

Interactive comment on “Mammal faunal response to the Paleogene hyperthermals ETM2 and H2” by A. E. Chew

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Received and published: 11 June 2015

I wish to preface this with an apology that I was unable to finish and post this response sooner. Clyde's review required extensive consideration and came at a busy time.

Clyde presents two fundamental criticisms of this project and other more detailed criticisms that are addressed in the following. The two main criticisms pertain to the precision of (1) the stratigraphic framework that ties together the fossil localities of the Fifteenmile Creek (FC) in the south-central Bighorn Basin and (2) the stratigraphic correlations that tie the FC fossil framework to the isotope records of the McCullough Peaks. Clyde's position is that neither is precise enough to support the hypothesis of this paper. With the first concern I disagree for the reasons discussed below. With the second concern I agree in that I also believe it is impossible to precisely correlate

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the isotope and fossil sections given available information. It was a mistake to provide a discussion and “rough correlation” of common biostratigraphic and geomagnetic events in both areas, my misguided purpose for which was to demonstrate that the CIEs in the McCullough Peaks isotope records and the faunal events described herein occur in common, limited stretches of stratigraphic section (<140 m stratigraphic thickness compared with total section thicknesses >700-3000 m) that document a brief (~450 ka according to Abels et al., 2012) interval of the early Eocene in the Bighorn Basin. Clyde does not dispute this and I believe the fundamental hypothesis of this paper remains valid but clearly needs to be restated in a way that avoids the misapprehension of it hinging on a precise correlation. To be perfectly clear, I have removed all discussion of, and reference to, the rough correlation I originally attempted to make as outlined below. I have also explicitly restated my hypothesis along the lines of Clyde and colleagues' work in the McCullough Peaks (Abels et al., 2012), on which this paper is largely based. Abels et al. (2012) hypothesized that the McCullough Peaks CIEs are related to ETM2 and H2 based on their “proximity” to the C24r-C24n.3n magnetic polarity reversal and the Wasatchian 4-Wasatchian 5 biozone boundary, and the pattern of the excursions in one of their two isotope sections (Abels et al., 2012: p. 1). The hypothesis of this paper can be similarly stated: two faunal events described in the FC section are hypothesized to be related to the McCullough Peaks isotope excursions based on the proximity of the C24r-C24n.3n magnetic polarity reversal and the Wasatchian 4-Wasatchian 5 biozone boundary, and the pattern of faunal change within each event. Clyde and colleagues compare isotope records, so perhaps it could be argued that the precision of the evidence required for a convincing argument is less for their hypothesis than for the one presented in this paper. However, their comparison is of a terrestrial record with marine records, for which there is no particular expectation of congruence. This project compares similar records from within the same sedimentary basin, separated by ~60 km distance. Within this brief interval, there were two pronounced CIEs interpreted to represent significant climatic and environmental change AND two pronounced, rapid, and appropriately scaled (in terms of section thickness)

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events of significant faunal change. The hypothesis that they are related is more reasonable and parsimonious than the alternative, which is that the faunas were immune to the climatic and environmental change indicated by the isotope excursions, instead experiencing within this brief interval two other, unassociated episodes of significant change related to some as-yet unknown external perturbations or to intrinsic controls. Clyde suggests that this hypothesis is not sufficiently supported without directly-related isotope data. I argue that directly-related isotope data would constitute a critical test of the hypothesis presented herein, but such data are not currently available. In the following, I address Clyde's major and lesser concerns in detail.

1) Major concern: stratigraphic framework of fossils. In his review, Clyde writes "The Fifteenmile Creek *composite* section (~700 meters thick) used in this study ties together some 410 fossil localities in an area that is roughly 30 km x 40 km by correlating some 44 different local sections (Bown et al., 1994)." This statement is inaccurate. The entire Fifteenmile Creek (FC) composite stratigraphic section is ~700 meters thick and was created by Bown et al. (1994) from 44 different local sections measured over an area ~3000 km². There are more than 1000 localities tied to the composite section. The 410 localities included in this analysis come from a subset of the FC section (290-510m) and are found along the FC (i.e., excluding the Elk Creek area, which is known to be more poorly resolved) in an area that is roughly 40 km by 15 km, although localities and sections only occupy ~300 km² of this area. Here, the section is based on 11 major local sections (PD, RWC, RS, RSA, PSB, SD, BW, NF, NFE, S, SF, TM, see Bown et al., 1994, Table 7), and several additional smaller sections that in many cases connect the longer ones. The endpoints of each local section are considerably less than 0.5 km apart in their sequence along the FC, with the exception of a distance of ~5 km between the RSA and SD sections.

Clyde continues "Although this [the south-central Bighorn Basin] is certainly one of the most densely sampled regions of the world for fossil mammals, the stratigraphic uncertainty in the correlations between local sections and fossil localities must be on

