

# Reworked pollen reduces apparent floral change during the Paleocene-Eocene Thermal Maximum

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## ABSTRACT

Plant megafossils from the Paleocene-Eocene Thermal Maximum (PETM) in the Bighorn Basin, north-central Wyoming, USA, document a dramatic shift in floral composition, whereas palynofloral change from the same sections has appeared to be more subtle. We investigated this discrepancy by quantifying pollen preservation and measuring the stable carbon isotope composition of specific pollen taxa. Pollen grains belonging to two common latest Paleocene taxa are poorly preserved in PETM samples, and their  $\delta^{13}\text{C}_{\text{pollen}}$  is similar during the latest Paleocene and PETM. In contrast, pollen grains of a thermophilic taxon that became more abundant during the PETM are pristine, and the  $\delta^{13}\text{C}_{\text{pollen}}$  of PETM specimens is  $\sim 4\text{‰}$  lower than that of latest Paleocene specimens. More broadly, pollen grains belonging to lineages currently centered in temperate climates are poorly preserved when found in PETM samples, whereas in the same samples, pollen belonging to lineages now centered in the tropics are well preserved. These differences in preservation and isotopic composition indicate extensive redeposition of older pollen grains during the PETM. Increased abundance of Cretaceous palynotaxa in PETM samples confirms erosion and redeposition, likely resulting from more episodic and intense precipitation. Exclusion of reworked palynotaxa from analyses reveals that, as in the megafloora, temperate taxa were absent during the PETM at the time when dry tropical taxa briefly appeared. Major climate changes like the PETM may commonly destabilize landscapes, increase reworking, and thus smooth patterns of change in microfloras, leading to underestimates of the rate and magnitude of floral response to past global change.

## INTRODUCTION

During the Paleocene-Eocene Thermal Maximum (PETM), ca. 56 Ma, a massive release of isotopically light carbon to the ocean-atmosphere system generated a negative carbon isotope ( $\delta^{13}\text{C}$ ) excursion (CIE) of  $4\text{‰}$ – $5\text{‰}$  and global warming of  $4$ – $8$  °C (McInerney and Wing, 2011). Prior work on megaflooras across the PETM in the Bighorn Basin, north-central Wyoming, USA, showed major change in composition across the hyperthermal event (Wing et al., 2005; Wing and Currano, 2013). Nearly half of 91 common megafloreal taxa had no occurrences in the CIE body, although they occurred both before and after the PETM in the study area (range-gap taxa). Nearly a quarter of the megafloora occurred only during the PETM

(PETM-only taxa). Range-gap taxa typically have living relatives distributed in temperate climates, whereas living relatives of PETM-only taxa grow in dry tropical climates. Wing and Currano (2013) interpreted range gaps as local extirpations caused by hotter, drier climate and PETM-only distributions as geographic range expansions responding to the same climate change. Although Wing et al. (2005) found rare occurrences of tropical palynomorphs (e.g., *Brosipollis*, Bombacoideae) in the PETM, they did not find range-gap palynotaxa, even among plant families for which megafossil records showed range gaps (e.g., Cupressaceae).

The absence of range gaps in the palynoflora might reflect the greater sampling radius of typical palynomorph assemblages compared

with highly local leaf assemblages (Jacobson and Bradshaw, 1981; Ferguson, 1985), implying that local populations of range-gap taxa did persist in the basin, but not close to environments of leaf deposition. Alternately, range gaps in the palynoflora might have been closed by Paleocene palynomorphs being eroded and redeposited during the PETM, a process that leaf fossils are too fragile to undergo (Ferguson, 1985).

We used the preservational state and stable carbon isotopic composition of range-through palynotaxa to test the hypothesis that they were reworked from Paleocene sediments. Paleocene pollen grains redeposited during the CIE body should reflect the stable carbon isotopic composition of the Paleocene atmosphere rather than the PETM atmosphere because pollen preserves the  $\delta^{13}\text{C}$  signature of atmospheric  $\text{CO}_2$  at the time of growth (Farquhar et al., 1989; Jahren, 2004). Such grains should also be less well preserved than autochthonous PETM pollen.

## METHODS

### Geologic Setting

The Paleocene Fort Union Formation and Paleocene–Eocene Willwood Formation of north-central Wyoming are well exposed in the northwest-southeast-oriented Bighorn Basin (BHB). The PETM has been identified in many parts of the BHB as a 30–45-m-thick sequence of fluvial rocks and paleosols (Koch et al., 1992; Bowen et al., 2001; Rose et al., 2012; Baczynski et al., 2013; van der Meulen et al., 2020). We collected plant microfossils from five types of fluvial subenvironments characterized by lithology, internal structure, geometry, proximity to paleochannels, and size (Table S1 in the Supplemental Material<sup>1</sup>). The age of each sample was

<sup>1</sup>Supplemental Material. Expanded methods, taxonomic considerations, Tables S1–S8, and Figures S1–S3. Please visit <https://doi.org/10.1130/GEOL.S.21005416> to access the supplemental material, and contact editing@geosociety.org with any questions.

