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A preliminary test of the press-pulse extinction hypothesis: Palynological indicators of vegetation change preceding the Cretaceous-Paleogene boundary, McCone County, Montana, USA

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ABSTRACT

Many workers consider the Cretaceous-Paleogene extinction the archetypal catastrophic pulse event caused solely by the Chicxulub bolide impact. However, based on a global scale analysis of marine animals, the Cretaceous-Paleogene boundary is a candidate for an extinction enhanced by the coincidence of press and pulse disturbances. We make a preliminary test of key predictions of the press-pulse hypothesis using palynological data. We document a local palynological extinction of 21% at the Cretaceous-Paleogene boundary, which is consistent with extinction rates of 15% to 30% at other localities in the Hell Creek type area and throughout North America. We also find a decline in the number of dicot angiosperm pollen taxa between –3.5 m and –2.5 m below the boundary. We document a low-palynospecies-richness interval between –1.4 m and –1.0 m that includes extirpation, but not extinction, of some palynospecies. These changes in species richness are not correlated with changes in depositional style or pollen preservation, indicating that they may represent a biological rather than entirely taphonomic signal. Review and reanalysis of previously published data from other localities in the western interior of North America suggest similar declines in species richness within approximately the same stratigraphic interval. However, many of the species absent during the low-species-richness interval reappeared before the Cretaceous-Paleogene boundary, suggesting changes in community structure and composition before the terminal Cretaceous event—a key prediction of the press-pulse hypothesis—rather than gradual extinction in the latest Cretaceous.

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INTRODUCTION

Many scientists studying the Cretaceous-Paleogene transition have concluded that the terminal Cretaceous bolide impact at Chicxulub was the single cause of the extinctions associated with this stratigraphic boundary (e.g., Schulte et al., 2010). However, some researchers still challenge this interpretation, citing the instability of the Maastrichtian environment and selectivity of extinctions as suggestive of a more nuanced mechanism (e.g., Archibald et al., 2010). Keller (e.g., 2003, 2005) and her colleagues have been among the most vocal, proposing that environmental perturbation produced by Deccan Trap volcanism combined with the consequences of an extraterrestrial impact better explain latest Maastrichtian biotic change and extinction selectivity than does the single-cause model. Keller et al. (2003) have further proposed a pair of impacts, one ~300,000 yr before the end of the Cretaceous and a second at the Cretaceous-Paleogene boundary, to explain the full range of available data. White and Saunders (2005) observed that during the Phanerozoic, flood basalt volcanism and large impacts both occurred more frequently than did major extinctions, suggesting that these catastrophes alone were not sufficient to produce significant declines in biological diversity. They modeled the statistical probability of impact, volcanism, and elevated extinction to demonstrate that these events were likely to coincide three times within the last 300 m.y. White and Saunders (2005) speculated that major extinctions required the juxtaposition of two major environmental disruptions, while volcanism or impact alone could only generate low-magnitude extinction events. Arens and West (2008) tested this hypothesis against available data at the global scale and developed an ecological mechanism to explain the observed pattern.

In modern ecosystems, the contrast between long-term environmental stress (press disturbance) and instantaneous catastrophic destruction (pulse disturbance) has been recognized by ecologists for decades (Bender et al., 1984). Under press stress, species that cannot tolerate, adapt to, or escape from environmental change are reduced in abundance or eliminated from a region over time. In contrast, pulse disturbance causes immediate mass mortality (Bender et al., 1984). Press disturbance forces the ecosystem into a new ecological equilibrium as stress-tolerant species replace those intolerant to the new conditions. In contrast, pulse disturbance wipes the ecological slate clean, and the subsequent ecosystem composition and structure are determined by differential survival, dispersal, and other stochastic effects rather than a permanent change in environmental conditions (Bender et al., 1984).