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the order of at least +/- 10 meters (and probably more) given the difficulty of tracing beds through the low-lying outcrops in this area and the prevalence of "cut and fill" channel structures (Bown et al., 1994). This study, however, assigns a single meter level to each fossil locality with no error." In fact, in Bown et al. (1994), localities were tied by meter level to the FC stratigraphic section with no error reported. Bown and colleagues' method of sampling and their stratigraphic framework were designed to be resolved to meter-level, as described in their monograph in detail (1994: p. 9-15, emphasis mine): "In 1974, it was discovered that a suite of geographic localities in the Sand Creek-No Water Creek area of Willwood badlands (pl. 2) yielded abundant vertebrate fossils from a single, exceptionally continuous bed. . . Further collecting in that area in 1975 demonstrated that the vast majority of Willwood fossils there could be precisely related to the beds that produced them. . . Shortly thereafter, other exceptionally productive, stratigraphically explicit fossil occurrences were also discovered in Willwood rocks exposed in the drainages of Elk and Fifteenmile Creeks. . . Recent collecting operations in the Fifteenmile Creek drainage. . . were undertaken, following the 1974 season, with the specific goal of collecting large samples of Willwood vertebrates with tight stratigraphic controls tied to fossil provenances in paleosols. Field collecting began to be consciously restricted to specific stratigraphic intervals that could be related to fossil provenances, and these are almost invariably in paleosols. . . This technique has afforded greater stratigraphic resolution than was possible in the study of Schankler (1980) [in the Elk Creek], in his correlation of the strictly geographic YPM localities (nearest 1.0 m instead of 10.0 m), for which bed provenance was unknown and commonly could not be reconstructed." It is apparent that great care was undertaken in collecting efforts along the FC from 1975-1994 (and thereafter) to ensure tight stratigraphic control and that the authors believed they were able to achieve meter-level stratigraphic resolution. Given that one meter of section is approximately half the height of the average stratigrapher, this does not seem to be a particularly extraordinary or unreasonable achievement. The FC composite stratigraphic section is the culmination of 20 years of work by a skilled stratigrapher (Bown) and has been widely accepted

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and in general use for ~20 years.

In my own experience in the central and southern part of the Bighorn Basin, I have never had any reason to doubt the FC stratigraphic section; the outcrops are relatively flat and stacked, and can be viewed for miles in any direction from any point of elevation. However, I am not a stratigrapher and do not feel qualified to answer criticisms directed at work that is not mine. I asked Bown, the primary author of the FC section, to respond to Clyde's statement "...the stratigraphic uncertainty in the correlations between local sections and fossil localities must be on the order of at least +/- 10 meters (and probably more) given the difficulty of tracing beds through the low-lying outcrops in this area and the prevalence of "cut and fill" channel structures (Bown et al., 1994)". By email, he responded "No, this is inaccurate. If you know where to go, there is almost no covered area in any of the sections, but some of them required a [lot] of walking". In clarification in a subsequent email, he wrote "There is no difficulty in relating the fossil localities to one another by meter levels, but the problem of the scours makes it difficult to relate events (originations, disappearances) in time—but that is a problem with both the Antelope Creek/Elk Creek and the Fifteenmile Creek sections..." I would add that it is also a problem in the McCullough Peaks, where Clyde and colleagues note (Abels et al., 2012: p 1) that the ETM2-H2 interval "is characterized by increased development of channel sandstone complexes and large mud-filled scours." These apparently do not interfere with correlations between localities and sections in the FC any more than they do in the McCullough Peaks. Bown concludes "...there is no error involved at all". While there are undoubtedly occasional errors associated with individual localities, Bown is strongly convinced that there is no widespread, systematic error in the assessment of the stratigraphic position of localities within the FC section on the order of 10 meters or more. There have been no subsequent studies to test the integrity of the FC section, but nor does Clyde provide any specific evidence to support that there is systematic error in the FC section.

Clyde's argument appears to rest on the premise that the FC section is too big and

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complex (i.e., encompasses a large area and is based on too many local sections) to be resolved to meter level without large errors. I do not believe either size or complexity is a particular barrier to resolution; the FC composite stratigraphic section is the culmination of 20 years of work by a skilled stratigrapher. The local sections are comprehensive, closely spaced and cover all of the area in question. Although Clyde led a group that measured paleomagnetic sections in other parts of the south-central Bighorn Basin (at Sand, Antelope, Dorsey and Elk creeks), he has not to my knowledge participated in paleontological fieldwork here or along the FC. Clyde's criticism appears to be based on his extensive experience in the McCullough Peaks, where structure is undoubtedly different from that in the south-central part of the basin. Clyde describes fossil localities in the McCullough Peaks as "encompass[ing] approximately 10 meters of vertical section" (Clyde, 2001: p. 113) and explains the difficulty in correlating neighboring sections there in an email to me describing his recent, unpublished work on the Gilmore Hill section: "the data that show the new correlation are part of Abby's Ph.D. thesis and will be included in a paper she is writing up this summer. To figure this out, we had to sample multiple parallel sections along the MP escarpment and trace beds by walking them out...It took us many summers of field work just to get the correlations right across the escarpment where we can walk between the various sites." It is undoubtedly the case that the position and correlation of localities and sections in the McCullough Peaks are more complex than in the central and southern part of the basin.

On one further point, Clyde writes "ETM2 and H2 where they have actually been identified by isotopic data in the northern part of the basin are each only ~20 meters thick (and would likely be less than that in the southern part of the basin where sediment accumulation rates are lower)". This is in fact the case; faunal events B-1 and B-2 are 12-13 meters thick. This coincides very closely with expectation, given that the McCullough Peaks section is roughly twice as thick as the FC section in the upper levels, as described by Clyde (2001).

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2) Major concern: precise correlation between the isotope and fossil stratigraphic sections. In his review, Clyde writes “Chew chooses to tie these two frameworks together using the C24r-C24n geomagnetic reversal and the Biohorizon B faunal event. However, there is no discussion of the large uncertainty associated with the correlation of these tie points except to say that “these are rough predictions” (line 14, p. 1376). Can “rough predictions” provide the kind of precise stratigraphic correlation necessary to support the conclusions (and title) of the paper? Unfortunately, I don’t think so.” I agree that it is impossible to precisely correlate the McCullough Peaks isotope sections with the FC section given available information and as previously stated it was not my intention. To be absolutely clear on this, I have removed all discussion of, and reference to, the rough correlation I originally attempted to make as follows. I have reworded the abstract (p. 1372 lines 13-18) to reflect the hypothesis as restated (borrowing the phrasing of Abels et al., 2012) above. I have also modified Figures 2 and 4 to explicitly separate the McCullough Peaks and FC records and remove all visual reference to rough correlation and prediction.