interpolated from its stratigraphic position relative to horizons of known age (e.g., magnetic reversals, onset of the CIE, end of the CIE body), assuming uniform long-term rates of sediment accumulation between dated levels. Previous work established that the CIE body represents ~100 k.y. (Westerhold et al., 2018; van der Meulen et al., 2020), had mean annual temperatures ~5 °C higher than the latest Paleocene (Fricke and Wing, 2004; Wing et al., 2005), and had a drier or more seasonally dry climate (Wing et al., 2005; Kraus and Riggins, 2007; Kraus et al., 2013; Baczynski et al., 2016). The CIE recovery is estimated to have been ~40 k.y. in duration and was characterized by decreasing temperature and increasing floodplain wetness (Wing et al., 2005; Adams et al., 2011; Baczynski et al., 2016; van der Meulen et al., 2020).

### Palynology

Palynomorphs were recovered from 40 samples (Fig. S1; Table S2) using a modified standard palynological process (see the Supplemental Material for additional details). Every fossil palynomorph was scored as corroded, degraded, and/or broken, following the terms of Cushing (1967) (Fig. S2). The classes are not mutually exclusive. Thermal maturity of grains was assessed using the palynomorph darkness index (PDI) of Goodhue and Clayton (2010). Palynomorphs affected by two or more forms of damage were considered deteriorated.

### Carbon Isotope Analysis

For each individual carbon isotope measurement of pollen ( $\delta^{13}\text{C}_{\text{pollen}}$ ), 30–40 grains of the

selected pollen taxon were identified under light microscopy from the residue of a single sample. These grains were transferred by micropipette to a drop of ultrapure water that was combusted using a spooling-wire microcombustion device. The  $\delta^{13}\text{C}_{\text{pollen}}$  values of the resulting  $\text{CO}_2$  gas were measured using an isotope ratio mass spectrometer (IRMS). The methods are described more fully in the Supplemental Material and in Nelson (2012). Weight percent total organic carbon (%TOC) and carbon isotopic measurements of TOC ( $\delta^{13}\text{C}_{\text{TOC}}$ ) were measured using an elemental analyzer IRMS as described by Baczynski et al. (2013). The *n*-alkane carbon isotope values ( $\delta^{13}\text{C}_{n\text{-}C_{29}}$ ) were determined via gas chromatography IRMS using methods described in the Supplemental Material and by Baczynski et al. (2016, 2018).

## RESULTS

### Pollen Preservation

Samples from the CIE body had high proportions of deteriorated palynomorphs and dinoflagellates compared with those from before and after, though four samples from the last 150 k.y. of the Paleocene had intermediate levels (Fig. 1). Deteriorated grains in PETM samples included clearly reworked Mesozoic taxa (e.g., *Aequitriradites ornatus*, *Classopollis classoides*, *Aquilapollenites quadrilobus*, and marine dinoflagellates; Table S3) as well as those with Paleocene and younger ranges (e.g., *Caryapollenites veripites*, *Momipites leffingwellii*, and *Ulmipollenites krempii*). The proportion of dinoflagellates and deteriorated grains varied by depositional environment, but abandoned

channel fills, the only environment distributed throughout the sequence, showed an increase during the CIE body (Fig. 1).

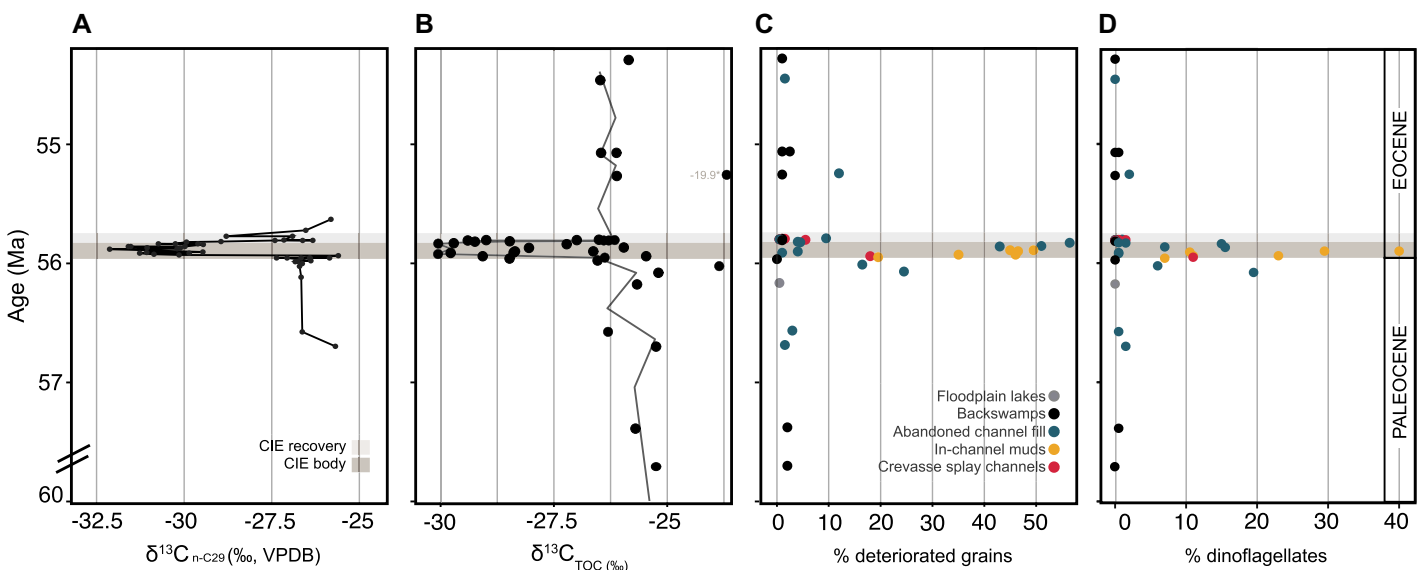
We examined the preservation of two temperate palynotaxa, the conifer *Cupressacites hiatipites* and the walnut relative *Caryapollenites veripites*, during the PETM, as these palynotaxa are relatively common in Paleocene rocks and therefore more likely to be reworked. More than 75% of *C. hiatipites* and *C. veripites* grains from the CIE body were deteriorated, whereas <5% from before and after were deteriorated (*T* value <0.02; Fig. 2; Table S8). In contrast, the palm *Arecipites tenuixinous*, which likely preferred warmer climates, is pristinely preserved throughout the sequence.

