

Cite as: T. R. Lyson *et al.*, *Science* 10.1126/science.aay2268 (2019).

# Exceptional continental record of biotic recovery after the Cretaceous–Paleogene mass extinction

T. R. Lyson<sup>1\*</sup>, I. M. Miller<sup>1</sup>, A. D. Bercovici<sup>1,2</sup>, K. Weissenburger<sup>1</sup>, A. J. Fuentes<sup>3</sup>, W. C. Clyde<sup>3</sup>, J. W. Hagadorn<sup>1</sup>, M. J. Butrim<sup>4</sup>, K. R. Johnson<sup>2</sup>, R. F. Fleming<sup>4</sup>, R. S. Barclay<sup>2</sup>, S. A. MacCracken<sup>2,5</sup>, B. Lloyd<sup>6</sup>, G. P. Wilson<sup>7</sup>, D. W. Krause<sup>1,8</sup>, S. G. B. Chester<sup>9,10,11</sup>

<sup>1</sup>Denver Museum of Nature and Science, 2001 Colorado Boulevard, Denver, CO 80205, USA. <sup>2</sup>National Museum of Natural History, Smithsonian Institution, 10th Street and Constitution Avenue, NW, Washington, DC 20560, USA. <sup>3</sup>University of New Hampshire, 56 College Road, Durham, NH 03824, USA. <sup>4</sup>Wesleyan University, Middletown, CT 06459, USA. <sup>5</sup>University of Maryland, College Park, 4291 Fieldhouse Drive, College Park, MD 20742, USA. <sup>6</sup>Colorado College, Colorado Springs, CO 80903, USA. <sup>7</sup>University of Washington, 251 Life Sciences Building, Seattle, WA 98195-1800, USA. <sup>8</sup>Stony Brook University, Stony Brook, NY 11794, USA. <sup>9</sup>Brooklyn College, City University of New York, 2900 Bedford Avenue, Brooklyn, NY 11210, USA. <sup>10</sup>The Graduate Center, City University of New York, 365 Fifth Avenue, New York, NY 10016, USA. <sup>11</sup>New York Consortium in Evolutionary Primatology, New York, NY 10024, USA.

\*Corresponding author. Email: tyler.lyson@dmns.org

We report a time-calibrated stratigraphic section in Colorado that contains unusually complete fossils of mammals, reptiles, and plants, and elucidates the drivers and tempo of biotic recovery during the poorly known first million years after the Cretaceous–Paleogene mass extinction (KPgE). Within ~100 thousand years (ka) post-KPgE, mammalian taxonomic richness doubled and maximum mammalian body mass increased to near pre-KPgE levels. A three-fold increase in maximum mammalian body mass and dietary niche specialization occurred at ~300 ka post-KPgE, concomitant with increased megafloral standing species richness. The appearance of additional large mammals occurred by ~700 ka post-KPgE, coincident with the first appearance of Leguminosae (bean family). These concurrent plant and mammal originations and body mass shifts coincide with warming intervals, suggesting climate influenced post-KPgE biotic recovery.

The Cretaceous–Paleogene (K–Pg) boundary marks Earth’s most recent mass extinction, when over 75% of species, including non-avian dinosaurs, went extinct (1). In the terrestrial realm, the mass extinction was followed by a radiation of modern clades, particularly placental mammals (2), crown birds (3), and angiosperms (4). The drivers (5–8) and tempo (9, 10) of the K–Pg mass extinction (KPgE) have been hotly debated and the patterns of terrestrial recovery in the first million years after the KPgE remain poorly understood. The extinction of all large-bodied vertebrates (5) undoubtedly impacted the post-KPgE taxonomic, ecologic, and body-mass diversification of various clades, but the lack of a well-studied fossil record has left the factors influencing ecosystem recovery unknown. Here we provide a detailed and temporally constrained terrestrial fossil record from this critical interval.

Fossils of terrestrial and freshwater organisms from the first million years after the KPgE are exceedingly rare worldwide, hindering our knowledge of post-KPgE taxonomic and ecological radiations. Thus far, the most fossiliferous sections from this time interval occur in the Williston, San Juan, Hanna, and Denver basins along the eastern margin of the Rocky Mountains in North America (11, 12). In all of these study areas, discontinuous outcrops result in composite stratigraphic sections, plant fossil localities are geographically widely spaced, vertebrate-bearing horizons are sparse and

separated by long temporal gaps, complete vertebrate fossils are exceptionally rare, and age control is variable (10–17). The Williston Basin has the most comprehensive fossil record with excellent age control, but the vertebrate specimens are fragmentary (10, 12, 13). The San Juan Basin preserves a well-studied early Paleocene vertebrate record but does not record the K–Pg boundary itself (16). Moreover, overlying Paleocene rocks only contain two vertebrate fossil-bearing horizons within the first one million years post-KPgE (16). The Hanna Basin K–Pg section is rich in fragmentary vertebrate fossils, but has structurally complex strata and lacks a detailed chronostratigraphic framework (17). Finally, the Denver Basin has well-documented Cretaceous and Paleocene strata, a precisely dated K–Pg boundary, and abundant, geographically dispersed plant fossils, but, prior to this study, a sparse and fragmentary vertebrate fossil record (14, 15, 18, 19).

## Corral Bluffs Study Area, Denver Basin, Colorado, USA

We developed a new high-resolution stratigraphic framework in the Corral Bluffs study area, a single continuous (physically traceable) (~27 km<sup>2</sup>) outcrop from the Denver Basin that preserves the biotic recovery of a terrestrial ecosystem in the first million years post-KPgE (20) (Fig. 1 and fig. S1). This stratigraphy is tied to the Geomagnetic Polarity

Time Scale (GPTS 2012) using paleomagnetics and a CA-ID-TIMS U-Pb-dated volcanic ash (20). For comparison, ages using an alternative age model based on work in the Denver Basin (18) are also provided in data files S1 to S14. The study area contains an exceptionally dense vertebrate (299 localities) and megafloral (65 localities) record with fossils occurring at more than 150 stratigraphic levels in the ~250 m thick sequence (Fig. 1). The extensive and nearly continuous outcrop belt spans the last ~100 thousand years (ka) of the Cretaceous and first ~1 Ma of the Paleocene. It includes four North American Land Mammal Age (NALMA) interval zones, four palynostratigraphic biozones, three magnetochron boundaries, two U-Pb radiometric dates, and the palynologically defined K-Pg boundary, yielding a locally derived, high-resolution chronostratigraphic framework (Fig. 1, figs. S2 to S5, and supplementary materials) (20). Together, these data provide an unprecedented opportunity to assess the biotic recovery of a terrestrial ecosystem following the KPgE.

Vertebrate fossils in the Corral Bluffs succession are unusually complete for this time period, and are found in a range of depositional environments, and represent a diversity of taxa and body sizes (Figs. 1 and 2). Most are three-dimensionally preserved in hydroxyapatite concretions and are found in all observed facies, often as articulated skeletons or skulls with intact delicate structures such as middle ear and hyoid elements (Fig. 2). Among vertebrate specimens preserved in concretions, mammalian, turtle, and crocodilian crania (Fig. 2, A to T) and turtle shells (Fig. 2, U to X) are most common. Individual fossils range in size from ~3 mm<sup>2</sup> (isolated teeth) to larger forms such as 1.5 m-long, articulated crocodilian skeletons. Plant fossils also span the size spectrum across all observed facies, including microscopic palynomorphs as well as seeds, leaves, roots, branches, and in situ saplings, and large stumps and logs (Fig. 3).

We recognize sixteen mammalian taxa, eight of which are based on cranial remains, including the first occurrence of the late Puerian (Pu3) index taxon *Taeniolabis taoensis* (Fig. 2, K and L) from the Denver Basin. Cranial size and lower first molar area were used to estimate mammalian body mass – an important feature that impacts many aspects of the biology and ecology of mammals (Fig. 4) (21). Given that there appears to be bias toward large vertebrates in our dataset (supplementary materials and data file S11), we focused on maximum mammalian body mass. Large bodied mammals disappear at the K-Pg boundary (10), but returned to near pre-KPgE levels within 100 ka after the K-Pg boundary (Fig. 4). Subsequent shifts in maximum mammalian body mass occurred at the Pu1/Pu2 and near the Pu2/Pu3 transitions, ~300 and ~700 ka post-KPgE, respectively (Fig. 4). In addition, the pattern and abundance of vertebrates preserved in all paleoenvironments suggest that by ~700 ka post KPgE the largest mammals (25+ kg) were spatially partitioned across the

landscape. We observe a strong pattern of association between taxa and facies (Fig. 4) indicating that baenid turtles (Fig. 2, Q to T) and *Taeniolabis taoensis* (Fig. 2, K and L) lived in or near river channel margins whereas chelydroid turtles (Fig. 2, W and X) and the large peritychid mammals *Ectocionus ditrignonius* (Fig. 2, C, D, G, and H) and *Carsiptychus coarctatus* (Fig. 2, I and J) primarily occupied distal portions of the floodplain (Fig. 4).