Arens and West (2008) scaled this ecological dichotomy into evolutionary time. In their model, press disturbances alter community composition by placing multigenerational stress on populations. Press disturbances do not necessarily cause high mortality, but they alter population size by a variety of mechanisms such as changing patterns of competition, reproduction, growth, or dispersal. Press stress may precipitate geographic range change as organisms track preferred habitat. Eventually, press stress may render some species endangered over all or part of their ranges. Conversely, an environmental change that constitutes deleterious press stress for some organisms may favor others, resulting in a long-term change in the equilibrium composition and structure of the ecosystem. In contrast, pulse disturbances are sudden catastrophic events that cause extensive mortality. In a pulse event, survival or extinction is determined by whether a species fortuitously possesses traits that confer survival advantage under the "different rules" operating during and after catastrophes (Gould, 1985). Alternatively, survival may be serendipitous or the consequence of large population sizes and wide geographic ranges (although the buffering effect of large geographic ranges has been shown to be reduced during times of elevated extinction; Payne and Finnegan, 2007). In theory, either press or pulse disturbances of sufficient magnitude could cause extinction. However, in an analysis of extinction proportions for marine animals during the Mesozoic and Cenozoic, elevated extinction occurred more frequently when press and pulse mechanisms coincided (Arens and West, 2008). Since the Cretaceous-Paleogene extinction emerged from that global analysis as a clear example of press-pulse coincidence, it offers a useful laboratory in which to begin to test the predictions of the press-pulse ecological model. Because the press-pulse model is fundamentally an ecological model with patterns observed at the global level presumably emergent from ecosystem-scale patterns, the next step in testing the press-pulse hypothesis is to examine its predictions at various ecosystem and regional scales.

The press-pulse model of extinction at the Cretaceous-Paleogene boundary makes specific predictions that contrast with

TABLE 1. PREDICTIONS OF THE SINGLE-CAUSE CATASTROPHIC MODEL OF EXTINCTION AT THE CRETACEOUS-PALEOGENE BOUNDARY CONTRASTED WITH THE PRESS-PULSE MODEL

Press-pulse model	Single-cause catastrophic model
Evidence of both press and pulse disturbance, with press disturbance beginning before pulse.	Evidence only of catastrophic disturbance. Any press disturbance is minor.
Biotic response (e.g., extirpation, relative abundance or range change) to press disturbance.	Negligible change in community composition and structure prior to catastrophe.
Extinction associated with pulse disturbance.	Extinction associated with catastrophe.
Survivors generally those species that were increasing in relative abundance or that were expanding ranges in response to press stress.	Survivors generally those species that possessed traits favorable during the "different rules" of the catastrophe itself.

those of the single-catastrophe model (some of which are summarized in Table 1). In particular, the press-pulse model requires the initiation of press stress before the pulse disturbance, and it requires that species respond differentially to this press disturbance. This may include a local loss of biological diversity, with the potential for associated loss of ecosystem resistance and resilience (see foundational discussions of these concepts in Pimm, 1984; Tilman and Downing, 1994). This contrasts with the catastrophic model in which biological communities are diverse and resistant to environmental change until the moment of catastrophe. In this study, we offer preliminary evidence from the palynological record that latest Maastrichtian plant communities in one site within the type area of the Hell Creek Formation were in flux prior to the terminal Cretaceous impact (pulse disturbance), and we speculate on the nature of the underlying press stress.

GEOLOGIC AND LITHOSTRATIGRAPHIC SETTING

The Bug Creek drainage in McCone County, northeastern Montana, has been extensively studied for the abundant, time-averaged vertebrate assemblages recovered from incised Paleocene-age paleochannels (Lofgren et al., 1990; Lofgren, 1995). Although the Bug Creek region is infamous for the reworked fauna from the incised paleochannels, away from these channels the uppermost Hell Creek Formation at the Russell Basin locality (Fig. 1) is characterized by regularly bedded, variegated siderite-bearing siltstone that represents typical episodic deposition on a stable flood plain (Fastovsky and Dott, 1986; Fastovsky, 1987). These siltstones are buff to gray, commonly weakly bedded, and structureless, with variable fractions of silt-, sand-, and clay-sized particles. Very fine-grained sand interbeds with a basal lag of plant hash and uncommon internal ripple lamination occur within the silts. These sand interbeds represent proximal flood events. Clays are generally mixed-layer smectite-illite, which produce the characteristic "popcorn weathering" associated with this lithology (Fastovsky and Dott, 1986). The section studied here (Fig. 2) was measured in the stable floodplain facies more than 3 km from the nearest incised paleochannels and is thus not subject to the reworking that has plagued stratigraphic analysis of classic Bug Creek vertebrate fossil localities. Exposure at this site is good and shows episodic terrestrial sedimentation through the interval studied (Retallack, 1994). This section was chosen because it has been studied by a number of previous workers (e.g., Tschudy et al., 1984; Retallack, 1994; Hotton, 2002) whose work provided useful context.