In the paragraph in the Methods section (p. 1375-1376) that discusses the FC and McCullough Peaks sections, I have deleted the second half of the sentence on p. 1375 lines 25-26. There follows an existing, detailed discussion of the uncertainty of the stratigraphic position of the biostratigraphic events in the McCullough Peaks (p. 1376 lines 3-8) and to the preceding lines 1-3 (p. 1376) I have added that the CIEs are found “in 60-70 meter thick intervals of mixed geomagnetic polarity between the C24 reversed and C24 normal geomagnetic zones”. I have replaced lines 8-11 (p. 1376) with: “The C24r-C24n geomagnetic shift and the nearly simultaneous Biohorizon B biostratigraphic events are also known in the FC section. The C24r-C24n geomagnetic shift occurs at ~455 m in two local paleomagnetic sections measured through the Dorsey and Elk creeks (Clyde et al., 2007). The latter is associated with a 30 meter zone of mixed geomagnetic polarity. The last appearance of *Haplomylus* (and also the condylarth *Ectocion osbornianus* originally described by Schankler (1980) as part of the suite of biostratigraphic events at the beginning of Biohorizon B) and the first

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appearance of *Bunophorus* occur at ~381 m (this project, Fig. 2) in the FC section.” Finally, in this paragraph, I have deleted lines 11-17 (p. 1376) and inserted the following: “The uncertainties in the stratigraphic position of the C24r-C24n geomagnetic shift and the biostratigraphic events at the beginning of Biohorizon B in the McCullough Peaks, as well as pronounced variation in sediment accumulation rate around Biohorizon B in the FC (Bown and Kraus, 1993), preclude precise correlation between the McCullough Peaks isotope sections and the FC fossil record. However, the common occurrence of the C24r-C24n geomagnetic shift and the biostratigraphic events at the beginning of Biohorizon B in both areas indicates that the ~85 meter stretch of the FC section described here documents the interval of Bighorn Basin time in which the CIEs of the McCullough Peaks occur (Fig. 2).”

Finally, in the first paragraph of the Results section, I have deleted the middle part of the sentence on line 24, p. 1381 and line 1 p. 1382. In the first paragraph of the Discussion section, I have reworded lines 25-27 of p. 1383 and line 1 of p. 1384 to read: “There are indications that faunal events B-1 and B-2 are related to the CIEs identified in the McCullough Peaks and thus represent response to the ETM2 and H2 hyperthermals. Faunal events B-1 and B-2 occur above the distinctive biostratigraphic events of Biohorizon B and in close proximity to the C24r-C24n geomagnetic shift, as do the CIEs in the McCullough Peaks (Abels et al., 2012).” At the end of this paragraph in the Discussion section, I modify the final lines (11-12 of p. 1384) to read: “For discussion purposes, it is hypothesized here that there is a relationship between the McCullough Peaks CIEs, ETM2 and H2, and faunal events B-1 and B-2. A critical test of this hypothesis requires directly related isotope data, which are presently unavailable.”

Clyde’s subsequent criticisms of the “precise” stratigraphic correlation between the FC and McCullough Peaks sections have been essentially addressed by the revisions just described. I will nevertheless respond to each criticism individually. Clyde writes “More recent work in this area has shown clearly that the event labeled H2 in the Gilmore Hill section in Abels et al., 2012 is actually ETM2 (this was presented at the Ferrara

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2014 CBEP meeting and is the basis for D'Ambrosia et al., 2014 and Snell et al., 2014 and the details will be part of an upcoming paper by D'Ambrosia based on her Ph.D. thesis work). This pushes the position of Biohorizon B down ~25 meters relative to the hyperthermals and thus fundamentally alters the correlation of the faunal turnover events to the isotopic anomalies (the faunal peaks identified by Chew will now fall below the isotope peaks by ~25 meters)." I am happy to learn about this unpublished revision of the Gilmore Hill section, information which has evidently been shared with Clyde's student and colleagues but of which I was not aware until now. (Clyde states that this was presented at CBEP but it is not described in either D'Ambrosia et al., 2014, or Snell et al., 2014, which present other research. I attended both talks and took detailed notes, and spoke with Clyde during the meeting, but missed this important information). While certainly relevant to this paper, it does not alter the fundamental relationship of the isotope excursions and faunal events B-1 and B-2 to the biostratigraphic events at the beginning of Biohorizon B. That is, those biostratigraphic events still occur below ETM2 and faunal event B-1. If the biostratigraphic events are now thought to occur ~25 meters lower than the ETM2 isotope excursion in the McCullough Peaks, this translates to a more modest 10-13 meter difference in the FC section, given the differences in section thickness (Clyde, 2001). The additional ~25 meters of thickness between the biostratigraphic events and the ETM2 isotope excursion in the Gilmore Hill section are still less than the ~35 meters of uncertainty associated with the biostratigraphic events in that section.

