend to favor smaller congeners. Faunal response at ETM2 and H2 is distinctive in its high proportion of species losses potentially related to heightened species vulnerability in response to the changes already underway at the beginning of the EECO. Faunal response at ETM2 and H2 is also distinctive in high proportions of beta richness, suggestive of increased geographic dispersal related to transient increases in habitat (floral) complexity and/or precipitation or seasonality of precipitation. These results suggest that rapid ecological changes, increased heterogeneity in species incidence, and heightened species vulnerability and

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to all meter levels within each bin in each series and then averaged by meter level across all bins. To test the accuracy of resolution of the binning protocol, the binned, averaged parameters are compared with (sample-size biased) parameters calculated from specimen data binned by meter level where possible.

5 Each binning series provides species abundance data and the levels of species first and last appearances within the stratigraphic range of this dataset. An algorithm is used to standardize these data by randomly sampling (without replacement) each bin to a sample size of 100 specimens. This process is repeated a specified number of times. From each run through each binning series the algorithm tabulates species first and last appearances and the total number of range-through species per bin (assumed present
10 if found in bins above and below a gap). The algorithm is modified from a previous version (Chew, 2009a) to discount first and last appearances that occur outside of the stratigraphic range of this dataset to reduce edge effects (Foote, 2000). From each set of repeated runs for each binning series, average first and last appearance and
15 range-through species data are produced per bin, as well as the average number of times each species occurs in each bin. The latter are multiplied by the species' relative abundance in each bin to create standardized proportional relative abundances.

2.3 Paleoecological parameters

To characterize the FC mammal fauna, fundamental concepts in paleoecology are parameterized, including diversity, the interplay between species richness and the evenness of abundance distributions, and turnover, compositional change through evolution and migration. These are complex, multifactorial concepts and diversity in particular
20 is often oversimplified (Magurran, 2004). Here, diversity is represented as variation in the average number of species in assemblages (alpha richness), the differentiation in richness between assemblages (beta richness), the equality of species relative abundances (evenness) and the commonness of one or a few species (dominance). Turnover is characterized by rates of species first and last appearances. Most of the
25 parameters are dependent on sample size and are standardized or calculated from

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ized proportional relative abundances. The first is the well-known Probability of Inter-specific Encounter, PIE, index (Hurlburt, 1971), which is the inverse of Simpson's dominance index standardized for finite collection size.

$$\text{PIE} = 1 - \left[\sum_{i=1}^s n_i(n_i - 1) / N(N - 1) \right], \quad (1)$$

where n_i is the number of specimens of species "i" and N is the total number of specimens in a sample. Though widely employed as a descriptor of the "evenness" of species abundance distributions, PIE is strongly correlated with the proportional relative abundance of the two most common species in these data (mainly equid and hypsodontid species; Spearman's $\rho = -0.49$ to -0.84 , $p = 0.00$). To avoid confusion, it is referred to here as an index of "inverse dominance". The second index is a modification of rank-abundance analysis (Fig. 3), in which species are ranked from most to least abundant and their natural-log transformed relative abundances are plotted against ranks (Magurran, 2004). Rank-abundance curves provide a visual representation of an abundance distribution that is shaped by the majority of the species present in a sample. The slopes of exponential trendlines fitted to the curves are directly comparable between samples (Fig. 3, as in Caron and Jackson, 2008). The fit of the trendlines for these data is high ($R^2 > 0.75$) and the slopes of the trendlines are shallow and negative (< -0.1). The reciprocal of the absolute value of the slopes is used to transform them into an index of "inclusive abundance". The two indices have values between zero and one. Higher values of inverse dominance indicate higher evenness through decreased dominance of the sample by a few taxa. Higher values of inclusive abundance indicate higher evenness through a more equal distribution of the abundances of the majority of the species in the sample. The two indices are summed as an index of evenness.

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2.3.3 Turnover

Rates of species first, F , and last, L , appearances are highly dependent on sample size. Standardized, instantaneous per-taxon rates are calculated for series of consecutive samples of equal time (as in Alroy, 2000; Chew, 2009a; Foote, 2000).

$$F = -\ln[(RS - FA - LA)/(RS - LA)] \quad (2)$$

and

$$L = -\ln[(RS - FA - LA)/(RS - FA)], \quad (3)$$

where FA is the number of first appearances, LA is the number of last appearances and RS is the range-through richness of each sample. Turnover is the sum of these rates.