Paleosol development in the uppermost Hell Creek beds at this locality is generally weak. Root traces are common, but other evidence of pedogenesis (e.g., pedon structure, slickensides, clay films) is rare, suggesting that depositional events were frequent (<100 yr intervals) and time-stratigraphic resolution is high. Two weakly developed paleosols occur in the section (Fig. 2; Retallack, 1994) and represent geologically brief depositional hiatuses. The lower was classified as the Maka pedotype by Retallack (1994; Fig. 2 herein). This pedotype is characterized by root traces, but soil formation has not progressed far enough to generate structure or the formation of clay films. This degree of soil development is typical of vegetated floodplains in which depositional events are frequent. Retallack (1994) estimated that Maka soils of the Hell Creek Formation formed rapidly (100–500 yr). The Sikahk pedotype was described at approximately –50 cm in Russell Basin (Retallack, 1994). (Throughout this paper, the

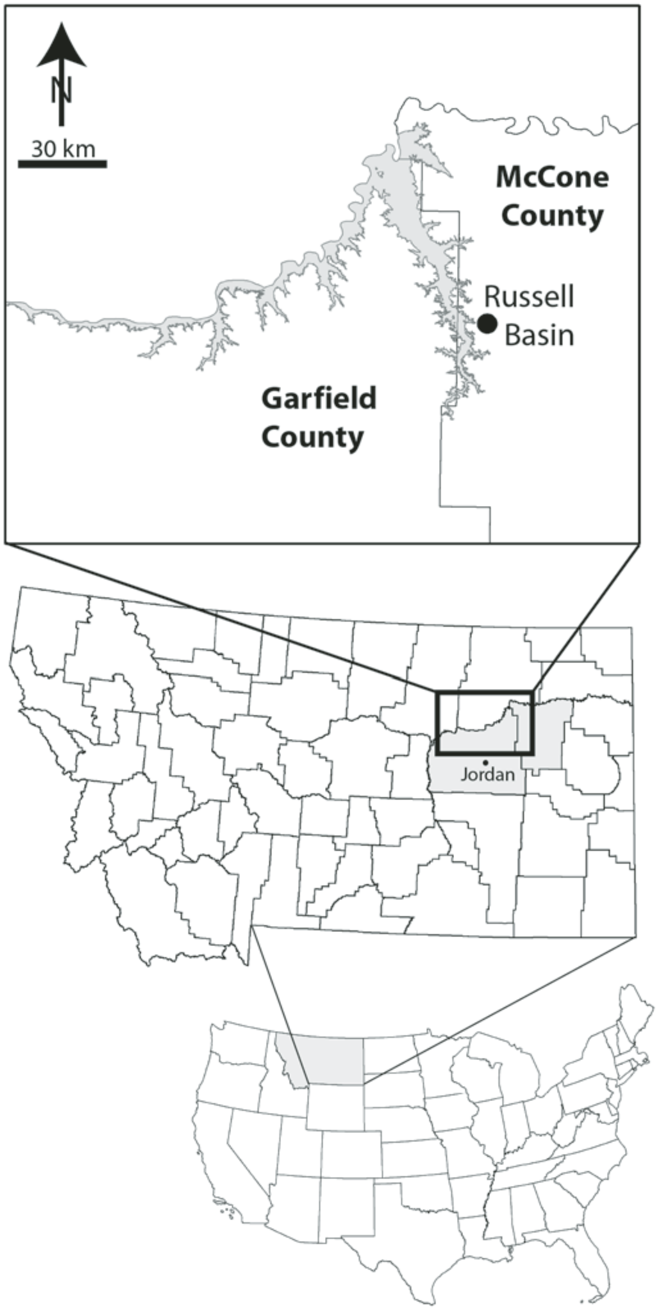

Figure 1. The location of the Russell Basin palynological section in McCone County, Montana. UCMP locality number PB97020, 40°40′25″N, 106°11′05″W, Bug Creek, Montana, quadrangle, section 10, T. 22 N, R. 43 E.