Clyde continues "These tie points also have uncertainties in the Fifteen Mile Creek section (unknown for Biohorizon B because it is assigned a single meter level despite previous arguments that it lasted ~300 ky [Chew 2009] and ~13 meters for the C24r-24n reversal [Clyde et al., 2007])." Clyde's concern regarding my assignment of a single meter level to "Biohorizon B" in the FC section stems from a typo. Lines 3-5 on p. 1376 are as follows: "Biostratigraphic events at the beginning of Biohorizon B are also loosely tied to the McCullough Peaks isotope sections, including the last appearance of the condylarth *Haplomylus speirianus* and the first appearance of the

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artiodactyl *Bunophorus etsagicus*." I then refer to the "nearly simultaneous Biohorizon B stratigraphic events" in line 9. This should read biostratigraphic events. I hope it then becomes clear that the 381-meter level is not assigned to "Biohorizon B", which I myself have described previously and in this paper as an event spanning 25-40 meters of stratigraphic thickness, but rather to the level at which *Haplomylus* (and *Ectocion*) disappear and *Bunophorus* appears. This does happen nearly simultaneously in the FC section (clearly illustrated in Figure 2) and is documented in the supplementary information. In addition, Clyde describes a ~13 meter error for the C24r-24n reversal in the FC section, by which I assume he refers to the 30 meter zone of intermediate geomagnetic polarity described in the Elk Creek Rim local paleomagnetic section of Clyde et al. (2007: p. 854). The C24r-24n reversal was assigned to the approximate middle of this zone in the Elk Creek Rim local section to coincide with the level of the reversal in the Dorsey Creek local paleomagnetic section. In the Dorsey Creek local paleomagnetic section, the C24r-24n reversal occurs at "the ~200 m level" with no error described apart from two cryptochrons ~80 m and ~160 m below this level (2007: p. 854). The ~200 m level of the Dorsey Creek local paleomagnetic section corresponds with 455 m in the FC section, whereas there is confusion over the correlation of the Elk Creek and FC sections (Clyde et al., 2007: p. 856-857), which is why no Elk Creek localities are included in this analysis. I chose to describe the C24r-24n reversal as occurring at 455 m (without reported error) in the FC section based on the local paleomagnetic section (Dorsey Creek) that can be directly correlated with the FC section, and to maintain the separation of the Elk and Fifteenmile creeks as clearly advocated in Clyde et al. (2007). However, as Clyde here suggests that this zone should be interpreted as error in the level of the C24r-24n reversal in the FC section, I have modified Figure 2 accordingly.

Clyde concludes that "The easiest and most obvious solution to this problem is to isotopically sample the Fifteenmile Creek localities from which the fossils come so an isotope record showing the precise position of ETM2 and H2 is directly tied to the fossils being analyzed." As Clyde is aware, this is a research priority for which I and

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colleagues have been trying to obtain funding for several years. When we are able to isotopically sample the FC localities, we plan to use the directly related isotope data to test the hypothesis presented herein.

3) Less significant concerns: use of the term EECO. In his review, Clyde writes “In several places in the paper, Chew suggests that ETM2 and H2 occur during the beginning of the EECO (e.g. line 9 in Abstract, p. 1372) but these events (which are older than 53.5 Ma, Zachos et al. 2010) occur before the EECO (which is 53-51 according to Chew – line 10, p. 1373 - and are considered even younger by many others). This misstatement is repeated many times in the paper and I suggest rewording to align with Line 8 in Introduction (p. 1373) that says “in the approach to the Early Eocene Climate Optimum (EECO)”.” These are not “misstatements”. They are entirely consistent with my discussion of the EECO in the Introduction, p. 1374, lines 23-26, and in more detail in the Discussion section, p. 1386. Zachos et al. (2001: p. 687) first described the EECO as the peak of “a pronounced warming trend” at 52-50 Ma. Zachos et al. subsequently described the peak as lasting from 53-51 Ma (2008: p. 279), which has led to some confusion over which definition to use (e.g., Eberle and Greenwood, 2012; Hofmann et al., 2012; Hyland et al., 2013; Hyland and Sheldon, 2013; Krause et al., 2010; Pross et al., 2012; Smith et al., 2012; Smith et al., 2010b; Wilf et al., 2003; Woodburne et al., 2009a; Woodburne et al., 2009b). I chose the more recent Zachos et al. definition of 53-51 Ma (and attributed this correctly on line 10, p. 1373) for several reasons, the most compelling of which was Clyde’s own recent recalibration of the early to middle Eocene part of the GPTM based on 29 ash-fall tuffs from five Laramide foreland basins (including the Bighorn Basin) in western North America (Tsukui and Clyde, 2012). In this convincing work, Tsukui and Clyde conclude (2012: “Implications of the new calibration”) that the EECO “is ~2.2 m.y. in duration from 52.9 to 50.7 Ma. This is ~1 m.y. longer than has been previously proposed.” I am aware of evidence from terrestrial records suggesting that the EECO was older (e.g., Pross et al., 2012). However, I prefer the more recent Zachos et al. (2008) assignment of the 53 Ma start date for the EECO Ma as it aligns with Tsukui and Clyde (2012) and

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with a volcanic ash layer in the south-central part of the Bighorn Basin, which has been dated at 52.9 ± 0.19 Ma (Smith et al., 2010a; Smith et al., 2004) and which lies ~40 m above the beginning of Wa-7 (latest Wasatchian North American Land Mammal Age biozone). The major faunal changes of the Wa-7 biozone have long been recognized (Stucky, 1990) and Wa-7 is generally included in the faunal change at the beginning of the EECO (e.g., Hyland and Sheldon, 2013; Tsukui and Clyde, 2012; Woodburne et al., 2009a; Woodburne et al., 2009b).