We recognize 233 plant morphospecies in our study area (supplementary materials). Despite lower sampling of Cretaceous strata (11 Cretaceous localities vs. 54 Paleocene localities), richness of dicotyledonous (dicot) leaf morphospecies from raw species counts at localities in the last ~100 ka of the Cretaceous (-18–0 m; 7 localities, 777 specimens, most speciose locality  $n = 31$ ) and the first ~100 ka of the Paleocene (0–20 m; 6 localities, 1,019 specimens, most speciose locality  $n = 13$ ) indicates that earliest Paleocene dicot diversity was less than half that of the latest Cretaceous (fig. S6). Additionally, 46% of Cretaceous dicot leaf morphospecies that occur at more than one site do not occur in any of our Paleocene localities. A comparable study with similar time bins from the Williston Basin estimated 57% extinction in dicot leaf morphospecies at the K-Pg boundary (22). Leaf mass per area (LMA), a proxy for carbon investment and ecological strategy in plants (23), decreased in both maximum and minimum values across the K-Pg boundary (Fig. 1 and fig. S7) consistent with a shift to faster growth strategies. Megafloral standing richness and LMA are lowest in the earliest Paleocene, but exceed pre-KPgE levels within ~300 ka (Fig. 1 and fig. S7).

Following the KPgE, many angiosperm clades diversified (4). The Corral Bluffs section preserves the oldest known occurrence of the Leguminosae, or bean family, as evidenced by fossil seedpods and leaflets dated to 65.35 Ma (Fig. 3, J and K). The oldest previously recognized legume (24) is based on wood and leaflets (25) from early Paleocene rocks of Argentina (26), whereas the earliest legume seedpods are not recognized until the late Paleocene (~58 Ma) of Colombia (27). Our discovery supports (i) a nearly synchronous first appearance of legumes in North America and southern South America; (ii) a rapid diversification for the group in the earliest Paleocene (24); and (iii) their apparent origination in the Western Hemisphere.

Relative changes in leaf-estimated mean annual temperature (LMAT) (Fig. 1, fig. S6, and supplementary materials) from our section track paleotemperature proxies from sections elsewhere in the world. Corral Bluffs experienced a 4.6 °C cooling ( $22.1 \pm 2.7$  °C 1SE to  $17.5 \pm 3.4$  °C 1SE) during the last ~100 ka of the Cretaceous, comparable to cooling estimates derived from LMAT (28) and carbonate-clumped isotopes (29) from the Williston Basin, and δ<sup>18</sup>O of benthic foraminifera from the South Atlantic (30). For the first time, we corroborate (31) a warm interval immediately post-K-Pg

in a terrestrial section. Here we observe a 5.1 °C warming event ( $17.5 \pm 3.4$  °C 1SE to  $22.6 \pm 3.5$  °C 1SE) occurred from the K-Pg boundary through the first ~60 ka of the Paleocene, similar to the ~5 °C in ~100 ka warming pulse inferred from  $\delta^{18}\text{O}$  of phosphatic fish scales from the El Kef K-Pg section of Tunisia (31). A second ~150 ka interval (65.80–65.65 Ma) shows an initial warming of 2.2 °C ( $21.1 \pm 3.3$  °C 1SE to  $23.3 \pm 2.9$  °C 1SE) over ~30 ka, sustained temperatures for ~50 ka, and then 3.0 °C cooling ( $22.7 \pm 2.8$  °C 1SE to  $19.7 \pm 3.1$  °C 1SE) over ~70 ka at the top of magnetochron C29r. This event corresponds with the Danian C2 carbon isotopic excursion and inferred warming interval observed in marine (32) and terrestrial (33) strata. Sampling between these warming intervals is limited and an alternative hypothesis is a general warming trend from the K-Pg boundary to the magnetochron C29r/29n boundary. A third 2.9–3.2 °C warming pulse ( $18.0 \pm 3.3$  °C 1SE to  $20.9 \pm 3.0$  °C 1SE to  $17.7 \pm 3.5$  °C 1SE) over ~10 ka is tentatively recognized ~700 ka post-KPgE.

### Paleotemperature and Ecosystem Recovery

The timing of these warming intervals corresponds with changes in plant richness and taxonomic composition and, likely due to additional food sources, coincident shifts in mammalian taxonomic composition, ecologic diversification, and expansion in the range of maximum mammalian body mass (Fig. 4). A mammalian taxonomic increase has been documented elsewhere in the Denver Basin, within the first 100 ka of the Paleocene, from nine species found in the earliest Pu1 faunas to 21 species found in later Pu1 faunas (34, 35). Maximum mammalian body mass increased through this interval to near pre-KPgE levels, from the largest known Lancian mammal (~8 kg) to the largest known Pu1 mammal (~6 kg), coincident with the first post-KPgE warming episode (Fig. 4 and figs. S8 and S9). The Pu1/Pu2 transition occurred ~300 ka after the KPgE and was marked by the appearance of varied and large (20+ kg) peritychid mammals. The appearance of larger-bodied peritychid mammals, particularly the herbivorous, hard-object feeder *Carsioptrychus coarctatus* (Fig. 2, I and J) (37, 38), marks a notable dietary niche specialization in the earliest Paleocene moving from the largely omnivorous/insectivorous diet found in Pu1 mammals (39) to a more herbivorous diet found in some Pu2 mammals. This dietary shift is correlated with a three-fold increase in maximum mammalian body mass compared to Pu1 faunas (Figs. 1 and 4 and figs. S8 and S9). The Pu1/Pu2 transition was coincident with the onset of a high plateau in megafloral standing richness, an increase of LMA beyond pre-KPgE levels, a doubling of the diversity of *Momipites* spp. [fossil juglandaceous (walnut family) pollen (Fig. 3I)], and the second early Paleocene warming interval (Figs. 1 and 4). The diversification of Juglandaceae taxa with small, winged seeds to later taxa with larger wingless seeds is hypothesized to reflect a transition

from wind to animal transport (36). This hypothesis is supported by the close correlation between diversification reflected in fossil juglandaceous pollen and the appearance of several large herbivorous peritychid mammals whose specialized and enlarged premolars are thought to be for hard-object feeding (37, 38). Finally, the appearance of legumes co-occurred with a tentatively recognized short warming pulse and shift in maximum mammalian body mass. Specifically, two large-bodied mammals appear within ~700 ka post-KPgE (Fig. 4) – the herbivorous multituberculate *Taeniolabis taoensis* (~34 kg) and the omnivorous triodontid archaic ungulate *Eoconodon coryphaeus* (~47 kg) (Fig. 2, A and B). These data suggest that earliest Paleocene warming pulses may have played an important role in post-KPgE ecosystem recovery, perhaps by facilitating immigration and/or in situ co-evolution of flora and fauna.

The transition from an ecosystem characterized by a small-bodied mammalian fauna, post-“disaster” ferns, and low diversity plant communities to one exhibiting a larger-bodied mammalian fauna and more ecologically and taxonomically complex forests mirrors modern post-disaster ecological successions, but on a much longer timescale (typically  $10^4$ – $10^5$  years for recoveries from global mass extinctions versus  $10$ – $10^2$  years for modern local-regional ecological recoveries) (40). The overall and long-term recovery we observe has recently been described as an aspect of “Earth system succession” (40). This concept proposes that global ecological succession following mass extinctions is intrinsically paced by the interactions of the biosphere and geosphere, both of which may be knocked out of equilibrium (40). The low-diversity, small-bodied mammalian fauna and low-diversity forests dominated by ferns and palms, often indicative of ecological disequilibrium, suggest that a period of ecosystem disequilibrium lasted for up to ~100 ka post-KPgE in our research area. A period of ecosystem “recovery” followed ~100 – 300 ka post-KPgE when megafloral diversity steadily increased. At ~300 ka post-KPgE we see several additional signs of ecosystem “recovery”, including i) the increase and then plateau of megafloral standing richness; ii) LMA exceeding pre-KPgE levels; iii) diversification of Juglandaceae, a potentially energy-rich food source for mammals; and iv) the first significant taxonomic diversification, dietary specialization (e.g., increased herbivory), and increase in maximum body mass of mammals (Pu1/Pu2). Finally, spatial niche partitioning, appearance of several additional large (30+kg) mammals, and expansion of mammalian body mass disparity continues through ~700 ka at the Pu2/Pu3 boundary, all further indications of ecosystem “recovery.” These changes are correlated with the arrival of plant taxa (e.g., legumes) that would have offered mammals new calorie-dense food sources. Taken together, our record places time estimates on the patterns of biotic recovery in Earth system succession and

demonstrates that several aspects of ecosystem “recovery” occurred within ~300 ka post-KPgE (Fig. 3).

The pattern of warming pulses correlated with biotic change during the earliest Paleocene demonstrates a strong relationship between the biosphere and geosphere. The Deccan Traps of the Indian subcontinent represent repeated and voluminous volcanic eruptions (>10<sup>6</sup> km<sup>3</sup> of magma) during the post-KPgE Earth system succession (6, 7). These eruptions might have induced warming pulses via the release of greenhouse gases (e.g., CO<sub>2</sub>) (7). Recent work on the timing of these eruptions (6, 7) places ~70% of the total volume within the 300–400 ka window roughly coincident with the earliest Paleocene warming pulse(s) observed at Corral Bluffs and the temporally correlated shifts in biotic recovery (Figs. 1 and 4). Although not a feedback of the biosphere-geosphere system, Deccan eruptions likely influenced atmospheric chemistry, in turn shaping Earth system succession and post-KPgE ecosystem recovery (Fig. 4). Detailed records of post-mass extinction biotic recovery, such as the one presented here, will provide a critical framework for predicting ecosystem recovery following mass extinction events including the one we currently face (41).