### Carbon Isotope Measurements

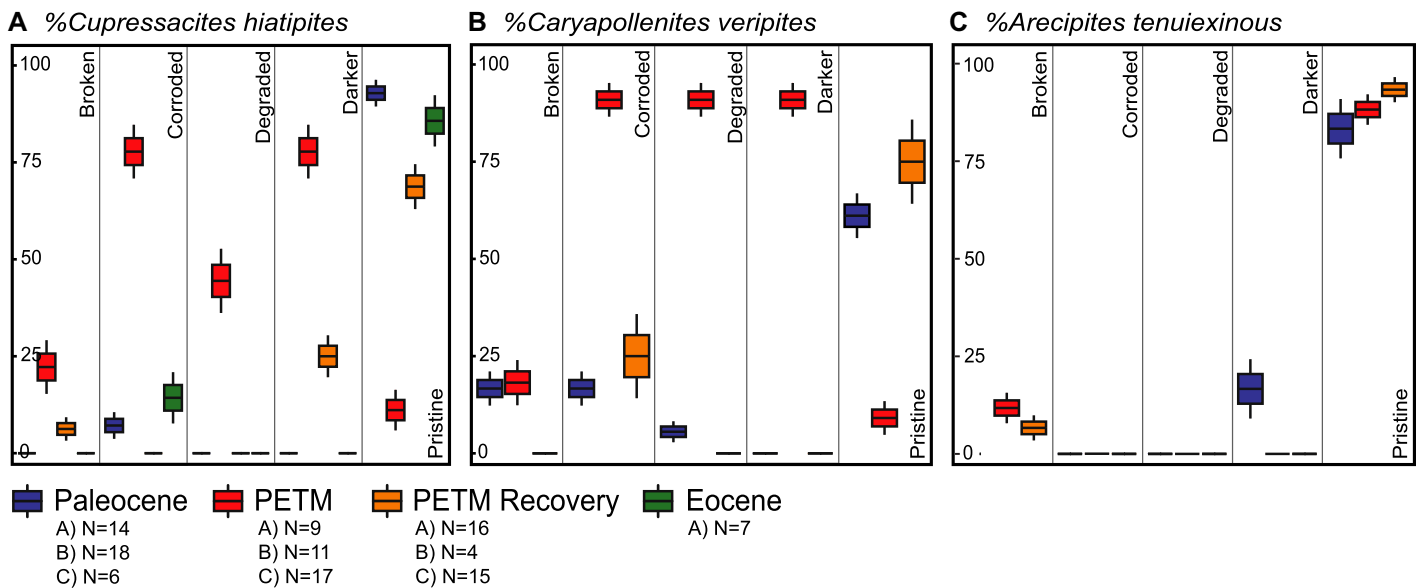
The carbon isotope composition of bulk organic matter ( $\delta^{13}\text{C}_{\text{TOC}}$ ) ranged from –30.1‰ to –23.9‰ through the sequence. The median values were –25.7‰ for the Paleocene, –28.2‰ for the CIE body, –27.0‰ for the CIE recovery, and –26.1‰ for the post-PETM Eocene (Fig. 1). During the CIE body,  $\delta^{13}\text{C}_{\text{TOC}}$  values were found to be positively correlated with the proportion of deteriorated palynomorphs in samples ( $R^2 = 0.76$ , *P* value < 0.0010; Fig. S3).

The carbon isotope composition of C29 *n*-alkanes ( $\delta^{13}\text{C}_{n\text{-}C_{29}}$ ) showed the expected 4‰–5‰ negative CIE associated with the PETM in addition to the sudden onset and rapid recovery, consistent with previous observations (Fig. 1; Table S6; Baczynski et al., 2013).