3 Results

The parameters calculated from the one-meter bins and averaged from the coarser binning series correspond closely, indicating an appropriate level of resolution in the averaged parameters (Fig. 4). Three overlapping peaks occur in both sets of parameters (370–394, 405–417 and 435–448 m), significantly refining previous work at a coarser resolution (20 m thick intervals, ≈ 100 ka), in which a single, 40 m thick interval (370–410 m) of biotic change was identified in this part of the FC section (Chew, 2009a). This analysis demonstrates two distinct events within that 40 m zone, separated by ~ 10 m (~ 60 ka) of pre-event parameter values. The lowest peak is the longest (~ 150 ka) and is distinguished by high turnover driven by many species first appearances (Fig. 4). It contains the distinctive biostratigraphic events conventionally referred to Biohorizon B (Bown et al., 1994b; Chew, 2009a; Schankler, 1980), including the last appearances of the condylarth genera *Haplomyilus* and *Ectocion* and the first appearance of the artiodactyl *Bunophorus* (Table 1). The middle and upper peaks correspond closely (within

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< 10 m, Fig. 4) to the predicted levels of the ETM2 and H2 CIEs, are comparatively short (~ 60–~ 70 ka), and are distinguished by increases in diversity driven by beta richness (Fig. 4). The middle peak was previously thought to be part of Biohorizon B and the upper peak falls within a longer interval of previously recognized, heightened and fluctuant diversity after Biohorizon B (Chew, 2009a; Chew and Oheim, 2013; Schankler, 1980). The middle and upper peaks are referred to here as faunal events B-1 and B-2 given their close association with Biohorizon B. Although faunal event B-1 encompasses more species first and last appearances than Biohorizon B (Table 1), appearance rates (Fig. 4) demonstrate that turnover is less pronounced at the faunal events in relation to higher standing richness and neither event appears to warrant the term “biohorizon”.

Focusing on the averaged parameters from the binned data, the turnover and diversity changes at faunal events B-1 and B-2 are highly significant. Two-sample Kolmogorov–Smirnov tests of the evenness and turnover parameters indicate that the parameter distributions above (and excluding) Biohorizon B vary significantly from their distributions in the ~ 240 ka prior to Biohorizon B (Table S4, K–S p values < 0.000). Mann–Kendal tests indicate significant trends in a number of the parameters, but the absolute value of all trend slopes is < 0.001 (Table S4) and it is unlikely that these trends influence the significance of the differences. Alpha richness is not significantly different after Biohorizon B compared with before, but the peaks in gamma richness at ETM2 and H2 are driven by beta richness (Fig. 4), which is significantly different (Table S4, K–S p = 0.002). Mann–Kendal tests indicate significant and opposing trends from before-to-after Biohorizon B in beta richness, but these also have absolute slope values of ~ 0.01 (Table S4) that are unlikely to greatly influence the significance of the differences in parameter distribution. Apart from inclusive abundance, the averaged parameters are significantly correlated with average carbon isotope value (Spearman’s ρ = 0.35–0.83, p ≤ 0.04) when the McCullough Peaks isotope record (Abels et al., 2012) is aligned with the FC section between faunal events B-1 and B-2.

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4.2 Characteristics of ETM2 and H2

ETM2 and H2 are set in the context of pronounced climatic, environmental and faunal change attributed to the onset of warming at the EECO (Chew, 2009a; Woodburne et al., 2009). Leaf margin analysis of scattered floras (Wing et al., 1991) and isotope ratios of paleosol hematites (Bao et al., 1999; Wing et al., 2000) indicate that MAT rose from a low of ~ 11 to $\sim 16^\circ\text{C}$ around the time of H2. Although the rate of this temperature increase is unknown, there is no evidence of a CIE in the McCullough Peaks isotope sections of Abels et al. (2012) to suggest a hyperthermal mechanism. Coincident lithological changes, such as increased sediment accumulation rate and common channel sandstones and mud-filled scours, may reflect tectonic activity on the southern edge of the basin (Bown and Kraus, 1993) and/or marked increases in temperature, precipitation and/or seasonality of precipitation (as in Foreman, 2014; Foreman et al., 2012). At the same time, floras began to transition to subtropical and tropical species (Wilf, 2000; Wing et al., 2000), indicating the possible development of a canopy that would account for coincident changes in soil moisture (Bown and Kraus, 1993) and temperature (Snell et al., 2013). Biohorizon B, the largest faunal event in the FC record after the PETM, coincides with the onset of this change and marks a major turning point in faunal diversity that has been correlated with jumps in generic alpha richness and turnover across North America (Chew and Oheim, 2013; Woodburne et al., 2009). In the FC record, Biohorizon B is distinguished by a burst of new species that were not immigrants, heralding long-term increases in alpha richness and evenness (Fig. 4, Chew and Oheim, 2013). There is also a proliferation of body sizes at this time, although abundance shifts tend to favor relatively smaller species (Fig. 5, Bown et al., 1994a). These results support the interpretation of Woodburne et al. (2009) that there was major evolutionary innovation in the lead-up to the EECO.