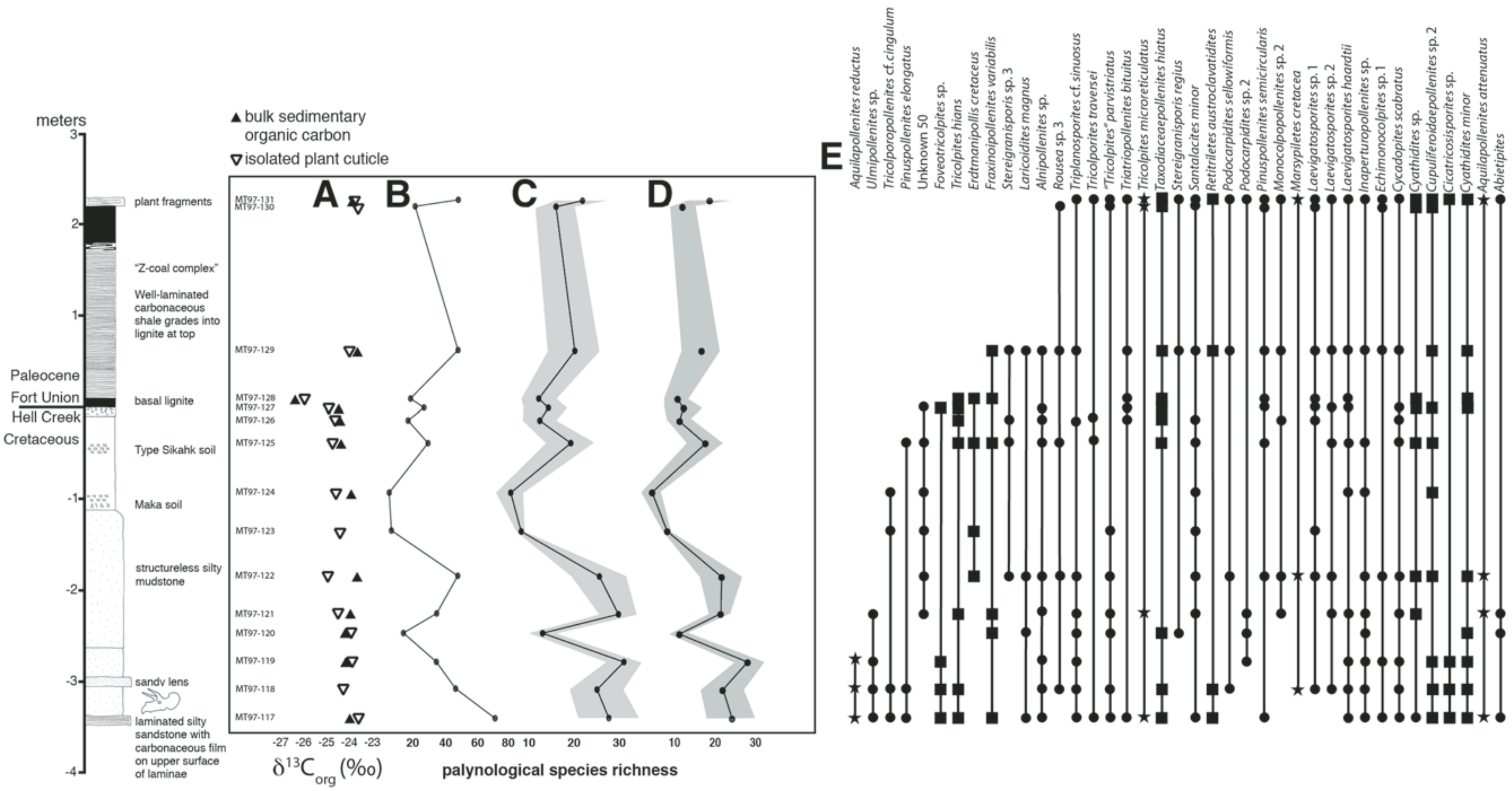

Figure 2. Lithostratigraphy, carbon isotope stratigraphy, and palynological species richness data for the Russell Basin section. Stratigraphic position is noted relative to the Cretaceous Hell Creek–Paleogene Fort Union (Khc/PgFtu) formational contact in meters; highest articulated dinosaur and associated Lancian microvertebrates in this section are noted by cartoon ceratopsian skull. Soil taxonomy is from Retallack (1994). Sample numbers correspond to Appendix. (A) Carbon isotope data for bulk sedimentary organic carbon (filled triangles) and isolated plant cuticle (open triangles). (B) Palynological species richness for all taxa (N = 165 taxa) based on actual counts, for which sample sizes varied. (C) Rarefaction estimates of palynological species richness based on a conservative subsample (N = 50 grains per sample, N = 165 taxa). Closed circles represent rarefaction estimates; gray field represents the 99% confidence interval of estimation. (D) Rarefaction estimates of palynological species richness based on a conservative subsample (N = 50 grains) of only those taxa that could be identified to genus or species (N = 110). (E) Stratigraphic distribution of the 39 most regionally common and locally abundant palynomorph species that meet the conservative 20% stratigraphic abundance criteria for accuracy in stratigraphic distribution (Meldahl, 1990). Species with last appearances that have been used to mark the terminal Cretaceous extinction at some sections in the Williston Basin of North Dakota (Nichols and Johnson, 2002) are indicated with stars. Other taxa typical of the Cretaceous from North Dakota (Nichols and Johnson, 2002; Bercovici et al., 2009) and the type area in Montana (Hotton, 2002) are indicated by squares.