Each measurement of  $\delta^{13}\text{C}_{\text{pollen}}$  was made on 30–40 grains of a specific pollen type from



**Figure 1.** Changes in  $\delta^{13}\text{C}_{n\text{-}C_{29}}$ ,  $\delta^{13}\text{C}_{\text{TOC}}$  (TOC—total organic carbon), palynomorph preservation, and dinoflagellate abundance during the latest Paleocene and early Eocene in Bighorn Basin (north-central Wyoming, USA). (A)  $\delta^{13}\text{C}_{n\text{-}C_{29}}$  of pollen samples. (B)  $\delta^{13}\text{C}_{\text{TOC}}$  of pollen samples. Eocene sample with  $\delta^{13}\text{C}_{\text{TOC}} = -19.9\text{‰}$  contained abundant carbonate shell fragments that may not have been entirely eliminated by acid treatment. Trend line is a two-point moving average for samples with <10% deteriorated grains. (C) Changes in palynomorph preservation with sample age. (D) Changes in dinoflagellate percent with sample age. Symbol colors in C and D indicate depositional environments of the samples (see key). Sample age calculations are given in the Supplemental Material (see footnote 1). CIE—carbon isotope excursion; VPDB—Vienna Peedee belemnite reference.



**Figure 2. Proportions of deteriorated and/or pristine pollen grains of (A) *Cupressacites hiatipites*, (B) *Caryapollenites veripites*, and (C) *Arcipites tenuixinous* in samples from the late Paleocene (blue), Paleocene-Eocene Thermal Maximum (PETM) body (red), PETM recovery (orange), and early Eocene (green) of the Bighorn Basin (north-central Wyoming, USA) (see Table S8 [see footnote 1]). Box and whisker plots show minimum, first quartile, median, third quartile, and maximum proportion of grains with each damage/preservation type.**

a single rock sample. The error of individual measurements was calculated from the mass of carbon in the sample (Fig. 3; see the Supplemental Material). If we measured more than one group of pollen grains from a sample, we present their error-weighted mean value. The mean  $\delta^{13}\text{C}_{\text{pollen}}$  of late Paleocene *C. hiatipites* was  $-22.6\text{‰}$  ( $N = 2$ ), and the mean  $\delta^{13}\text{C}_{\text{pollen}}$  of *C. veripites* from the same sample was  $-26.1\text{‰}$  ( $N = 2$ ). Latest Paleocene *A. tenuixinous* had a mean  $\delta^{13}\text{C}_{\text{pollen}}$  of  $-26.8\text{‰}$ . *C. hiatipites* from the CIE body had  $\delta^{13}\text{C}_{\text{pollen}}$  of  $-23.5\text{‰}$  ( $N = 1$ ), and *C. veripites* from the CIE body had  $\delta^{13}\text{C}_{\text{pollen}}$  of  $-26.6\text{‰}$  ( $N = 1$ ). *A. tenuixinous* from the CIE body had a  $\delta^{13}\text{C}_{\text{pollen}}$  of  $-30.8\text{‰}$  ( $N = 4$ ; Fig. 3; Table S4).