## REFERENCES AND NOTES

- D. M. Raup, J. J. Sepkoski Jr., Mass extinctions in the marine fossil record. *Science* **215**, 1501–1503 (1982). doi:[10.1126/science.215.4539.1501](https://doi.org/10.1126/science.215.4539.1501) Medline
- M. A. O’Leary, J. I. Bloch, J. J. Flynn, T. J. Gaudin, A. Giallombardo, N. P. Giannini, S. L. Goldberg, B. P. Kraatz, Z.-X. Luo, J. Meng, X. Ni, M. J. Novacek, F. A. Perini, Z. S. Randall, G. W. Rougier, E. J. Sargis, M. T. Silcox, N. B. Simmons, M. Spaulding, P. M. Velasco, M. Weksler, J. R. Wible, A. L. Cirranello, The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* **339**, 662–667 (2013). doi:[10.1126/science.1229237](https://doi.org/10.1126/science.1229237) Medline
- R. O. Prum, J. S. Berv, A. Dornburg, D. J. Field, J. P. Townsend, E. M. Lemmon, A. R. Lemmon, A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**, 569–573 (2015). doi:[10.1038/nature15697](https://doi.org/10.1038/nature15697) Medline
- S. Magallón, L. L. Sánchez-Reyes, S. L. Gómez-Acevedo, Thirty clues to the exceptional diversification of flowering plants. *Ann. Bot.* **123**, 491–503 (2019). doi:[10.1093/aob/mcy182](https://doi.org/10.1093/aob/mcy182) Medline
- P. Schulte, L. Alegret, I. Arenillas, J. A. Arz, P. J. Barton, P. R. Bown, T. J. Bralower, G. L. Christeson, P. Claeys, C. S. Cockell, G. S. Collins, A. Deutscher, T. J. Goldin, K. Goto, J. M. Grajales-Nishimura, R. A. F. Grieve, S. P. S. Gulick, K. R. Johnson, W. Kiessling, C. Koeberl, D. A. Kring, K. G. MacLeod, T. Matsui, J. Melosh, A. Montanari, J. V. Morgan, C. R. Neal, D. J. Nichols, R. D. Norris, E. Pierazzo, G. Ravizza, M. Rebolledo-Vieyra, W. U. Reimold, E. Robin, T. Salge, R. P. Speijer, A. R. Sweet, J. Urrutia-Fucugauchi, V. Vajda, M. T. Whalen, P. S. Willumsen, The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. *Science* **327**, 1214–1218 (2010). doi:[10.1126/science.1177265](https://doi.org/10.1126/science.1177265) Medline
- B. Schoene, M. P. Eddy, K. M. Samperton, C. B. Keller, G. Keller, T. Adatte, S. F. R. Khadri, U-Pb constraints on pulsed eruption of the Deccan Traps across the end-Cretaceous mass extinction. *Science* **363**, 862–866 (2019). doi:[10.1126/science.aau2422](https://doi.org/10.1126/science.aau2422) Medline
- C. J. Sprain, P. R. Renne, L. Vanderkluysen, K. Pande, S. Self, T. Mittal, The eruptive tempo of Deccan volcanism in relation to the Cretaceous-Paleogene boundary. *Science* **363**, 866–870 (2019). doi:[10.1126/science.aav1446](https://doi.org/10.1126/science.aav1446) Medline
- J. D. Archibald, W. A. Clemens, K. Padian, T. Rowe, N. Macleod, P. M. Barrett, A. Gale, P. Holroyd, H. D. Sues, N. C. Arens, J. R. Horner, G. P. Wilson, M. B. Goodwin, C. A. Brochu, D. L. Lofgren, S. H. Hurlbert, J. H. Hartman, D. A. Eberth, P. B. Wignall, P. J. Currie, A. Weil, G. V. R. Prasad, L. Dingus, V. Courtillot, A. Milner, A. Milner, S. Bajpai, D. J. Ward, A. Sahni, Cretaceous extinctions: Multiple causes. *Science* **328**, 973–973, author reply 975–976 (2010). doi:[10.1126/science.328.5981.973-a](https://doi.org/10.1126/science.328.5981.973-a) Medline
- D. A. Pearson, T. Schaefer, K. R. Johnson, D. J. Nichols, J. P. Hunter, “Vertebrate biostratigraphy of the Hell Creek formation in southwestern North Dakota and northwestern South Dakota” in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, D. J. Nichols, Eds. (Geological Society of America Special Paper, vol. 361, 2002) pp. 145–167.
- G. P. Wilson, “Mammalian extinction, survival, and recovery dynamics across the Cretaceous-Paleogene boundary in northeastern Montana, USA,” in *Through the End of the Cretaceous in the Type Locality of the Hell Creek Formation in Montana and Adjacent Areas*, G. P. Wilson, W. A. Clemens, J. R. Horner, J. H. Hartman, Eds. (Geological Society of America Special Paper, ed. 503, 2014) pp. 365–392.
- D. J. Nichols, K. R. Johnson, *Plants and the K-T boundary*, (Cambridge University Press, MA, 2008).
- D. L. Lofgren, J. A. Lillegraven, W. A. Clemens, P. D. Gingrich, T. E. Williamson, “Paleocene biochronology: the Puercan through Clarkforkian Land Mammal Ages” in *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*, M. O. Woodburne, ed., (Columbia University Press, New York, New York, 2004), pp. 43–105.
- K. R. Johnson, “Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression” in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, D. J. Nichols, Eds. (Geological Society of America Special Paper, vol. 361, 2002) pp. 329–391.
- R. G. Reynolds, K. R. Johnson, Synopsis of the stratigraphy and paleontology of the uppermost Cretaceous and lower Tertiary strata in the Denver Basin, Colorado. *Rocky Mt. Geol.* **38**, 171–181 (2003). doi:[10.2113/gsrocky.38.1.171](https://doi.org/10.2113/gsrocky.38.1.171)
- J. J. Eberle, Puercan mammalian systematics and biostratigraphy in the Denver Formation, Denver Basin, Colorado. *Rocky Mt. Geol.* **38**, 143–169 (2003). doi:[10.2113/gsrocky.38.1.143](https://doi.org/10.2113/gsrocky.38.1.143)
- T. E. Williamson, *The Beginning of the Age of Mammals in the San Juan Basin, New Mexico: Biostratigraphy and Evolution of Paleocene Mammals of the Nacimiento Formation* (New Mexico Museum of Natural History and Science Bulletin ed. 8, 1996).
- J. A. Lillegraven, J. J. Eberle, Vertebrate faunal changes through Lancian and Puercan time in southern Wyoming. *J. Paleontol.* **73**, 691–710 (1999). doi:[10.1017/S0022336000032510](https://doi.org/10.1017/S0022336000032510)
- W. C. Clyde, J. Ramezani, K. R. Johnson, S. A. Bowring, M. M. Jones, Direct high-precision U-Pb geochronology of the end-Cretaceous extinction and calibration of Paleocene astronomical timescales. *Earth Planet. Sci. Lett.* **452**, 272–280 (2016). doi:[10.1016/j.epsl.2016.07.041](https://doi.org/10.1016/j.epsl.2016.07.041)
- M. Dechesne, R. G. Reynolds, P. E. Barkmann, K. J. Johnson, “Denver Basin Geologic Maps: Bedrock Geology, Structure and Isopach Maps of the Upper Cretaceous through Paleogene Strata between Greeley and Colorado Springs, Colorado. 1: 250,000. 15 maps and 3 cross sections: Colorado Geological Survey,” Colorado Geological Survey, 15 (2011).
- A. J. Fuentes, W. C. Clyde, K. Weissenburger, A. Bercovici, T. R. Lyson, I. M. Miller, J. Ramezani, M. D. Schmitz, K. R. Johnson, Constructing a timescale of biotic recovery across the Cretaceous–Paleogene boundary, Corral Bluffs, Denver Basin, Colorado. *bioRxiv* 10.1101/636951 (2019). doi:[10.1101/636951](https://doi.org/10.1101/636951)
- S. S. Hopkins, “Estimation of body size in fossil mammals” in *Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities*, D. A. Croft, D. F. Su, S. W. Simpson, Eds. (Springer, 2018), pp. 7–22.
- P. Wilf, K. R. Johnson, Land plant extinction at the end of the Cretaceous: A quantitative analysis of the North Dakota megafloral record. *Paleobiology* **30**, 347–368 (2004). doi:[10.1666/0094-8373\(2004\)030<0347:LPFATE>2.0.CO;2](https://doi.org/10.1666/0094-8373(2004)030<0347:LPFATE>2.0.CO;2)
- B. Blonder, D. L. Royer, K. R. Johnson, I. Miller, B. J. Enquist, Plant ecological strategies shift across the Cretaceous-Paleogene boundary. *PLOS Biol.* **12**, e1001949 (2014). doi:[10.1371/journal.pbio.1001949](https://doi.org/10.1371/journal.pbio.1001949) Medline