In marine records, the pronounced warming trend that led to the peak temperatures of the EECO warming occurred “from the mid-Paleocene (59 Ma) to early Eocene (52 Ma)” (Zachos et al., 2001: p. 687). In the Bighorn Basin, this warming trend was interrupted by a ~2 my period of cool, static temperature (Bao et al., 1999; Wing et al., 2000). Pronounced warming resulting in the EECO began as this cool period came to an end at or around Biohorizon B and was continuous through the upper part of the section (Bao et al., 1999; Fricke and Wing, 2004; Snell et al., 2013; Wilf, 2000; Wing et al., 2000). Woodburne et al. (2009a; 2009b) argued explicitly that the “major faunal reorganization” of Wa-7 in faunas across the North American interior was part of the “EECO initial diversification”, which began in Wa-6 as “reflected in an increase in diversity” coincident with rising temperatures and more diverse, tropical floras (Woodburne et al., 2009a: p. 13400). Chew and Oheim (2013) argued that there is no evidence of an increase in diversity in Wa-6 in the FC fossil record. There is, however, a major shift in faunal dynamics, including increased diversity, at the beginning of Wa-5, which is comparatively short in the FC record (~45 meters thick compared with ~160 meters thickness for Wa-6). This implies that, at least in the FC record, the EECO initial diversification began in Wa-5 at or just after Biohorizon B, which is the largest faunal turnover event after the Paleocene-Eocene Thermal Maximum turnover in this record. The McCullough Peaks CIEs and hence ETM2 and H2 unquestionably occurred after Biohorizon B and before the peak temperatures of the EECO. Thus, I have described them throughout this paper as occurring in EECO-related warming (i.e., not within the optimum itself) and the EECO initial faunal diversification. I have specifically described

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the position of the CIEs and hence ETM2 and H2 as follows:

1. Abstract, line 9, p. 1372: "The later hyperthermals [ETM2 and H2] occurred following the onset of warming at the Early Eocene Climatic Optimum (EECO)"
2. Introduction, lines 7-9, p. 1373: "...including several hyperthermals (intervals of geologically rapid global warming) in the approach to the Early Eocene Climatic Optimum (EECO)"
3. Discussion, lines 2-4, p. 1386: "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)."
4. Discussion, lines 14-16, p. 1387: "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."
5. Summary, lines 18-20, p. 1389: "ETM2 and H2 are set in the context of pronounced climatic, environmental and faunal change related to the onset of the EECO."

I have further described the period after Biohorizon B as follows:

6. Abstract, line 21, p. 1372 and repeated in the Summary, lines 20-22, p. 1389: "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."
7. Introduction, line 20, p. 1374: "The dense, highly-resolved, well-documented mammal record from the Fifteenmile Creek (FC) in the south-central part of the Bighorn Basin (Fig. 1) chronicles almost the entire early Eocene from the PETM to the EECO (Bown et al., 1994b)."
8. Introduction, lines 23-26, p. 1374: "Biohorizon B marks a major turning point in faunal diversity (Chew and Oheim, 2013) that has been correlated with paleoecolog-

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ical change across North America attributed to the onset of warming at the EECO (Woodburne et al., 2009)."

9. Discussion, lines 24-25, p. 1386: "These results support the interpretation of Woodburne et al. (2009) that there was major evolutionary innovation in the lead-up to the EECO."
10. Discussion, lines 27-28, p. 1388: "The latter changes are more consistent with the Bighorn Basin record of the beginning of the EECO."

Clyde describes bullets 1, 3-8 and 10 as misstatements because the "events [ETM2 and H2] (which are older than 53.5 Ma, Zachos et al. 2010) occur before the EECO". None of these statements places the events within the optimum, with the possible exception of bullet 10, although the statement in bullet 10 does not refer to the position of the McCullough Peaks CIEs and hence ETM2 and H2. These statements could be construed as inaccurate if the optimum itself includes significant warming that is distinct from the warming at and after Biohorizon B that directly resulted in the optimum (and which would contradict the term 'optimum'). In fact, there is some evidence of a zone of peak temperatures near the end of Wa-7, which is in the middle of the EECO (beginning between 51.7 Ma and 50.9 Ma (Hyland et al., 2013; Hyland and Sheldon, 2013). I do not believe it is likely that this could be easily confused for the warming at the beginning of the EECO, but I am happy to use the unobjectionable and most precise characterization of this interval, the "approach to" and "lead-up to" the EECO, as in bullets 2 and 9. I have altered bullets 1, 3-6, 8 and 10 accordingly. The statement in bullet 7 is correct; the FC section chronicles almost the entire early Eocene from the PETM to the first part of Wa-7, which is in the EECO. For clarity, I have changed this to the "beginning of the EECO".

4) Less significant concerns: future projections for biotic change. Clyde's concern was echoed in Huber's online review and discussed in our back and forth exchanges. In response to Huber's comments and clarifications, I have deleted the last sentence of

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the Abstract and the repetition of this sentence in the Summary (p. 1372 lines 26-27 and p. 1 lines 1-2, p. 1389 line 26 and p. 1390 lines 1-2) and the last paragraph of the Discussion (section 4.3, p. 1388-p. 1389), in which I speculated about the possible implications of this study for future anthropogenic change. Huber points out that warming of the magnitude of the early Eocene hyperthermals is not likely to be replicated in our future. Thus, the changes documented here are not directly analogous for the future, although as Huber points out they may pertain to other areas under certain scenarios of future warming. Clyde's concern here is addressed by these deletions.