Faunal events B-1 and B-2 are distinct intervals of change set within the context of Biohorizon B. Abundance, evenness, dominance and body size trends were initiated at, or before, Biohorizon B (e.g., some long-term increases in size and the relative

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abundance of dominant species, see Chew, 2009a, b; Chew and Oheim, 2013) and carried through faunal events B-1 and B-2. However, faunal events B-1 and B-2 are unique in their higher proportions of species loss, which nearly equal the proportions of new species at each event (Table 2). Nearly half of the turnover at faunal events B-1 and B-2 occurs within lineages, with correspondingly small proportions ($\leq 6\%$) of generic events. In contrast, and in spite of their widely different mechanisms, both the PETM and Biohorizon B are characterized by bursts of new species, including many new genera, and comparatively few losses. The PETM was a transient episode of ecological change, including immigration and body size adjustment, whereas Biohorizon B involved marked evolutionary change (Woodburne et al., 2009). Both events were initiated by significant climatic and environmental disturbance that ended ≥ 1 ma periods of relatively static conditions; warm and moist before the PETM and cool and dry before Biohorizon B (Kraus et al., 2013; Kraus and Riggins, 2007; Snell et al., 2013; Wilf, 2000; Wing et al., 2000). In contrast, the rapid warming of ETM2 and H2 occurred soon after the onset of the climatic and environmental disturbance related to the EECO and Biohorizon B. Faunal structure may have been comparatively unstable as communities were adjusting to changing conditions, perhaps leaving more species vulnerable to further change. The turnover within lineages at faunal events B-1 and B-2 suggests that more species were lost through evolutionary transitions at ETM2 and H2.

Faunal events B-1 and B-2 are also unique in their high proportions of beta richness (Table 2). Beta richness reflects heterogeneity in species incidence patterns (Collins and Simberloff, 2009; Colwell et al., 2004; Gotelli and Colwell, 2001) that may occur through specialization for dispersed microhabitats and/or heightened ecological interactions that prompt species to seek out or avoid each other (e.g., competition, predation). Previous analysis identified a rise in beta richness in the ~ 2 ma after Biohorizon B to which both mechanisms may have contributed (Fig. 3, Chew and Oheim, 2013; Woodburne et al., 2009). A coincident long-term increase in alpha richness (Fig. 3, Chew and Oheim, 2013; Woodburne et al., 2009) implies that there were more species packed into the available space of the landscape, increasing the potential for ecologi-

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cal interactions. Increased habitat complexity as subtropical and tropical floras became more established implies more opportunities for microhabitat specialization (Chew and Oheim, 2013; Wing et al., 2000; Woodburne et al., 2009). The proportions of new species and alpha richness are not particularly high at faunal events B-1 and B-2, suggesting that the temporary peaks in beta richness at ETM2 and H2 are probably not related to an acceleration of species packing and heightened ecological interactions. Instead, they may represent increased microhabitat specialization in response to transient increases floral complexity, perhaps heightened by the more seasonal, possibly more intense and episodic, precipitation suggested by transient lithological changes (Abels et al., 2012).