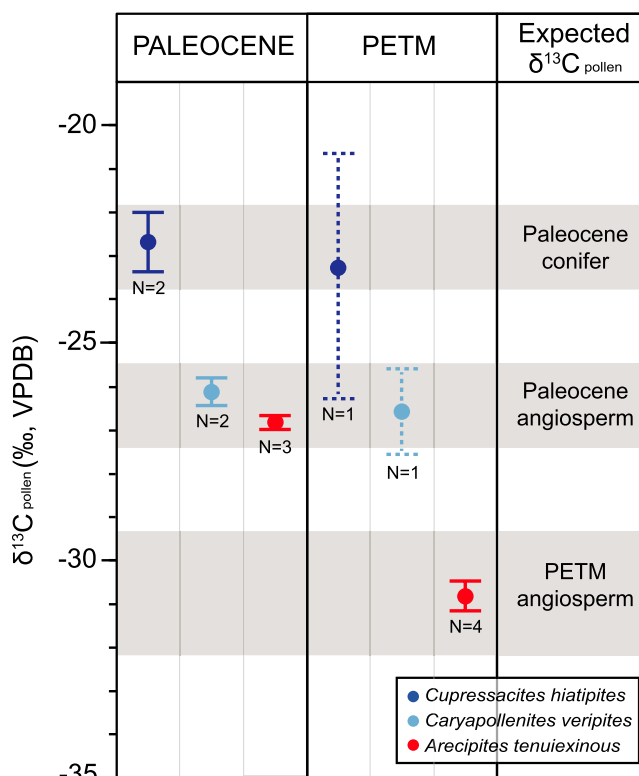
### DISCUSSION

The carbon isotope composition and preservational state of palynomorphs are consistent with the hypothesis that many organic microfossils were eroded from Paleocene (and older) rocks and redeposited during the CIE body in the Bighorn Basin. The  $\delta^{13}\text{C}_{\text{pollen}}$  of *C. hiatipites* and *C. veripites* shifted only fractionally and insignificantly negative from the latest Paleocene to the CIE body, consistent with most or all of the grains being products of photosynthesis from the Paleocene rather than PETM atmosphere (Fig. 3). Specimens of these taxa from the CIE body were also generally poorly preserved (Fig. 2), consistent with erosion from (slightly) older sediments and redeposition during the CIE body. In contrast, the  $\delta^{13}\text{C}_{\text{pollen}}$  of *A. tenuixinous* shifted  $\sim 4\text{‰}$  from the latest Paleocene to the CIE body, consistent with photosynthesis from a CIE atmosphere  $\sim 4\text{‰}$  more negative than the latest Paleocene

atmosphere, which agrees with the magnitude of the CIE observed in *n*-alkanes and mammalian tooth enamel (Fig. 3; Koch et al., 1992; Secord et al., 2012; Baczynski et al., 2016). Specimens of *A. tenuixinous* from the CIE body were also well preserved and commonly occurred in clusters, providing independent evidence they were autochthonous and not

eroded, transported, and redeposited from older rocks (Farley, 1990).

We considered alternative hypotheses to explain the absence of a negative shift in the  $\delta^{13}\text{C}$  values of *C. veripites* and *C. hiatipites*. Each of these palynotaxa might represent more than one closely related biological species (see the Supplemental Material; pollen of related species



**Figure 3. Expected and observed  $\delta^{13}\text{C}_{\text{pollen}}$  of three pollen taxa. Expected ranges of  $\delta^{13}\text{C}_{\text{pollen}}$  (gray bars) were calculated from measured  $\delta^{13}\text{C}_{n-C_{29}}$  values (Fig. 1; Table S5 [see footnote 1]) from which we subtracted a lipid-specific enrichment of  $\varepsilon = 4.3$  and accounted for an average 3‰ difference in  $\delta^{13}\text{C}$  of angiosperms and gymnosperms (Diefendorf et al., 2011).  $\delta^{13}\text{C}_{\text{pollen}}$  of *A. tenuixinous* (palm) from carbon isotope excursion (CIE) body is  $\sim 4\text{‰}$  more negative than that from the latest Paleocene, reflecting an expected shift caused by a change in the isotopic composition of atmosphere. In contrast, temperate taxa *C. veripites* and *C. hiatipites* have similar  $\delta^{13}\text{C}_{\text{pollen}}$  in the Paleocene and CIE body, consistent with being reworked. Solid bars are standard error of the mean calculated for samples with replicates.**

Dashed bars are expected instrumental accuracy for samples with no replicates. VPDB—Vienna Pee Dee belemnite reference.

may not be distinguishable). If the hypothetical species within *C. veripites* and *C. hiatipites* that lived during the PETM had ~4‰ less preference for <sup>12</sup>C than the Paleocene species producing the same pollen types, this would offset the CIE in the atmosphere and result in similar δ<sup>13</sup>C<sub>pollen</sub> values in the Paleocene and PETM, as we observed. Similarly, changes in photosynthesis and/or stomatal conductance, resulting from decreased water availability, could have reduced discrimination against <sup>13</sup>C in plants growing during the CIE (Diefendorf et al., 2010). These alternative hypotheses, though, require species and/or physiologic changes in unrelated plant groups that exactly offset the difference between the pre-CIE and the CIE body carbon isotope values, while a third species, *A. tenuixinous*, displayed a carbon isotopic change very similar to that observed in δ<sup>13</sup>C<sub>TOC</sub> and δ<sup>13</sup>C<sub>n-C29</sub>. These alternative hypotheses also do not explain the poor preservational state of the former two taxa during the CIE. The reworking hypothesis is more parsimonious and therefore preferred here.

Other evidence for elevated reworking during the CIE body is seen in higher proportions of deteriorated palynomorphs and Cretaceous dinoflagellates. Taxonomic identifications (Table S3) of the reworked palynomorphs and dinoflagellates suggest the dominant sources for fine reworked organic matter were the easily eroded Cretaceous and Paleocene mud rocks around the Bighorn Basin margin. Both the source and increased amount of reworking are consistent with prior studies of the isotopic and maceral composition of dispersed organic matter in multiple sections (Bataille et al., 2013; Baczynski et al., 2013, 2016, 2019; Denis et al., 2021). We

do not attribute the increase in the proportion of reworked palynomorphs to decreasing production of pollen and spores during the PETM because sedimentary concentrations of organic microfossils remained high, at least in some depositional environments (Table S5).