5) Technical corrections.

Title. Clyde suggests it should be changed to "Mammal faunal changes near Paleogene hyperthermals ETM2 and H2". I prefer "Mammal faunal change in the zone of the Paleogene hyperthermals ETM2 and H2".

Abstract p.1372, line 9. See response 3) Less significant concerns: use of the term EECO. Abstract p.1372, line 12. Changed according to suggestion and also the Introduction, p. 1374, lines 13-14. Abstract p.1372, line 19. Changed to "is not driven by immigration" according to suggestion. Abstract p.1372, line 19. See response 3) Less significant concerns: use of the term EECO. Abstract p. 1373, line 1-2. See response 3) Less significant concerns: future projections for biotic change.

Introduction p. 1373, line 8-9. See response under 3) Less significant concerns: use of the term EECO. Introduction p. 1373, line 21. Changed according to suggestion. Introduction p. 1374, line 20. See response 3) Less significant concerns: use of the term EECO. Introduction p. 1374, line 25. See response 3) Less significant concerns: use of the term EECO.

Methods and materials p. 1375, line 12. See description of "red 1" in Rose et al. (2012: p. 9 and Fig. 6).

Methods and materials p. 1376, line 4: Clyde writes "I would argue that the "biostrati-

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graphic events at the beginning of Biohorizon B" are not "loosely tied" in the McCullough Peaks sections since the fossil localities there are tied directly (by bed tracing of usually less than 1 km) to the isotope sections. Delete "loosely." The statement refers to the position of the biostratigraphic events within the McCullough Peaks isotope sections, and is accurate given that the taxa in question "co-occur at a single locality (MP 122, ~5 km west of the nearest isotope section) that was traced to near the middle of a ~35 m thick gap between them in the isotope sections (Fig. 2)" (lines 6-8, p. 1376, summarizing Abels et al., 2012: supplementary material, p. 5). I would call this a "loose" correlation (with the Gilmore Hill section and hence the Upper Deer Creek section).

Methods and materials p. 1376, line 8-15. See response 2) Major concern: precise correlation between the isotope and fossil stratigraphic sections.

Methods and materials p. 1376, line 21. Changed to: "Neighboring localities along the Elk Creek (Fig. 1) have also been tied to the FC section but are excluded from this analysis (as advocated in Clyde et al., 2007) because of differences in section thickness (up to 70 m, Bown et al., 1994) that would compromise resolution."

Methods and materials p. 1377, line 3. No change suggested.

Methods and materials p. 1377, line 20. Clyde writes: "More explanation is needed to explain how this analysis of randomly overlapping time bins of different length artificially increases the temporal resolution of the data when the raw data are not sufficiently resolved to begin with. A simple simulation would be helpful to illustrate the point. In essence, it seems to be arguing that you can get better temporal resolution than your original data set by a moving window averaging method but that sounds like a free lunch :)." The method does not increase the resolution, which I can see I have mistakenly implied in the wording of line 21, p. 1377: "to approximate meter level resolution" and lines 13-14, p. 1381 "indicating an appropriate level of resolution in the averaged parameters (Fig. 4)." This wording has been deleted. The underlying parameter pattern is extrapolated from multiple, overlapping bins, as is now more clearly explained in this

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paragraph and illustrated with a simulation in Fig. 3 as suggested. Please note: the simulation demonstrates a 30-50% amplification of signal fluctuation inherent in the binning process (i.e., not in the averaging of binned signals proposed here but in the binning itself) that may raise additional concerns. I did not go into this originally in the paper as the statistical significance of the B-1 and B-2 parameter peaks is based on comparison with averaged, binned initial parameter distributions that are subject to the same amplification. However, I am happy to add a line addressing this if Clyde/the editor feel it would be appropriate in light of the revisions to Fig. 3.

Methods and materials p. 1379, line 1. Changed according to suggestion.

Methods and materials p. 1380, line 23. Clyde writes: "Why sum these metrics instead of just plotting them separately to see if they agree? It seems like summing them unnecessarily masks them (and same question on Line 9, P. 1381)." All metrics, including alpha and beta richness, evenness and dominance, and rates of first and last appearance, are plotted separately in Figure 4 (and also in the revised Fig. 4) and discussed extensively (both individually and summed) in the Results section, p. 1381-1382 and Discussion section, p. 1386-1388.

Results p. 1381, line 18. Clyde writes "It is absolutely not possible to say with confidence that this 40 meter interval is the same as the ETM2 and H2 interval without having isotope data tied directly to the fossil localities (see detailed discussion above)." The sentence is: "This analysis demonstrates two distinct events within that 40 m zone, separated by ~10 m (~60 ka) of pre-event parameter values." The "40m zone" referred to in this sentence has nothing to do with the McCullough Peaks ETM2 and H2 interval. It refers to the previous sentence (lines 14-17): "Three overlapping peaks occur in both sets of parameters (370–394, 405–417 and 435–448m), significantly refining previous work at a coarser resolution (20m thick intervals, =~100 ka), in which a single, 40m thick interval (370–410 m) of biotic change was identified in this part of the FC section (Chew, 2009a)."