4.3 Implications for modern anthropogenic change

Aspects of faunal change in the Bighorn Basin record of the early Eocene are relevant for predicting modern anthropogenic effects. The PETM, ETM2 and H2 raised MAT in the Bighorn Basin to nearly the same absolute value ($\sim 20^{\circ}\text{C}$ given the proportionality of CIE and temperature, and long-term temperature trends at ETM2 and H2, Abels et al., 2012; Fricke and Wing, 2004; Wing et al., 2000). Extrapolating from current and projected regional rates of change, Wyoming's MAT ($\sim 8^{\circ}\text{C}$ according to US climate data) will approach this value in ~ 300 years even if emissions are stabilized before then, given the time scale of climate processes and feedbacks (Pachauri and Reisinger, 2007). This rate of warming far exceeds those of the past, implying that species-specific, rapid ecological adjustments (e.g., geographic range and body size changes) will probably occur in the near future as they did at the PETM, the interval with the highest rate of warming. River runoff and water availability are expected to decrease in the dry areas of western North America with ongoing climate change but precipitation and the frequency of heavy precipitation events are expected to increase across the rest of the continent with the contraction of the Greenland ice sheet (Pachauri and Reisinger, 2007). The latter changes are more consistent with the Bighorn Basin record of the beginning of the EECO. In addition, human activities such as urbanization, habi-

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5 tat degradation and fragmentation have already stressed many of the Earth's terrestrial faunas. Such stresses may be considered analogous to the faunal changes underway in the Bighorn Basin when ETM2 and H2 occurred. This suggests that increased heterogeneity in species incidence and heightened species vulnerability and loss may be expected across most of North America in the near future as occurred at ETM2 and H2 in the remote past.

5 Summary

10 This analysis highlights the importance of analytical resolution and the use of multiple parameters in the paleoecological analysis of whole communities. Two previously unsuspected episodes of faunal change most likely related to the ETM2 and H2 hyperthermals are identified. Comparison of diverse and complementary lines of evidence summarizing different functional and ecological groups allows the differentiation of superficially similar faunal response to these hyperthermals and the PETM. Faunal change at the PETM is characterized by pronounced turnover fueled by immigration and widespread decreases in body size. These changes are probably related to the combination of rapid warming and drying at the PETM. In contrast, faunal change at ETM2 and H2 is less extreme, does not include immigration, and involves a proliferation of body sizes, although abundance shifts tend to favor smaller sizes. ETM2 and H2 are set in the context of pronounced climatic, environmental and faunal change related to the onset of the EECO. Faunal response at ETM2 and H2 is distinctive in its high proportion of species losses potentially related to heightened species vulnerability in response to the changes already underway at the beginning of the EECO. Faunal response at ETM2 and H2 is also distinctive in high proportions of beta richness, suggestive of increased geographic dispersal related to transient increases in habitat (floral) complexity and/or precipitation or seasonality of precipitation. These results suggest that rapid ecological changes, increased heterogeneity in species incidence,

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and heightened species vulnerability and loss may be expected across most of North America in the near future in response to anthropogenically-driven climate change.

**The Supplement related to this article is available online at
doi:10.5194/cpd-11-1371-2015-supplement.**

5 *Acknowledgements.* This project was supported by the National Science Foundation Sedimentary Geology and Paleobiology program grants 0739718 and 0616430, and in part by the National Geographic Society Waitt Program grant W315-14. The author gratefully acknowledges the substantial efforts of K. Rose and students and volunteers who have collected, curated and catalogued the specimens on which the research is based. The collections are
10 housed at the Smithsonian National Museum of Natural History. Rarefaction software was downloaded from the University of Georgia Stratigraphy Lab webpage of S. Holland (<http://www.uga.edu/~strata/software/Software.html>) and from the University of Connecticut Ecology and Evolutionary Biology webpage of R. Colwell (<http://viceroy.eeb.uconn.edu/EstimateS/>). R. Chew wrote the algorithm to standardize species appearance data.

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Table 1. First and last appearances of species at Biohorizons B and faunal events B-1 and B-2. Species connected by dotted lines represent segments of individual lineages. Taxa in parentheses did not have first or last appearances within the significant intervals but are probably related to the event. Bold-faced taxa indicate the appearance or disappearance of a genus.