By evaluating the preservational state of palynological assemblages with light microscopy, we recognized nine palynotaxa that appeared to range through the PETM but were represented only by deteriorated, likely reworked, grains (Fig. 4). Removing these taxa from pollen sums revealed higher turnover in the PETM palynoflora than previously recognized and, specifically, that, as in the megafloora, there are range gaps for palynotaxa during the CIE body. These range-gap taxa represent 37% of the palynoflora, comprising a smaller proportion than in the megafloora, but far more than previously recognized. Significantly, the range-gap palynotaxa with known nearest living relatives belong to plant groups with high extant diversity in temperate climates (e.g., *Aesculus*, *Alnus*, *Carya*, *Platanus*). The patterns of turnover in the palynoflora are more congruent with the megafloora than previously recognized, and they bolster the hypothesis that many temperate plants were extirpated from the Bighorn Basin during the CIE body. New taxa from the CIE are illustrated and described by Korasidis et al. (2022).

Recently, the isotopic composition of individual planktic foraminifera tests at Ocean Drilling Program Site 865 in the mid-Pacific Ocean was used to demonstrate that turnover in faunal composition across the PETM was muted by mixing (Hupp et al., 2022). Although there is abundant evidence for increased flux

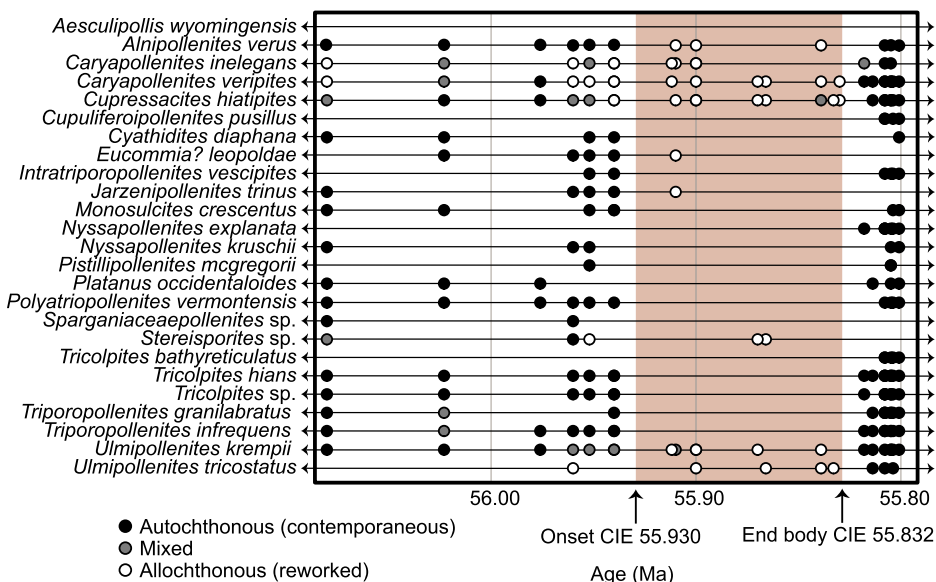
of terrestrial organic matter in marine deposits along many continental margins during the PETM (Handley et al., 2008; Carmichael et al., 2017; Lyons et al., 2019), there has been less attention paid to the possibility that erosion and redeposition could have reduced the apparent rate and magnitude of biotic turnover in organic microfossils. Unrecognized reworking of pollen and spores may disguise the distinctiveness of PETM palynofloras in many sections, and, more broadly, similar effects during other periods of rapid environmental change may reduce the apparent magnitude and rapidity of floral response to major disruptions in Earth history.

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#### REFERENCES CITED

- Adams, J.S., Kraus, M.J., and Wing, S.L., 2011, Evaluating the use of weathering indices for determining mean annual precipitation in the ancient stratigraphic record: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 309, p. 358–366, <https://doi.org/10.1016/j.palaeo.2011.07.004>.
- Baczynski, A.A., McInerney, F.A., Wing, S.L., Kraus, M.J., Bloch, J.I., Boyer, D.M., Secord, R., Morse, P.E., and Fricke, H.C., 2013, Chemostratigraphic implications of spatial variation in the Paleocene-Eocene thermal maximum carbon isotope excursion, SE Bighorn Basin, Wyoming: *Geochemistry Geophysics Geosystems*, v. 14, p. 4133–4152, <https://doi.org/10.1002/ggge.20265>.
- Baczynski, A.A., McInerney, F.A., Wing, S.L., Kraus, M.J., Morse, P.E., Bloch, J.I., Chung, A.H., and Freeman, K.H., 2016, Distortion of carbon isotope excursion in bulk soil organic matter during the Paleocene-Eocene thermal maximum: *Geological Society of America Bulletin*, v. 128, p. 1352–1366, <https://doi.org/10.1130/B31389.1>.
- Baczynski, A.A., Polissar, P.J., Juchelka, D., Schwieters, J., Hilkert, A., Summons, R.E., and Freeman, K.H., 2018, Picomolar-scale compound-specific isotope analyses: *Rapid Communications in Mass Spectrometry*, v. 32, p. 730–738, <https://doi.org/10.1002/rcm.8084>.
- Baczynski, A.A., McInerney, F.A., Freeman, K.H., Wing, S.L., and the Bighorn Basin Coring Project (BBCP) Science Team, 2019, Carbon isotope record of trace *n*-alkanes in a continental PETM section recovered by the Bighorn Basin Coring Project (BBCP): *Paleoceanography and Paleoclimatology*, v. 34, p. 853–865, <https://doi.org/10.1029/2019PA003579>.
- Bataille, C.P., Mastalerz, M., Tipple, B.J., and Bowen, G.J., 2013, Influence of provenance and preservation on the carbon isotope variations of dispersed organic matter in ancient floodplain sediments: *Geochemistry Geophysics Geosystems*, v. 14, p. 4874–4891, <https://doi.org/10.1002/ggge.20294>.
- Bowen, G.J., Koch, P.L., Gingerich, P.D., Norris, R.D., Bains, S., and Corfield, R.M., 2001, Refined isotope stratigraphy across the continental Paleocene-Eocene boundary on Polecat Bench in the northern Bighorn Basin, in: *Gingerich, P.D., ed., Paleocene-Eocene Stratigraphy and Biotic*