24. M. Lavin, P. S. Herendeen, M. F. Wojciechowski, Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the tertiary. *Syst. Biol.* **54**, 575–594 (2005). doi:10.1080/10635150590947131 Medline
25. M. Brea, A. B. Zamuner, S. D. Matheos, A. Iglesias, A. F. Zucol, Fossil wood of the Mimosoideae from the early Paleocene of Patagonia, Argentina. *Alcheringa* **32**, 427–441 (2008). doi:10.1080/03115510802417695
26. E. E. Comer, R. L. Slingerland, J. M. Krause, A. Iglesias, W. C. Clyde, M. S. Raigemborn, P. Wilf, Sedimentary facies and depositional environments of diverse early Paleocene floras, north-central San Jorge Basin, Patagonia, Argentina. *Palaios* **30**, 553–573 (2015). doi:10.2110/palo.2014.064
27. S. L. Wing, F. Herrera, C. A. Jaramillo, C. Gómez-Navarro, P. Wilf, C. C. Labandeira, Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 18627–18632 (2009). doi:10.1073/pnas.0905130106 Medline
28. P. Wilf, K. R. Johnson, B. T. Huber, Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous-Paleogene boundary. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 599–604 (2003). doi:10.1073/pnas.0234701100 Medline
29. T. S. Tobin, G. P. Wilson, J. M. Eiler, J. H. Hartman, Environmental change across a terrestrial Cretaceous-Paleogene boundary section in eastern Montana, USA, constrained by carbonate clumped isotope paleothermometry. *Geology* **42**, 351–354 (2014). doi:10.1130/G35262.1
30. J. S. K. Barnet, K. Littler, D. Kroon, M. J. Leng, T. Westerhold, U. Rohl, J. C. Zachos, A new high-resolution chronology for the late Maastrichtian warming event: Establishing robust temporal links with the onset of Deccan volcanism. *Geology* **46**, 147–150 (2017). doi:10.1130/G39771.1
31. K. G. MacLeod, P. C. Quinton, J. Sepúlveda, M. H. Negra, Postimpact earliest Paleogene warming shown by fish debris oxygen isotopes (El Kef, Tunisia). *Science* **360**, 1467–1469 (2018). doi:10.1126/science.aap8525 Medline
32. F. Quillévétré, R. D. Norris, D. Kroon, P. A. Wilson, Transient ocean warming and shifts in carbon reservoirs during the early Danian. *Earth Planet. Sci. Lett.* **265**, 600–615 (2008). doi:10.1016/j.epsl.2007.10.040
33. I. Gilmour, M. Gilmour, D. Jolley, S. Kelley, D. Kemp, R. Daly, J. Watson, A high-resolution nonmarine record of an early Danian hyperthermal event, Boltyshev crater, Ukraine. *Geology* **41**, 783–786 (2013). doi:10.1130/G34292.1
34. E. L. Dahlberg, J. J. Eberle, J. J. Sertich, I. M. Miller, A new earliest Paleocene (Puercan) mammalian fauna from Colorado's Denver Basin, USA. *Rocky Mt. Geol.* **51**, 1–22 (2016). doi:10.2113/gsrocky.51.1.1
35. M. D. Middleton, E. W. Dewar, "New mammals from the early Paleocene Littleton fauna (Denver Formation, Colorado)" in *Paleogene Mammals*, S. G. Lucas, K. E. Zeigler, P. E. Kondashov, Eds. (New Mexico Museum of Natural History and Science Bulletin, vol. 26, 2004) pp. 59–80.
36. K. D. Rose, *The Beginning of the Age of Mammals*. (Johns Hopkins University Press, Baltimore, Maryland, 2006).
37. J. D. Archibald, "Archaic ungulates ("Condylarthra")" in *Evolution of Tertiary Mammals of North America: Volume 1: Terrestrial Carnivores, Ungulates, and Ungulate Like Mammals*, C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. pp. 292 (1998).
38. E. W. Dewar, Functional diversity within the Littleton fauna (early Paleocene), Colorado: Evidence from body mass, tooth structure, and tooth wear. *PaleoBios* **23**, 1–19 (2003).
39. B. H. Tiffney, Seed size, dispersal syndromes, and the rise of the angiosperms: Evidence and hypothesis. *Ann. Mo. Bot. Gard.* **71**, 551–576 (1984). doi:10.2307/2399037
40. P. Hull, Life in the aftermath of mass extinctions. *Curr. Biol.* **25**, R941–R952 (2015). doi:10.1016/j.cub.2015.08.053 Medline
41. A. D. Barnosky, N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, E. A. Ferrer, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011). doi:10.1038/nature09678 Medline
42. R. G. Raynolds, "Synorogenic and postorogenic strata in the central Front Range, Colorado" in *Geologic History of the Colorado Front Range: Rocky Mountain Association of Geologists*, B. D. Boyland, S. S. Sonnenberg, Eds. (Rocky Mountain Association of Geologists, 1997), pp. 43–47.
43. R. G. Raynolds, Upper Cretaceous and Tertiary stratigraphy of the Denver Basin, Colorado. *Rocky Mt. Geol.* **37**, 111–134 (2002). doi:10.2113/3
44. D. E. Fastovsky, A. Bercovici, The Hell Creek Formation and its contribution to the Cretaceous-Paleogene extinction: A short primer. *Cretac. Res.* **57**, 368–390 (2016). doi:10.1016/j.cretres.2015.07.007
45. R. W. Brown, Cretaceous-Tertiary boundary in the Denver Basin, Colorado. *Bull. Geol. Soc. Am.* **54**, 65–86 (1943). doi:10.1130/GSAB-54-65
46. K. R. Johnson, M. L. Reynolds, K. W. Werth, J. R. Thomasson, Overview of the Late Cretaceous, early Paleocene, and early Eocene megafloras of the Denver Basin, Colorado. *Rocky Mt. Geol.* **38**, 101–120 (2003). doi:10.2113/gsrocky.38.1.101
47. K. P. Benson, Colorado College, "Floral diversity and paleoclimate of the latest Cretaceous and early tertiary deposits, Denver Basin, Colorado, USA" (1998).
48. J. F. Hicks, K. R. Johnson, J. D. Obradovich, D. P. Miggins, L. Taupe, Magnetostratigraphy of Upper Cretaceous (Maastrichtian) to lower Eocene strata of the Denver Basin, Colorado. *Rocky Mt. Geol.* **38**, 1–27 (2003). doi:10.2113/gsrocky.38.1.1
49. F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, *The Geologic Time Scale 2012*. (Elsevier, 2012).
50. J. G. Ogg, "Geomagnetic polarity timescale" in *The Geologic Time Scale*, F. M. Gradstein, J. G. Ogg, M. Schmitz, G. Ogg, Eds. (Elsevier, 2012), pp. 85–114.
51. D. J. Nichols, R. F. Fleming, Palynology and palynostratigraphy of Maastrichtian, Paleocene, and Eocene strata in the Denver Basin, Colorado. *Rocky Mt. Geol.* **37**, 135–163 (2002). doi:10.2113/4
52. R. S. Barclay, K. R. Johnson, W. J. Betterton, D. L. Dilcher, Stratigraphy and megaflora of a KT boundary section in the eastern Denver Basin, Colorado. *Rocky Mt. Geol.* **38**, 45–71 (2003). doi:10.2113/gsrocky.38.1.45
53. K. R. Johnson, D. J. Nichols, M. Attrep, C. J. Orth, High-resolution leaf-fossil record spanning the Cretaceous/Tertiary boundary. *Nature* **340**, 708–711 (1989). doi:10.1038/340708a0
54. B. Ellis et al., *Manual of Leaf Architecture*. (Cornell University Press, Ithaca, NY, 2009).
55. I. M. Miller, L. J. Hickey, The fossil flora of the Winthrop Formation (Albian-Early Cretaceous) of Washington State, USA. Part II: Pinophytina. *Bull. Peabody Mus. Nat. Hist.* **51**, 3–96 (2010). doi:10.3374/014.051.0104
56. I. W. Bailey, E. W. Sinnott, A botanical index of Cretaceous and Tertiary climates. *Science* **41**, 831–834 (1915). doi:10.1126/science.41.1066.831 Medline
57. J. A. Wolfe, Tertiary climatic fluctuations and methods of analysis of Tertiary floras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **9**, 27–57 (1971). doi:10.1016/0031-0182(71)90016-2
58. J. A. Wolfe, A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere: Data from fossil plants make it possible to reconstruct Tertiary climatic changes, which may be correlated with changes in the inclination of the earth's rotational axis. *Am. Sci.* **66**, 694–703 (1978).
59. J. Wolfe, Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere. *U.S. Geol. Surv. Prof. Pap.* **1106**, 1–37 (1979).
60. S. L. Wing, D. R. Greenwood, Fossils and fossil climate: The case for equable continental interiors in the Eocene. *Philos. Trans. R. Soc. B* **341**, 243–252 (1993). doi:10.1098/rstb.1993.0109
61. D. R. Greenwood, Fossil angiosperm leaves and climate: From Wolfe and Dilcher to Burnham and Wilf. *Cour. For. Sencken.* **258**, 95 (2007).
62. I. M. Miller, M. T. Brandon, L. J. Hickey, Using leaf margin analysis to estimate the mid-Cretaceous (Albian) paleolatitude of the Baja BC block. *Earth Planet. Sci. Lett.* **245**, 95–114 (2006). doi:10.1016/j.epsl.2006.02.022
63. D. J. Peppe, A. Baumgartner, A. Flynn, B. Blonder, "Reconstructing paleoclimate and paleoecology using fossil leaves" in *Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities*, D. A. Croft, D. F. Su, S. W. Simpson, Eds. (Springer, 2018), pp. 289–317.
64. D. R. Greenwood, P. Wilf, S. L. Wing, D. C. Christophe, Paleotemperature estimation using leaf-margin analysis: Is Australia different? *Palaios* **19**, 129–142 (2004). doi:10.1669/0883-1351(2004)019<0129:PFULAI>2.0.CO;2
65. K. M. Gregory-Wodzicki, Relationships between leaf morphology and climate, Bolivia: Implications for estimating paleoclimate from fossil floras. *Paleobiology* **26**, 668–688 (2000). doi:10.1666/0094-8373(2000)026<0668:RBLMAC>2.0.CO;2