Biohorizon B	
Disappearances – 379–392 m	Appearances – 370–394 m
<i>Ectocion</i> , <i>Haplomylus</i> , <i>Plagiomene</i>	<i>Ambloctonus</i> , <i>Anemorhysis pattersoni</i> , <i>Bunophorus</i> <i>grangeri</i> , <i>Bunophorus etsagicus</i> , <i>Cantius</i> new sp., <i>Chriacus gallinae</i> , <i>Copelemur</i> , <i>Homogalax</i> sp., <i>Hyopsodus minor</i> , <i>Minnipus</i> , <i>Palaeictops</i> , <i>Systemodon</i> , <i>Vulpavus</i> <i>australis</i>
<i>Cantius trigonodus</i> – <i>Hyopsodus wortmani</i> – <i>Prototomus martis</i> – <i>Prototomus</i> sp. –	<i>Cantius abditus</i> <i>Hyopsodus latidens</i> <i>Tritemnodon</i> <i>gigantea</i> <i>Prototomus secundarius</i>
Faunal event B-1	
Disappearances – 409–417 m	Appearances – 405–417 m
<i>Cardioloophus</i> , <i>Dissacus</i> sp., <i>Miacis exiguus</i> , <i>Microparamys scopaiodon</i> , <i>Pachyaena ossifraga</i> , <i>Pseudotetonius</i> , <i>Viverravus politis</i> , <i>Viverravus rosei</i> <i>Apheliscus insidiosus</i> – <i>Arenahippus pernix</i> – <i>Diacodexis metsiacus</i> – <i>Didymictis protenus</i> – (<i>Galecyon mordax</i> 357 m) – (<i>Thryptacodon antiquus</i> 360 m) –	<i>Anacodon</i> , <i>Apatemys rodens</i> , <i>Hyopsodus powellianus</i> , <i>Oxyaena forcipata</i> , <i>Phenacodus</i> sp., <i>Prolimnocyon</i> sp., <i>Steinius</i> , <i>Uintacyon</i> new sp. 1, <i>Xenicohippus grangeri</i> (<i>Apheliscus</i> sp. 423 m) <i>Eohippus</i> <i>angustidens</i> <i>Diacodexis secans</i> <i>Didymictis lysitensis</i> <i>Galecyon</i> sp. <i>Thryptacodon loisi</i>
Faunal event B-2	
Disappearances – 435–448 m	Appearances – 438–442 m
<i>Oxyaena intermedia</i> , <i>Prolimnocyon</i> sp., <i>Uintacyon rudis</i> <i>Esthonyx spatularius</i> – <i>Arenahippus</i> <i>aemulor</i> – <i>Prolimnocyon atavus</i> –	<i>Absarokius abbotti</i> , <i>Hexacodus</i> , <i>Phenacolemur willwoodensis</i> <i>Esthonyx</i> sp. <i>Protorohippus</i> <i>ventricolum</i> <i>Prolimnocyon antiquus</i>

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Table 2. Comparison of faunal change at the PETM and faunal events B-1 and B-2. Summary paleoecological parameter values are calculated for the entire PETM sample (Rose et al., 2012) and the entire faunal event B-1 and B-2 samples. Proportions of taxa lost at the PETM are based on the Clarkforkian (late Paleocene) Bighorn Basin mammal fauna described in Rose (1981). Proportions of change in body size at the PETM are from Secord et al. (2012). Proportions of change in body size at faunal events B-1 and B-2 are based on the total number of taxa for which body size can be assessed.

Parameter	PETM	B-1	B-2	Biohorizon B
Diversity				
Proportion of alpha richness	$\frac{29}{39}$	$\frac{24}{39}$	$\frac{23}{39}$	$\frac{26}{34}$
Proportion of beta richness	$\frac{10}{39}$	$\frac{15}{39}$	$\frac{16}{39}$	$\frac{8}{34}$
Proportion of evenness (inclusive abundance)	$\frac{0.92}{1.84}$	$\frac{0.92}{1.8}$	$\frac{0.91}{1.78}$	$\frac{0.92}{1.78}$
Proportion of dominance (inverse dominance)	$\frac{0.92}{1.84}$	$\frac{0.88}{1.8}$	$\frac{0.87}{1.78}$	$\frac{0.86}{1.87}$
Turnover				
Proportion of new species	$\frac{46}{58}$	$\frac{14}{78}$	$\frac{6}{77}$	$\frac{13}{70}$
Proportion of new genera	$\frac{20}{42}$	$\frac{3}{53}$	$\frac{2}{53}$	$\frac{8}{51}$
Proportion of species lost	$\frac{18}{39}$	$\frac{12}{78}$	$\frac{6}{77}$	$\frac{70}{70}$
Proportion of genera lost	$\frac{7}{39}$	$\frac{2}{53}$	$\frac{1}{53}$	$\frac{3}{51}$
Body size				
Proportion of genera in which body size decreases	$\frac{10}{26}$	$\frac{6}{35}$	$\frac{2}{35}$	$\frac{6}{32}$
Proportion of genera in which body size increases	$\frac{0}{26}$	$\frac{7}{35}$	$\frac{9}{35}$	$\frac{4}{32}$