**Figure 4. Temporal distribution of 25 common and long-ranging pollen and spore types in Bighorn Basin (north-central Wyoming, USA) during the Paleocene-Eocene transition. The overwhelming majority (35 of 37) of occurrences of these taxa during carbon isotope excursion (CIE) body are reworked as opposed to contemporaneous specimens.**

- Change in the Bighorn and Clarks Fork Basins, Wyoming: University of Michigan Papers on Paleontology 33, p. 73–88.
- Carmichael, M.J., Inglis, G.N., Badger, M.P., Naafs, B.D.A., Behrooz, L., Rimmelzwaal, S., Monteiro, F.M., Rohrssen, M., Farnsworth, A., Buss, H.L., and Dickson, A.J., 2017, Hydrological and associated biogeochemical consequences of rapid global warming during the Paleocene-Eocene thermal maximum: *Global and Planetary Change*, v. 157, p. 114–138, <https://doi.org/10.1016/j.gloplacha.2017.07.014>.
- Cushing, E.J., 1967, Evidence for differential pollen preservation in late Quaternary sediments in Minnesota: *Review of Palaeobotany and Palynology*, v. 4, p. 87–101, [https://doi.org/10.1016/0034-6667\(67\)90175-3](https://doi.org/10.1016/0034-6667(67)90175-3).
- Denis, E.H., Maibauer, B.J., Bowen, G.J., Jardine, P.E., Harrington, G.J., Baczynski, A.A., McInerney, F.A., Collinson, M.E., Belcher, C.M., Wing, S.L., and Freeman, K.H., 2021, Decreased soil carbon in a warming world: Degraded pyrogenic carbon during the Paleocene-Eocene thermal maximum, Bighorn Basin, Wyoming: *Earth and Planetary Science Letters*, v. 566, <https://doi.org/10.1016/j.epsl.2021.116970>.
- Diefendorf, A.F., Mueller, K.E., Wing, S.L., Koch, P.L., and Freeman, K.H., 2010, Global patterns in leaf  $^{13}\text{C}$  discrimination and implications for studies of past and future climate: *Proceedings of the National Academy of Sciences of the United States of America*, v. 107, p. 5738–5743, <https://doi.org/10.1073/pnas.0910513107>.
- Diefendorf, A.F., Freeman, K.H., Wing, S.L., and Graham, H.V., 2011, Production of *n*-alkyl lipids in living plants and implications for the geologic past: *Geochimica et Cosmochimica Acta*, v. 75, p. 7472–7485, <https://doi.org/10.1016/j.gca.2011.09.028>.
- Farley, M.B., 1990, Vegetation distribution across the early Eocene depositional landscape from palynological analysis: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 79, p. 11–27, [https://doi.org/10.1016/0031-0182\(90\)90103-E](https://doi.org/10.1016/0031-0182(90)90103-E).
- Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T., 1989, Carbon isotope discrimination and photosynthesis: *Annual Review of Plant Biology*, v. 40, p. 503–537, <https://doi.org/10.1146/annurev.pp.40.060189.002443>.
- Ferguson, D.K., 1985, The origin of leaf-assemblages—New light on an old problem: *Review of Palaeobotany and Palynology*, v. 46, p. 117–188, [https://doi.org/10.1016/0034-6667\(85\)90041-7](https://doi.org/10.1016/0034-6667(85)90041-7).
- Fricke, H.C., and Wing, S.L., 2004, Oxygen isotope and paleobotanical estimates of temperature and  $\delta^{18}\text{O}$ -latitude gradients over North America during the early Eocene: *American Journal of Science*, v. 304, p. 612–635, <https://doi.org/10.2475/ajs.304.7.612>.
- Goodhue, R., and Clayton, G., 2010, Palynomorph darkness index (PDI)—A new technique for assessing thermal maturity: *Palynology*, v. 34, p. 147–156, <https://doi.org/10.1080/01916121003696932>.
- Handley, L., Pearson, P.N., McMillan, I.K., and Pancost, R.D., 2008, Large terrestrial and marine carbon and hydrogen isotope excursions in a new Paleocene/Eocene boundary section from Tanzania: *Earth and Planetary Science Letters*, v. 275, p. 17–25, <https://doi.org/10.1016/j.epsl.2008.07.030>.
- Hupp, B.N., Kelly, D.C., and Williams, J.W., 2022, Isotopic filtering reveals high sensitivity of planktic calcifiers to Paleocene-Eocene thermal maximum warming and acidification: *Proceedings of the National Academy of Sciences of the United States of America*, v. 119, <https://doi.org/10.1073/pnas.2115561119>.