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Results p. 1382, line 28. Clyde writes "What is meant by "aligned" here. I am assuming it means independently correlated but it sounds like the patterns were wiggle matched which of course would not be appropriate. Assuming independent correlation, there are still all of the issues mentioned above (especially with respect to the updated position of Biohorizon B relative to ETM2 in McCullough Peaks sections)." The faunal events are independently correlated with the CIEs in the Upper Deer Creek section using the range end-points of species in this part of the section to delimit the stratigraphic range of faunal events B-1 and B-2. I modeled this particular correlation analysis on Clyde and colleagues' alignment of the CIEs from the Bighorn Basin and Walvis Ridge in order to illustrate "the close similarity between the large-scale carbon isotope changes across both hyperthermals" (Abels et al., 2012: p. 2, Fig. 2). Once aligned, I tested the correlation between the parameters calculated from averaged, resampled specimen data and the isotope data to determine whether the variation in the parameters and offsets in their peaks undermine the interpretation of coincident change. The unpublished data pertaining to the Gilmore Hill section and the position of Biohorizon B has no bearing on this alignment. I have changed the wording on p. 1382, line 28 from "aligned" to "independently correlated with the FC section using the stratigraphic ranges of faunal events B-1 and B-2 as determined from species range end-points."

Results p. 1383, line 3. D'Ambrosia et al. (2014) is more appropriately cited in the Discussion section, p. 1385, lines 2-4.

Discussion p. 1384, line 1. Clyde writes: "Similar to each other?" The sentence on line 1 seems fairly self-explanatory: faunal events B-1 and B-2 are "similar in all aspects of faunal change described here." As exhaustively described in the Results section, p. 1381-1383, faunal events B-1 and B-2 exhibit similar changes in richness, evenness, turnover and body size that are in many cases distinct from Biohorizon B.

Discussion p. 1384, line 4. Clyde writes: "Except earlier you indicated that immigration was not important at ETM2 and H2 but it certainly was at PETM." The sentence on line 4 seems fairly self-explanatory: "Change at faunal events B-1 and B-2 is superficially

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similar to that described at the only other well-known early Eocene hyperthermal, the PETM (Gingerich, 1989; Rose et al., 2012; Secord et al., 2012), including increases in diversity and turnover and a general shift towards smaller body size.” The superficial similarities include increases in diversity and turnover and smaller body sizes. In the very next paragraph, I describe in detail the differences between the PETM and faunal events B-1 and B-2, focusing on immigration and the extent of body size decrease.

Discussion p. 1385, line 1. Changed according to suggestion.

Discussion p. 1385, line 15: Clyde writes “Snell et al., 2014 should be cited here as it is the first to give absolute temp estimates for these hyperthermals in the Bighorn Basin.” Snell et al. (2014) dispute the scaling of CIE and temperature change as discussed in this sentence. I insert this reference as “(but see Snell et al., 2014).”

Discussion p. 1386, line 2. See response 3) Less significant concerns: use of the term EECO.

Discussion p. 1386, line 7: Clyde writes: “Not clear what this means given these are the sections where the CIEs are actually documented.” The sentence is: “there is no evidence of a CIE in the McCullough Peaks isotope sections of Abels et al. (2012) to suggest a hyperthermal mechanism”. I have added “at Biohorizon B” to the end of the sentence to clarify.

Discussion p. 1386, line 16: Clyde writes: “Onset of what change? To be clear, Biohorizon B does not correlate to ETM2 or H2 just as Abels et al 2012 argued and is further supported in this analysis.” The sentence is: “Biohorizon B, the largest faunal event in the FC record after the PETM, coincides with the onset of this change”. I have added “with the onset of this warming, lithological and floral change”, which are described in detail in the preceding part of the paragraph, p. 1386, lines 1-15 and which constitute the change to which this sentence refers.

Discussion p. 1387, line 10. Changed according to suggestion.

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Discussion p. 1388, line 16: See response 4) Less significant concerns: future projections for biotic change.

Summary p. 1389, line 10. See response 2) Major concern: precise correlation between the isotope and fossil stratigraphic sections.

Summary p. 1389, line 17. Changed to “is not fueled by immigration” according to suggestion. Summary p. 1389, line 20. See response 3) Less significant concerns: use of the term EECO.

Table 1 caption, p. 1398. Changed according to suggestion.

Figure 2, p. 1401. Clyde writes: “Could the peaks in abundance be driving your peaks in turnover? These should be shown side-by-side or correlated to make sure that sampling is still not influencing the turnover results.” I have revised Fig. 2 to show the entire size distribution of the binning series, rather than the subset that was originally pictured. I have revised Fig. 4 to show the averaged, binned sampling distribution (prior to standardization) side-by-side with the results to illustrate that there is no significant correlation except for richness. The correlation with alpha richness is weak ($r=0.28$, $p=0$) and with beta richness is strong ($r=0.91$, $p=0$). Previous analysis (Chew and Oheim, 2013) demonstrated significantly higher beta richness in this part of the section even in samples that were rigorously standardized for both sample size and area. Given the lack of correlation in the other parameters, the weak correlation with alpha richness, and the results of previous work just described, I do not believe that the significant correlation between the original sampling distribution and the beta richness parameter indicates uncorrected sample size bias but rather independent increases in preservation (sampling) and differentiation across the landscape (beta richness). I have added a paragraph describing and discussing Fig. 4 and these correlations in detail to the results section, beginning on line 25, p. 1382.

Figure 4, p. 1403 Clyde writes: “The relative spacing between ETM2 and H2 and the tie points shifts between the bottom bar (which I assume represents the McCullough

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Peaks record?) and the upper graphs. Why would that be if the McCullough Peaks spacing of these events is being used as the independent guide to interpreting the turnover curves? The caption needs a lot more detail to explain this as well as what all of the different color curves represent.” The first part of Clyde’s concern has been addressed in revisions in response 2) Major concern: precise correlation between the isotope and fossil stratigraphic sections. For increased clarity, the parameters have been color coded and this color coding is described in the revised figure caption as suggested.