66. R. J. Burnham, N. C. Pitman, K. R. Johnson, P. Wilf, Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. *Am. J. Bot.* **88**, 1096–1102 (2001). doi:[10.2307/2657093](https://doi.org/10.2307/2657093) Medline
67. D. R. Greenwood, Leaf margin analysis: Taphonomic constraints. *Palaios* **20**, 498–505 (2005). doi:[10.2110/palo.2004.P04-58](https://doi.org/10.2110/palo.2004.P04-58)
68. S. R. Manchester, Biogeographical relationships of North American Tertiary floras. *Ann. Mo. Bot. Gard.* **86**, 472–522 (1999). doi:[10.2307/2666183](https://doi.org/10.2307/2666183)
69. P. Wilf, When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* **23**, 373–390 (1997). doi:[10.1017/S0094837300019746](https://doi.org/10.1017/S0094837300019746)
70. D. L. Royer, L. A. Meyerson, K. M. Robertson, J. M. Adams, Phenotypic plasticity of leaf shape along a temperature gradient in *Acer rubrum*. *PLOS ONE* **4**, e7653 (2009). doi:[10.1371/journal.pone.0007653](https://doi.org/10.1371/journal.pone.0007653) Medline
71. D. L. Royer, P. Wilf, Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *Int. J. Plant Sci.* **167**, 11–18 (2006). doi:[10.1086/497995](https://doi.org/10.1086/497995)
72. S. A. Little, S. W. Kembel, P. Wilf, Paleotemperature proxies from leaf fossils reinterpreted in light of evolutionary history. *PLOS ONE* **5**, e15161 (2010). doi:[10.1371/journal.pone.0015161](https://doi.org/10.1371/journal.pone.0015161) Medline
73. J. A. Wolfe, G. R. Upchurch Jr., North American nonmarine climates and vegetation during the Late Cretaceous. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **61**, 33–77 (1987). doi:[10.1016/0031-0182\(87\)90040-X](https://doi.org/10.1016/0031-0182(87)90040-X)
74. S. L. Wing, G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, K. H. Freeman, Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* **310**, 993–996 (2005). doi:[10.1126/science.1116913](https://doi.org/10.1126/science.1116913) Medline
75. E. D. Curran, P. Wilf, S. L. Wing, C. C. Labandeira, E. C. Lovelock, D. L. Royer, Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1960–1964 (2008). doi:[10.1073/pnas.0708646105](https://doi.org/10.1073/pnas.0708646105) Medline
76. D. L. Royer, L. Sack, P. Wilf, C. H. Lusk, G. J. Jordan, Ü. Niinemets, I. J. Wright, M. Westoby, B. Cariglino, P. D. Coley, A. D. Cutter, K. R. Johnson, C. C. Labandeira, A. T. Moles, M. B. Palmer, F. Valladares, A.D., Fossil leaf economics quantified: Calibration, Eocene case study, and implications. *Paleobiology* **33**, 574–589 (2007). doi:[10.1666/070011](https://doi.org/10.1666/070011)
77. E. G. Kauffman, G. R. Upchurch, D. J. Nichols, "The Cretaceous-Tertiary boundary interval at south table mountain, near Golden, Colorado" in *Extinction Events in Earth History*, E. G. Kauffman, O. H. Walliser, Eds. (Springer, 1990), pp. 365–392.
78. P. D. Gingerich, Prediction of body mass in mammalian species from long bone lengths and diameters. *Contrib. Mus. Paleont. Univ. Mich.* **28**, 79–92 (1990).
79. C. M. Janis, J. Damuth, B. MacFadden, "Correlation of cranial and dental variables with body size in ungulates and macropodoids" in *Body Size in Mammalian Paleobiology, Estimation and Biological Implications*. J. D. Damuth, B. J. MacFadden, Eds. (Cambridge University Press, 1990), pp. 255–291.
80. E. Delson, C. J. Terranova, W. L. Jungers, E. J. Sargis, N. G. Jablonski, *Body Mass in Cercopithecidae (Primates, Mammalia): Estimation and Scaling in Extinct and Extant Taxa*. (Anthropological papers of the AMNH, vol. 83, 2000).
81. N. E. Campione, D. C. Evans, A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biol.* **10**, 60 (2012). doi:[10.1186/1741-7007-10-60](https://doi.org/10.1186/1741-7007-10-60) Medline
82. G. P. Wilson, E. G. Ekdale, J. W. Hoganson, J. J. Caleda, A. Vander Linden, A large carnivorous mammal from the Late Cretaceous and the North American origin of marsupials. *Nat. Commun.* **7**, 13734 (2016). doi:[10.1038/ncomms13734](https://doi.org/10.1038/ncomms13734) Medline
83. E. C. Kirk, S. Hoffmann, A. D. Kemp, D. W. Krause, P. M. O'Connor, Sensory anatomy and sensory ecology of *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **34**, 203–222 (2014). doi:[10.1080/02724634.2014.963232](https://doi.org/10.1080/02724634.2014.963232)
84. S. Legendre, in *Analysis of Mammalian Communities From the Late Eocene and Oligocene of Southern France (Palaeovertebrata)* (Laboratoire de Paleontologie de l'Universite des Sciences et Techniques du Languedoc, 1986), pp. 191–212.
85. P. D. Gingerich, Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. *J. Paleontol.* **48**, 895–903 (1974).
86. P. D. Gingerich, B. H. Smith, K. Rosenberg, Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *Am. J. Phys. Anthropol.* **58**, 81–100 (1982). doi:[10.1002/ajpa.1330580110](https://doi.org/10.1002/ajpa.1330580110) Medline
87. P. D. Gingerich, M. J. Schoeninger, Patterns of tooth size variability in the dentition of primates. *Am. J. Phys. Anthropol.* **51**, 457–465 (1979). doi:[10.1002/ajpa.1330510318](https://doi.org/10.1002/ajpa.1330510318) Medline
88. V. Vajda, A. Bercovici, The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: A template for other extinction events. *Global Planet. Change* **122**, 29–49 (2014). doi:[10.1016/j.gloplacha.2014.07.014](https://doi.org/10.1016/j.gloplacha.2014.07.014)
89. D. J. Nichols, K. R. Johnson, J. Hartman, "Palynology and microstratigraphy of Cretaceous-Tertiary boundary sections in southwestern North Dakota" in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, J. H. Hartman, K. R. Johnson, D. J. Nichols, Eds. (Geological Society of America Special Paper, vol. 361, 2002) pp. 95–143.
90. D. J. Field, A. Bercovici, J. S. Berv, R. Dunn, D. E. Fastovsky, T. R. Lyson, V. Vajda, J. A. Gauthier, Early evolution of modern birds structured by global forest collapse at the end-Cretaceous mass extinction. *Curr. Biol.* **28**, 1825–1831.e2 (2018). doi:[10.1016/j.cub.2018.04.062](https://doi.org/10.1016/j.cub.2018.04.062) Medline
91. R. H. Tschauder, "Palynological evidence for change in continental floras at the Cretaceous-Tertiary boundary" in *Catastrophes in Earth History: The New Uniformitarianism*, W. A. Berggren, J. A. Van Couvering, Eds. (Princeton University Press, Princeton, New Jersey, 1984), pp. 315–337.
92. R. H. Tschauder, C. L. Pillmore, C. J. Orth, J. S. Gilmore, J. D. Knight, Disruption of the terrestrial plant ecosystem at the cretaceous-tertiary boundary, Western interior. *Science* **225**, 1030–1032 (1984). doi:[10.1126/science.225.4666.1030](https://doi.org/10.1126/science.225.4666.1030) Medline
93. D. J. Nichols, R. F. Fleming, "Plant microfossil record of the terminal Cretaceous event in the western United States and Canada" in *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*, V. L. Sharpton, P. D. Ward, Eds. (Geological Society of America Special Paper, vol. 247, 1990) pp. 445–455.
94. D. J. Nichols, J. L. Brown, M. Attrep Jr., C. J. Orth, A new Cretaceous-Tertiary boundary locality in the western Powder River basin, Wyoming: Biological and geological implications. *Cretac. Res.* **13**, 3–30 (1992). doi:[10.1016/0195-6671\(92\)90026-M](https://doi.org/10.1016/0195-6671(92)90026-M)
95. A. Bercovici, V. Vajda, D. Pearson, U. Villanueva-Amadoz, D. Kline, Palynostratigraphy of John's Nose, a new Cretaceous-Paleogene boundary section in southwestern North Dakota, USA. *Palynology* **36** (sup1), 36–47 (2012). doi:[10.1080/01916122.2012.678695](https://doi.org/10.1080/01916122.2012.678695)
96. A. Bercovici, D. Pearson, D. Nichols, J. Wood, Biostratigraphy of selected K/T boundary sections in southwestern North Dakota, USA: Toward a refinement of palynological identification criteria. *Cretac. Res.* **30**, 632–658 (2009). doi:[10.1016/j.cretres.2008.12.007](https://doi.org/10.1016/j.cretres.2008.12.007)
97. D. J. Nichols, *Reevaluation of the Holotypes of the Wodehouse Pollen Species from the Green River Formation (Eocene, Colorado and Utah)*, (American Association of Stratigraphic Palynologists Foundation, 2010).
98. D. J. Nichols, H. L. Ott, Biostratigraphy and evolution of the *Momipites-Caryapollenites* lineage in the early Tertiary in the Wind River Basin, Wyoming. *Palynology* **2**, 93–112 (1978). doi:[10.1080/01916122.1978.9989167](https://doi.org/10.1080/01916122.1978.9989167)
99. D. J. Nichols, H. L. Ott, Neotypes for Paleocene species in the *Momipites-Caryapollenites* pollen lineage. *Palynology* **30**, 33–41 (2006). doi:[10.2113/gspalynol.30.1.33](https://doi.org/10.2113/gspalynol.30.1.33)
100. S. Palamarczuk, N. H. Landman, Dinoflagellate cysts from the upper Campanian Pierre Shale and Bearpaw Shale of the US Western Interior. *Rocky Mt. Geol.* **46**, 137–164 (2011). doi:[10.2113/gsrocky.46.2.137](https://doi.org/10.2113/gsrocky.46.2.137)
101. D. J. Nichols, "Palynostratigraphic framework for age determination and correlation of the nonmarine lower Cenozoic of the Rocky Mountains and great plains region" in *Cenozoic Systems of the Rocky Mountain Region*, R. G. Raynolds, R. M. Flores, Eds. (Rocky Mountain Section (SEPM), 2003) pp. 107–134.
102. D. J. Nichols, On the palynomorph-based biozones in Paleogene strata of Rocky Mountain basins. *Mt. Geol.* **46**, 105–121 (2009).
103. D. Nichols, S. Jacobson, R. Tschauder, "Cretaceous palynomorph biozones for the central and northern Rocky Mountain region in the United States" in *Geologic Studies of the Cordilleran Thrust Belt vol. II*, R. B. Powers, Ed. (Rocky Mountain Association of Geologists, Denver, Colorado, 1982).
104. D. J. Nichols, "A revised palynostratigraphic zonation of the nonmarine Upper Cretaceous, Rocky Mountain Region, United States" in *Mesozoic Systems of the*