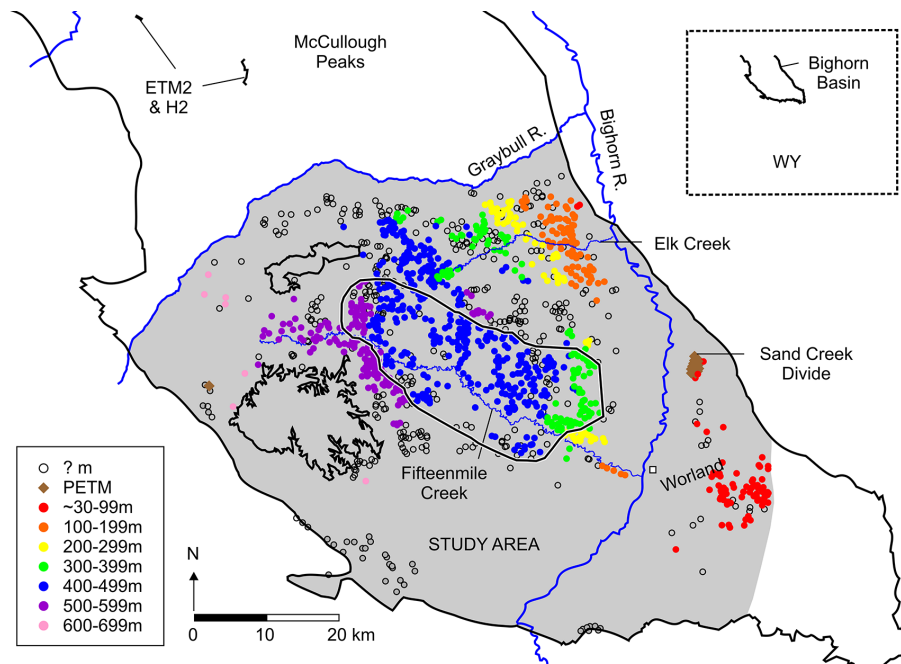


Figure 1. Fossil localities in the south-central part of the Bighorn Basin. Colored localities have been tied by meter level to the Fifteenmile Creek composite stratigraphic section of Bown et al. (1994b). Circled localities span the ETM2 and H2 hyperthermal levels (290–510 m) in the Fifteenmile Creek section. Isotope sections recording the ETM2 and H2 CIEs in the McCullough Peaks are from Abels et al. (2012).

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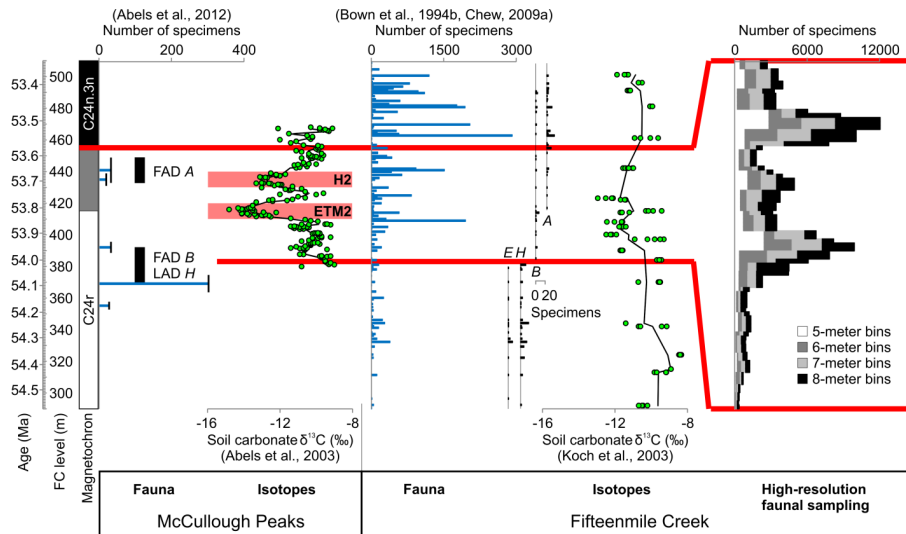