- Jacobson, G.L., and Bradshaw, R.H., 1981, The selection of sites for paleovegetational studies I: *Quaternary Research*, v. 16, p. 80–96, [https://doi.org/10.1016/0033-5894\(81\)90129-0](https://doi.org/10.1016/0033-5894(81)90129-0).
- Jahren, A.H., 2004, The carbon stable isotope composition of pollen: *Review of Palaeobotany and Palynology*, v. 132, p. 291–313, <https://doi.org/10.1016/j.revpalbo.2004.08.001>.
- 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, <https://doi.org/10.1038/358319a0>.
- Korasidis, V.A., Wing, S.L., Harrington, G., Demchuk, T., Gravenydyck, J., Jardine, P.E., and Willard, D., 2022, Biostratigraphically significant palynofloras from the Paleocene–Eocene boundary of the USA: *Palynology*, <https://doi.org/10.1080/01916122.2022.2115159> (in press).
- Kraus, M.J., and Riggins, S., 2007, Transient drying during the Paleocene-Eocene Thermal Maximum (PETM): Analysis of paleosols in the Bighorn Basin, Wyoming: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 245, p. 444–461, <https://doi.org/10.1016/j.palaeo.2006.09.011>.
- Kraus, M.J., McInerney, F.A., Wing, S.L., Secord, R., Baczynski, A.A., and Bloch, J.I., 2013, Paleohydrologic response to continental warming during the Paleocene-Eocene thermal maximum, Bighorn Basin, Wyoming: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 370, p. 196–208, <https://doi.org/10.1016/j.palaeo.2012.12.008>.
- Lyons, S.L., et al., 2019, Palaeocene–Eocene thermal maximum prolonged by fossil carbon oxidation: *Nature Geoscience*, v. 12, p. 54–60, <https://doi.org/10.1038/s41561-018-0277-3>.
- McInerney, F.A., and Wing, S.L., 2011, The Paleocene-Eocene thermal maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future: *Annual Review of Earth and Planetary Sciences*, v. 39, p. 489–516, <https://doi.org/10.1146/annurev-earth-040610-133431>.
- Nelson, D.M., 2012, Carbon isotopic composition of *Ambrosia* and *Artemisia* pollen: Assessment of a  $\text{C}_3$ -plant paleophysiological indicator: *The New Phytologist*, v. 195, p. 787–793, <https://doi.org/10.1111/j.1469-8137.2012.04219.x>.
- Rose, K.D., Chew, A.E., Dunn, R.H., Kraus, M.J., Fricke, H.C., and Zack, S.P., 2012, Earliest Eocene Mammalian Fauna from the Paleocene-Eocene Thermal Maximum at Sand Creek Divide, Southern Bighorn Basin, Wyoming: *University of Michigan Papers in Palaeontology* 36, 122 p.
- Secord, R., Bloch, J.I., Chester, S.G., Boyer, D.M., Wood, A.R., Wing, S.L., Kraus, M.J., McInerney, F.A., and Krigbaum, J., 2012, Evolution of the earliest horses driven by climate change in the Paleocene-Eocene thermal maximum: *Science*, v. 335, p. 959–962, <https://doi.org/10.1126/science.1213859>.
- van der Meulen, B., Gingerich, P.D., Lourens, L.J., Meijer, N., van Broekhuizen, S., van Ginneken, S., and Abels, H.A., 2020, Carbon isotope and mammal recovery from extreme greenhouse warming at the Paleocene-Eocene boundary in astronomically-calibrated fluvial strata, Bighorn Basin, Wyoming, USA: *Earth and Planetary Science Letters*, v. 534, <https://doi.org/10.1016/j.epsl.2019.116044>.
- Westerhold, T., Röhl, U., Donner, B., and Zachos, J.C., 2018, Global extent of early Eocene hyperthermal events: A new Pacific benthic foraminiferal isotope record from Shatsky Rise (ODP Site 1209): *Paleoceanography and Paleoclimatology*, v. 33, p. 626–642, <https://doi.org/10.1029/2017PA003306>.
- Wing, S.L., and Curran, E.D., 2013, Plant response to a global greenhouse event 56 million years ago: *American Journal of Botany*, v. 100, p. 1234–1254, <https://doi.org/10.3732/ajb.1200554>.
- Wing, S.L., Harrington, G.J., Smith, F.A., Bloch, J.I., Boyer, D.M., and Freeman, K.H., 2005, Transient floral change and rapid global warming at the Paleocene-Eocene boundary: *Science*, v. 310, p. 993–996, <https://doi.org/10.1126/science.1116913>.

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