- Rocky Mountain Region, USA.* (Rocky Mountain Section (SEPM), 1994), pp. 503–522.
105. R. Villar, J. Ruiz-Robledo, J. L. Ubera, H. Poorter, Exploring variation in leaf mass per area (LMA) from leaf to cell: An anatomical analysis of 26 woody species. *Am. J. Bot.* **100**, 1969–1980 (2013). doi:[10.3732/ajb.1200562](https://doi.org/10.3732/ajb.1200562) Medline
106. I. J. Wright, P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, R. Villar, The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004). doi:[10.1038/nature02403](https://doi.org/10.1038/nature02403) Medline
107. H. Poorter, U. Niinemets, L. Poorter, I. J. Wright, R. Villar, Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytol.* **182**, 565–588 (2009). doi:[10.1111/j.1469-8137.2009.02830.x](https://doi.org/10.1111/j.1469-8137.2009.02830.x) Medline
108. C. L. Gazin, Paleocene mammals from the Denver Basin, Colorado. *Washington Acad. Sci.* **31**, 289–295 (1941).
109. M. D. Middleton, University of Colorado, Boulder, “Early Paleocene vertebrates of the Denver Basin, Colorado” (1983).
110. J. H. Hutchison, Determinate growth in the Baenidae (Testudines): Taxonomic, ecologic and stratigraphic significance. *J. Vertebr. Paleontol.* **3**, 148–151 (1984). doi:[10.1080/02724634.1984.10011968](https://doi.org/10.1080/02724634.1984.10011968)
111. T. R. Lyson, J. L. Sayler, W. G. Joyce, A new baenid turtle, *Saxochelys giberti*, gen. et sp. nov., from the uppermost Cretaceous (Maastrichtian) Hell Creek Formation: Sexual dimorphism and spatial niche partitioning within the most speciose group of Late Cretaceous turtles. *J. Vertebr. Paleontol.* e1662428 (2019). doi:[10.1080/02724634.2019.1662428](https://doi.org/10.1080/02724634.2019.1662428)
112. P. Holroyd, J. H. Hutchison, Patterns of geographic variation in latest Cretaceous vertebrates: Evidence from the turtle component. *Spec. Pap. Geol. Soc. Am.* **361**, 177–190 (2002). doi:[10.1130/0-8137-2361-2.177](https://doi.org/10.1130/0-8137-2361-2.177)
113. J. H. Hutchison, A new eubaenine, *Goleremys mckennai*, gen. et sp. n., (Baenidae: Testudines) from the Paleocene of California. *Bull. Carneg. Mus. Nat. Hist.* **36**, 91–96 (2004). doi:[10.2992/0145-9058\(2004\)36\[91:ANFGMG\]2.0.CO;2](https://doi.org/10.2992/0145-9058(2004)36[91:ANFGMG]2.0.CO;2)
114. T. R. Lyson, W. G. Joyce, A new species of *Palatobaena* (Testudines: Baenidae) and a maximum parsimony and Bayesian phylogenetic analysis of Baenidae. *J. Paleontol.* **83**, 457–470 (2009a). doi:[10.1666/08-172.1](https://doi.org/10.1666/08-172.1)
115. T. R. Lyson, W. G. Joyce, A revision of *Plesioabaena* (Testudines: Baenidae) and an assessment of baenid ecology across the K/T boundary. *J. Paleontol.* **83**, 833–853 (2009b). doi:[10.1666/09-035.1](https://doi.org/10.1666/09-035.1)
116. P. A. Holroyd, G. P. Wilson, J. H. Hutchison, Temporal changes within the latest Cretaceous and early Paleogene turtle faunas of northeastern Montana. *Spec. Pap. Geol. Soc. Am.* **503**, 299–312 (2014). doi:[10.1130/2014.2503\(11\)](https://doi.org/10.1130/2014.2503(11))
117. W. G. Joyce, T. R. Lyson, A review of the fossil record of turtles of the clade Baenidae. *Bull. Peabody Mus. Nat. Hist.* **56**, 147–183 (2015). doi:[10.3374/014.056.0203](https://doi.org/10.3374/014.056.0203)
118. C. H. Ernst, R. W. Barbour, *Turtles of the World*. Washington, DC: Smithsonian Institution Press (1989).
119. G. E. Knauss, W. G. Joyce, T. R. Lyson, D. Pearson, A new kinosternoid from the Late Cretaceous Hell Creek Formation of North Dakota and Montana and the origin of the *Dermatemys mawii* lineage. *Paläontologische Zeitschrift* **85**, 125–142 (2011). doi:[10.1007/s12542-010-0081-x](https://doi.org/10.1007/s12542-010-0081-x)
120. T. R. Lyson, W. G. Joyce, J. J. W. Sertich, A new chelydroid turtle, *Lutemys warren*, gen. et sp. nov. from the Upper Cretaceous (Campanian) Kaiparowits Formation of southern Utah. *J. Vertebr. Paleontol.* **37**, e1390672 (2017). doi:[10.1080/02724634.2017.1390672](https://doi.org/10.1080/02724634.2017.1390672)
121. J. D. Damuth, B. J. MacFadden, “Introduction: body size and its estimation” in *Body Size in Mammalian Paleobiology: Estimation and Biological Implications* J. D. Damuth, B. J. MacFadden, Eds. (Cambridge University Press, Cambridge, 1990), pp. 1–10.
122. G. P. Wilson, A. R. Evans, I. J. Corfe, P. D. Smits, M. Fortelius, J. Jernvall, Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. *Nature* **483**, 457–460 (2012). doi:[10.1038/nature10880](https://doi.org/10.1038/nature10880) Medline
123. V. Millien, H. Bovy, When teeth and bones disagree: Body mass estimation of a giant extinct rodent. *J. Mammal.* **91**, 11–18 (2010). doi:[10.1644/08-MAMM-A-347R1.1](https://doi.org/10.1644/08-MAMM-A-347R1.1)