Supplementary information. Clyde writes: “(1) Why are some specimens from Elk Creek included when the text says they were not?” There are no Elk Creek specimens included. I believe Clyde’s confusion stems from my notations of species for which specimens are known in the Elk Creek outside of the stratigraphic range indicated by the FC specimens of this project. The Elk Creek specimens are not included here.

Supplementary information. Clyde writes: “(2) Many specimens have a level that says “~”. What does this mean? How much stratigraphic error is on these specimens compared to the others?” The only specimens with “~” related to meter level are from the locality D-1441 (~441 m), which includes 3 separate productive levels (lower, middle and upper) that span a stratigraphic thickness of 6 meters (438-444 m) as reported in Bown et al. (1994). This is not error.

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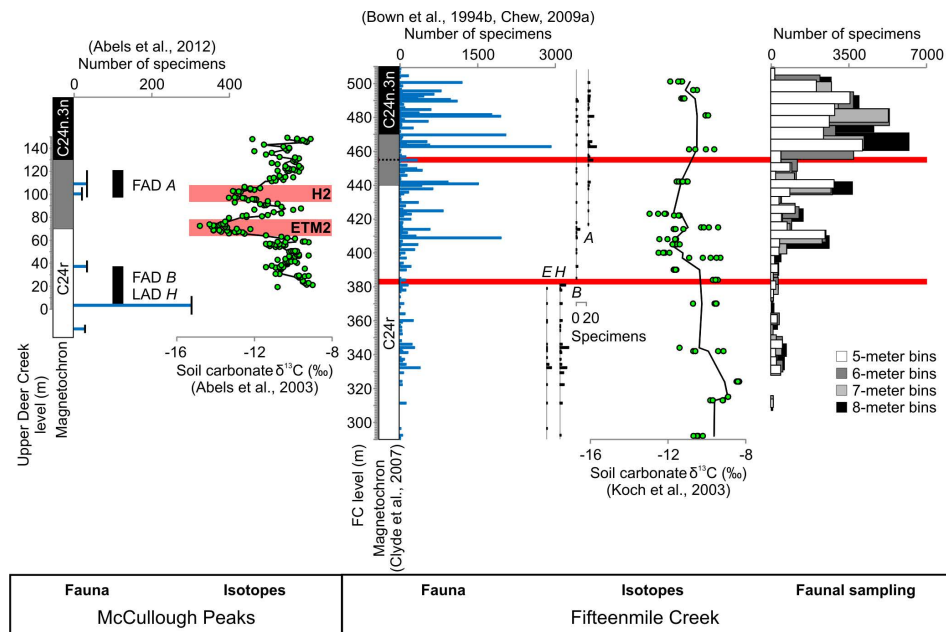


Fig. 1. Revised Fig. 2.

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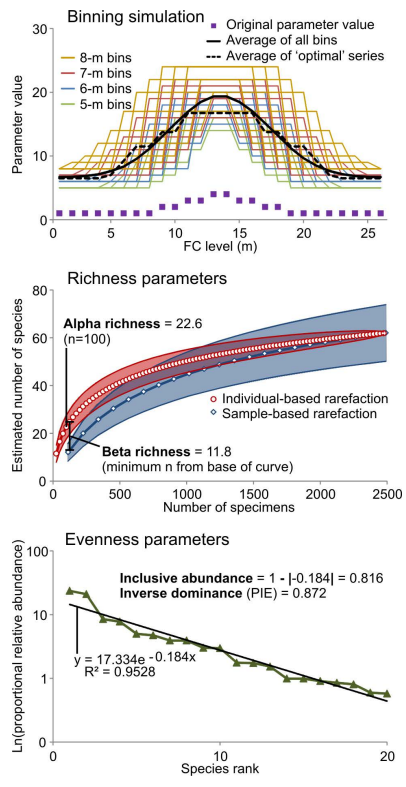


Fig. 2. Revised Fig. 3

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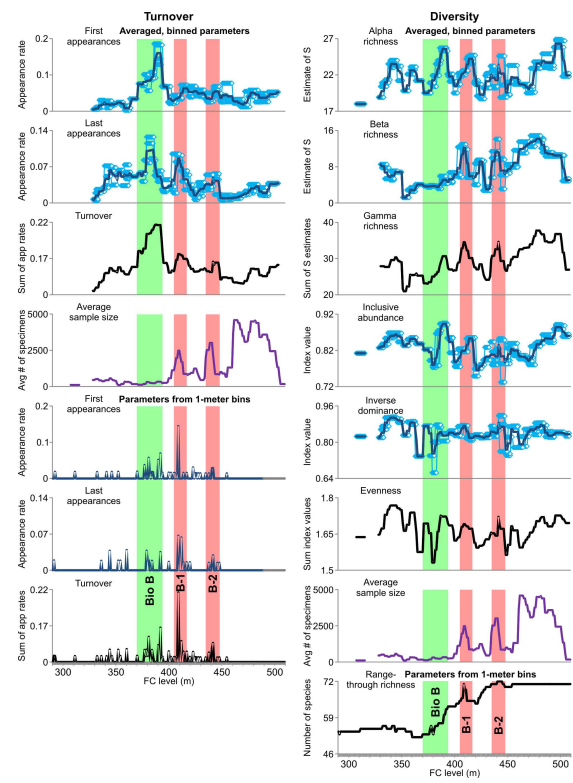


Fig. 3. Revised Fig. 4

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