Figure 2. Available fossil samples and carbon isotope data from the northern and south-central parts of the Bighorn Basin. Absolute ages are based on Tsukui and Clyde (2012). The McCullough Peaks sections (Abels et al., 2012) are tied to the Fifteenmile Creek (FC) section (Bown et al., 1994b) between two tie points indicated by thick red lines: the first (FAD) and last (LAD) appearances of distinctive taxa and the C24r-C24n geomagnetic shift. Distinctive taxa include *Bunophorus etsagicus* (*B*), *Haplomylus speirianus* (*H*), *Ectocion osbornianus* (*E*) and *Anacodon ursidens* (*A*). FC mammal fossils are binned into overlapping intervals for high-resolution paleoecological analysis.

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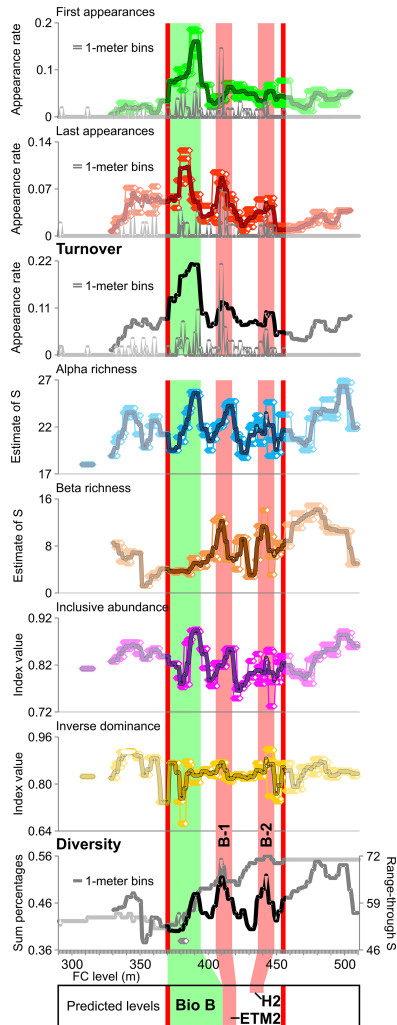
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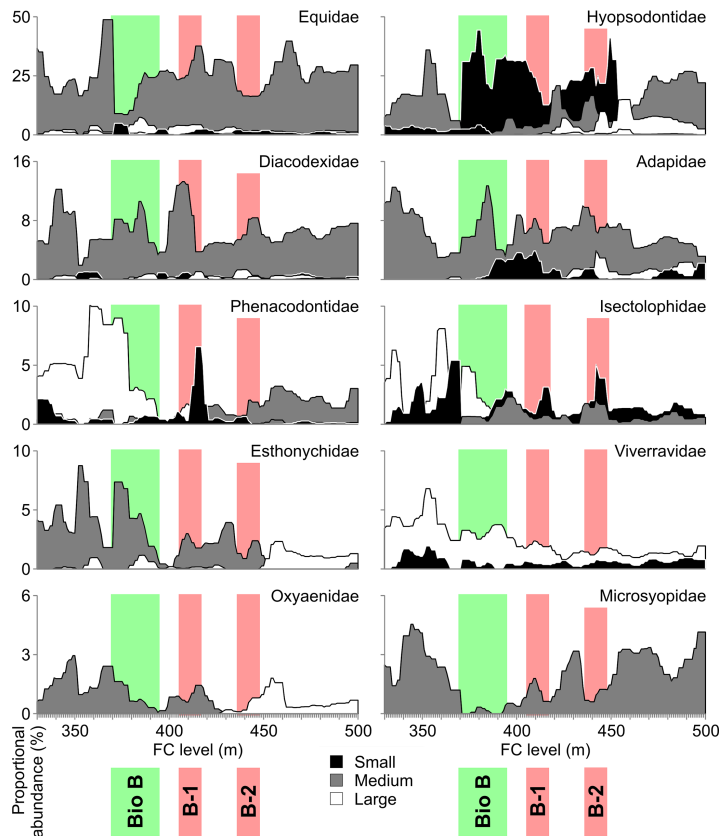


Figure 5. Changes in proportional relative abundance of species and comparative body sizes in the south-central Bighorn Basin fossil mammal fauna.

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