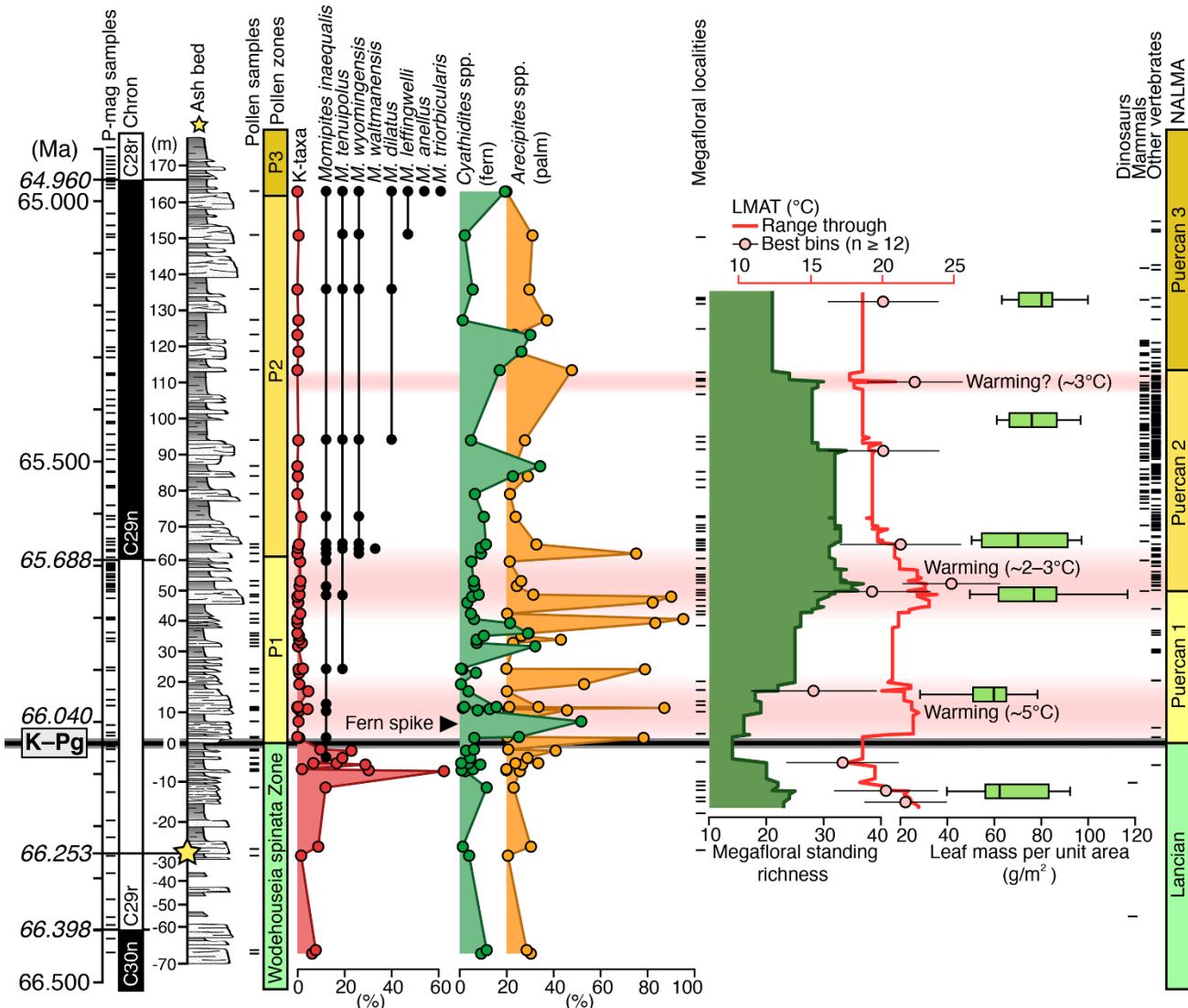
## ACKNOWLEDGMENTS

We thank Norwood Properties, City of Colorado Springs, Waste Management, Aztec Family Raceway, J. Hawkins, J. Hilaire, J. Carner, W. Pendleton, the Bishop Family, H. Kunstle for land access; J. Alicia, S. Begin, J. P. Cavigelli, H. Cochard, J. Englehorn, J. Groenke, F. Koether, L. Lacey, A. Lujan, B. Masek, B. Pittman, N. Toth for preparation of specimens; K. Getty, R. Hess, R. Lavie, S. Milito, Y. Rollot, P. Sullivan, J. Wyman, L. Taylor for field assistance; F. Cochard, L. Dougan, S. Luallin, R. Wicker, J. Wood, USGS National Unmanned Aircraft Systems team for photography; K. MacKenzie, N. Neu-Yagle for collections assistance; and B. Snellgrove for logistics. **Funding:** Funding was provided by The Lisa Levin Appel Family Foundation, M. Cleworth, Lyda Hill Philanthropies, David B. Jones Foundation, M.L. and S.R. Kneller, T. and K. Ryan, and J.R. Tucker as part of the Denver Museum of Nature & Science (DMNS) No Walls Community Initiative. **Author contributions:** T.R.L. and I.M.M. led the project; T.R.L. wrote and edited the manuscript in collaboration with I.M.M.; A.D.B., K.W., and S.G.B.C. were primary project participants; all authors collected and/or analyzed data and samples, interpreted results, and edited the manuscript. **Competing interests:** None declared. **Data and materials availability:** Fossil specimens and pollen slides all deposited at the DMNS. All data are available in supplementary materials.

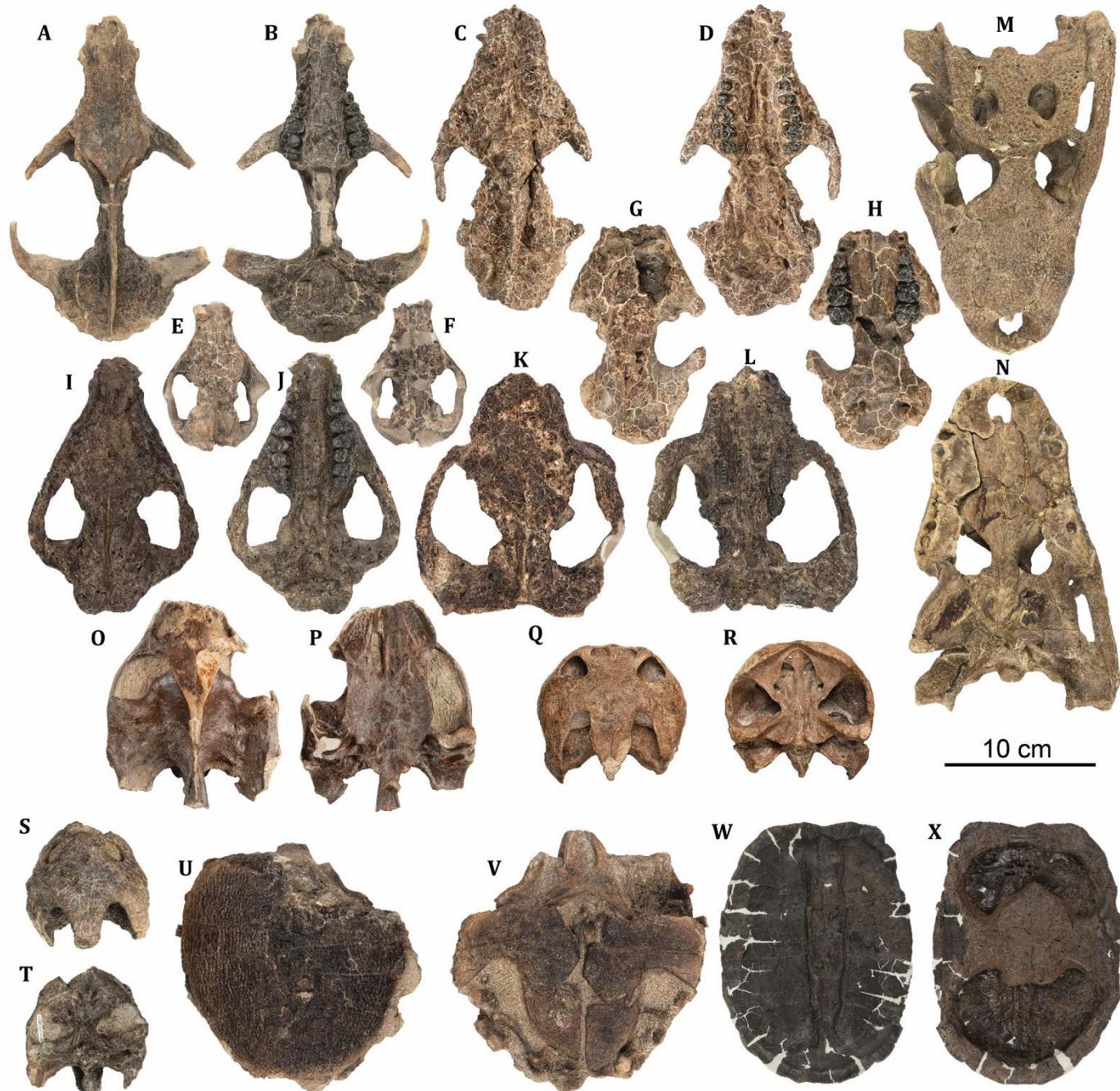
## SUPPLEMENTARY MATERIALS

[science.sciencemag.org/cgi/content/full/science.aay2268/DC1](https://science.sciencemag.org/cgi/content/full/science.aay2268/DC1)  
Materials and Methods  
Supplementary Text  
Figs. S1 to S9  
Table S1  
Data Files S1 to S14  
References (42–123)

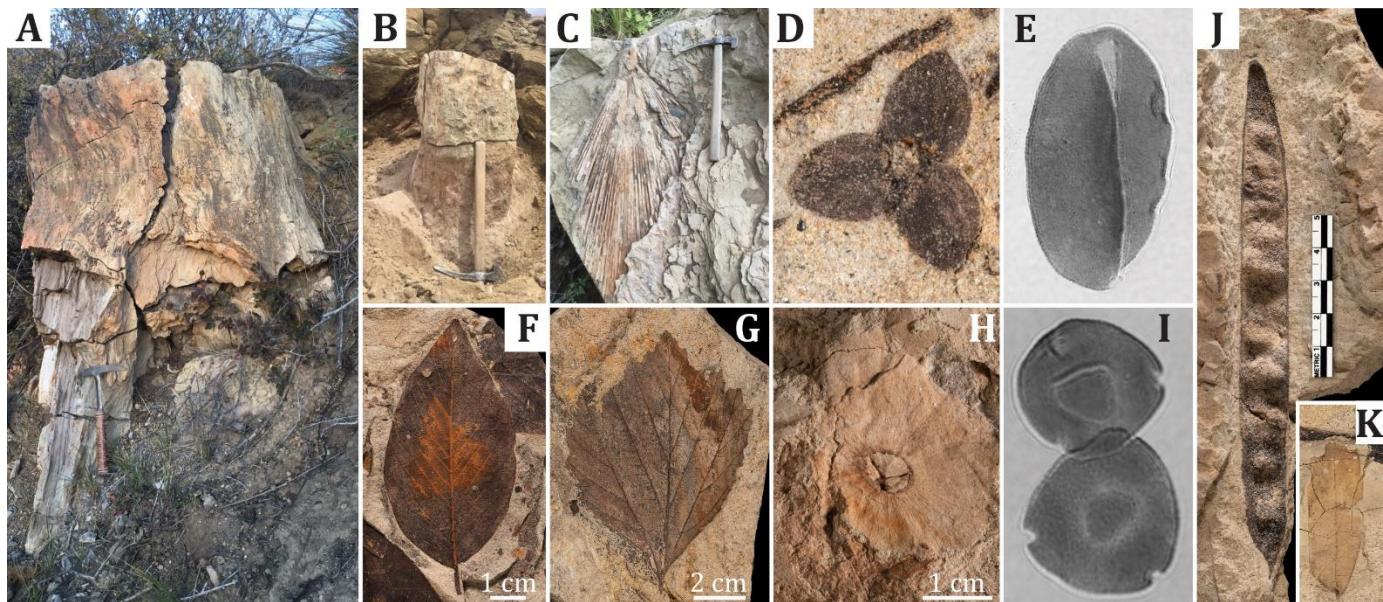
3 June 2019; accepted 15 October 2019  
Published online 24 October 2019  
10.1126/science.aay2268



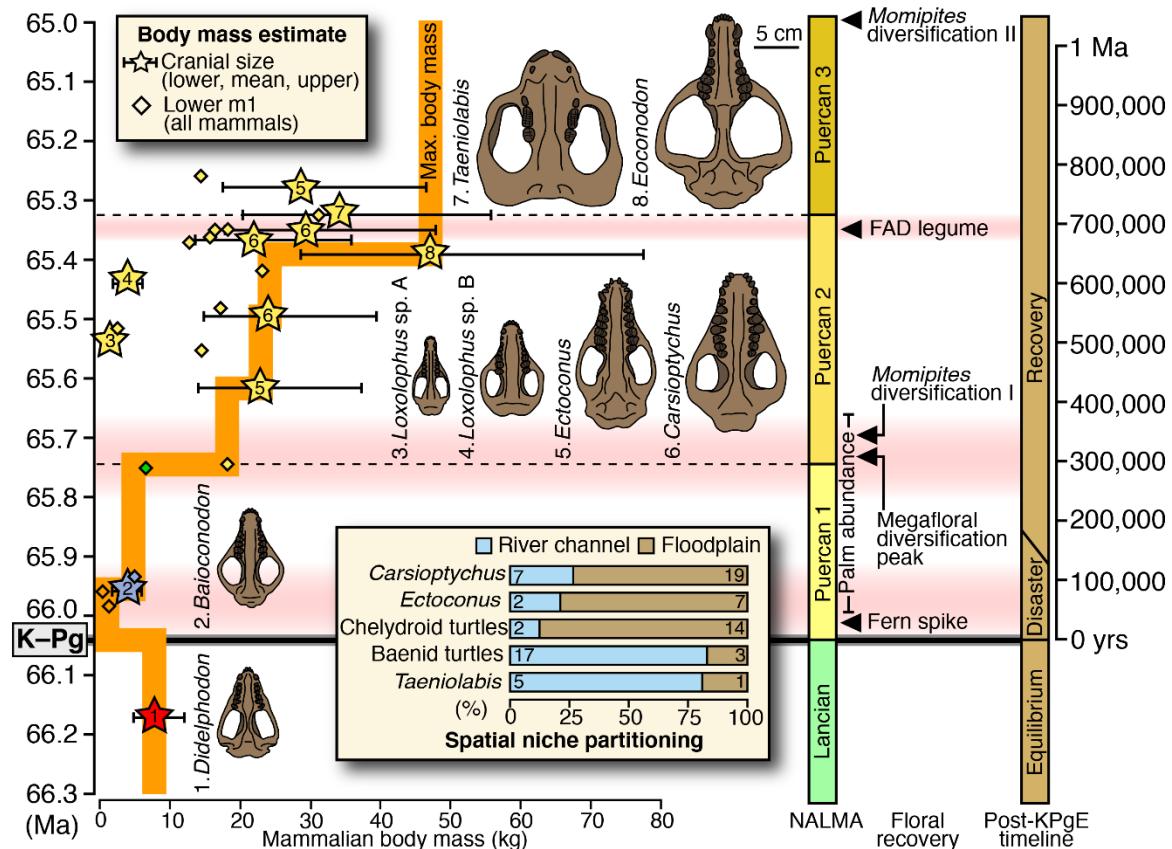
**Fig. 1. Temporally calibrated stratigraphic, floral, and faunal data for the K-Pg interval in the Corral Bluffs study area (fig. S1).** Stratigraphy is tied to the Geomagnetic Polarity Time Scale (GPTS 2012) using paleomagnetics and a CA-ID-TIMS U-Pb-dated ash (italicized dates) (20) (data file S1 and figs. S3 and S5). The composite lithostratigraphic log (figs. S2 to S5) is dominated by intercalated mudstone and sandstone, reflecting a variety of fluvial facies. Pollen zones (data file S3) are defined by diversification of *Momipites* spp. (fossil juglandaceous pollen) (Fig. 3I). The K-Pg boundary is demarcated by the decrease in abundance of Cretaceous pollen taxa (labeled as “K-taxa”) without recovery, and subsequent fern (*Cyathidites* spp.) spike (data file S2). Relative abundance (%) of fern (*Cyathidites* spp.) and palm (*Arecipites* spp.) (Fig. 3E) palynomorphs increased dramatically post-KPgE (data file S2); note palm pollen percentages are offset from scale by 20%. Standing richness of dicot morphospecies or megafloral standing richness is exclusive of species that occur at a single locality (data files S4 to S7). Leaf-estimated mean annual temperature (LMAT) calibrated with East Asian forests (data file S8 and fig. S6). Pink horizontal bars indicate hypothesized warming intervals. Estimated leaf mass per unit area (data files S9 and S10 and fig. S7); shown with box plots that represent the distribution of species-site pair means for each 30-m bin starting from the K-Pg boundary (supplementary materials). Boxplots are placed along the y-axis near each bin's stratigraphic midpoint, repositioned for visibility. See data file S11 and supplementary materials for placement of NALMAS. Tick marks next to GPTS, pollen zones, megafloral standing richness, and NALMAS show stratigraphic placement of samples and fossil localities (supplementary materials).



**Fig. 2. Representative selection of vertebrate fossils.** (A to R) Crania in dorsal and ventral views of *Eoconodon coryphaeus* [(A) and (B); DMNH.EPV.130976], *Ectoconus ditrigonus* [(C) and (D); DMNH.EPV.130985], *Loxolophus* sp. [(E) and (F); DMNH.EPV.132501], juvenile *Ectoconus ditrigonus* [(G) and (H); DMNH.EPV.132515], *Carsioptychus coarctatus* [(I) and (J); DMNH.EPV.95283], *Taeniolabis taoensis* [(K) and (L); DMNH.EPV.95284], cf. *Navajosuchus* [(M) and (N); DMNH.EPV.48541], *Axestemys infernalis* [(O) and (P); DMNH.EPV.132514], *Palatobaena* sp. [(Q) and (R); DMNH.EPV.134081], and (S and T) *Cedrobaena putorius* (DMNH.EPV.130982). (U to X) Turtle shells in dorsal and ventral views of *Gilmoremys* sp. [(U) and (V); DMNH.EPV.95454] and *Hoplochelys* sp. [(W) and (X); DMNH.EPV.95453]. All crania and shells to scale except for (W) and (X), which are scaled 1:2 compared to other specimens (10-cm scale bar).



**Fig. 3. Representative selection of plant fossils.** (A) In situ tree stump. (B to E) Palm fossils—in-situ stump (B), frond (C), flower (D; DMNH.EPI.45594), and *Arecipites* sp. pollen grain (E). (F and G) Most common smooth and toothed dicot morphospecies—(F) “*Rhamnus*” *goldiana* (DMNH.EPI.52262) and (G) *Platanites marginata* (DMNH.EPI.23281). (H and I) Walnut family flower and pollen—*Cyclocarya* sp. (DMNH.EPI.52272) and *Momipites tenuipolus* pollen grains preserved as a dyad (H). (J) Legume seedpod (DMNH.EPI.45540). (K) Legume leaflet (DMNH.EPI.45576). Rock hammer handle = 38 cm in (A) to (C); (D), flower is 5 mm wide; (E), pollen grain is 42 µm long; (I), each pollen grain has a 20 µm diameter; leaflet in (K) is scaled 2:1 compared to (J) (5-cm scale bar).



**Fig. 4.** Timeline of expansion of maximum body mass and niche space in earliest Paleocene mammals correlated with diversification and origination of key plant groups and warming intervals. Post-KPgE “disaster” ecosystems occur for less than 100 ka, ecosystem “recovery” occurs between ~100–300 ka, and overall post-KPgE ecosystem equilibrium occurs within ~300 ka. Mammalian body mass estimated based on cranial and lower first molar dimensions of specimens recovered from Pu1–Pu3 intervals (data files S13 and S14 and figs. S8 and S9). Data from Corral Bluffs study area (yellow) except for Pu1 mammals, which come from adjacent outcrops in the Denver Basin (West Bijou (no fill; orange), South Table Mountain (blue), and Alexander Locality (green)) and *Didelphodon* from North Dakota (red) (data files S13 and S14 and supplementary materials). Not plotted is distribution of other large (10–100+ kg) vertebrates (e.g., turtles, crocodilians, dinosaurs) found throughout the section (Fig. 1). Pink, blurred horizontal bars represent hypothesized warming intervals interpreted from LMAT. Niche partitioning graph showing environmental distribution of vertebrate groups (data file S12): *Carsioptychus*, *Ectoconus*, and chelydroid turtles predominantly associated with floodplain and ponded water facies; baenid turtles and *Taeniolabis* predominantly in river channel complexes and proximal to medial crevasse splay facies. FAD = first appearance datum.