0 stratigraphic datum is set at the Hell Creek–Fort Union formational contact; positive values are above the contact, and negative values are below.) This pedotype is characterized by a finely laminated lignitic O-horizon, which may be stained with jarosite. Root traces among coarse, blocky peds with slickensides characterize the A and B horizons. This paleosol likely represents a palustrine forest (Retallack, 1994). Paleotopography in the Russell Basin area suggests a local swale that may account for the presence of poorly drained soils before the onset of regionally developed swamps (lignite formation, Fig. 2) at and above the Hell Creek–Fort Union formational contact. Retallack (1994) estimated that the Sikahk paleosol resulted from 15 to 30 k.y. of soil development, and thus produced greater time averaging in its palynoflora and a larger interval of "missing time" than is characteristic of the rest of the sampled section.

The contact between the Hell Creek and Fort Union Formations occurs at the base of a series of thin (<1 m) lignite and carbonaceous mudstone beds (Fastovsky and Dott, 1986; Retallack, 1994). At the Russell Basin locality, the Cretaceous-Paleogene boundary can be bracketed biostratigraphically. A fragmentary skull of an articulated dinosaur and a surface concentration of typical Lancian microvertebrates (W.A. Clemens, 2001, personal commun.) occur approximately at −3 m (Fig. 2). Based on both the absence of typical Cretaceous pollen and the presence of typical Paleocene forms, Hotton (2002) placed the Cretaceous-Paleogene boundary at the base of the basal Fort Union lignite (Fig. 2). In North Dakota, palynological biostratigraphy has been extensively used to place the Cretaceous-Paleogene boundary (Nichols, 2002; Nichols and Johnson, 2002, 2008; Bercovici et al., 2009). Eight of the 30 species for which extinctions mark the Cretaceous-Paleogene boundary in North Dakota (Nichols and Johnson, 2002) were present at Russell Basin: *Aquilapollenites attenuatus*, *Aquilapollenites collaris*, *Aquilapollenites reductus*, *Leptopecopites pocockii*, *Liliacidites complexus*, *Marsypiletes cretacea*, *Tricolpites microreticulatus*, and *Tschudypollis retusus* (see Appendix). Of these, *A. attenuatus*, *A. reductus*, *M. cretacea*, and *T. microreticulatus* occurred with high stratigraphic confidence in our samples (Fig. 2E). The rest were found at low abundance in the basal three samples. The last appearance of *A. reductus* occurred below −2 m, at a stratigraphic position approximately equivalent to that of typical Lancian microvertebrates. The remaining three (*A. attenuatus*, *M. cretacea*, and *T. microreticulatus*) were found in low abundance in lignite samples at the top of the section sampled in this study (Fig. 2E) and may have been reworked or represent relic surviving populations that were ultimately unsustainable. Hotton (2002) noted that several of these forms, including *A. reductus* and *T. microreticulatus*, were rare in sediments above the Cretaceous-Paleogene boundary in sections where the boundary was marked by an iridium and shocked mineral anomaly. Bercovici et al. (2009) also noted that some typical Cretaceous taxa (e.g., *A. attenuatus*, *A. collaris*, *Erdtmanipollis cretaceus*, *T. microreticulatus*, and *L. pocockii*) occurred above the Cretaceous-Paleogene boundary in some localities. This suggests that palynostratigraphy may not place the Cretaceous-Paleogene boundary with precision in the Russell Basin data set. Therefore, we sought additional lines of evidence that would locate the Cretaceous-Paleogene boundary independent of fossil assemblages.

No confirmed Cretaceous-Paleogene boundary iridium or shocked mineral anomaly has been reported at this locality or elsewhere in McCone County, despite repeated attempts to find one. However, the stratigraphic position of the Cretaceous-Paleogene boundary can be identified independent of biostratigraphy using chemostratigraphic correlation (Arens and Jahren, 2000, 2002). We recorded a −1.6‰ carbon isotope anomaly at the base of the lowermost lignite (Fig. 2A; Appendix). Elsewhere in the region, carbon isotope excursions ranging from −2‰ to −2.5‰ were found in sediments immediately overlying the iridium- and shocked mineral–bearing Cretaceous-Paleogene boundary impact layer (Arens and Jahren, 2000). Based on the previous biostratigraphic and carbon isotope data, we concur with previous placements of the Cretaceous-Paleogene boundary coincident with the first lignite above articulated dinosaur remains in Russell Basin (Retallack, 1994; Hotton, 2002). Under this interpretation, the Cretaceous-Paleogene chronostratigraphic boundary coincides with the Hell Creek–Fort Union formational contact at this locality. The relatively low magnitude of the carbon isotope anomaly at Russell Basin and the absence of an Ir-enriched boundary clay argue that some section is missing at this locality (see Arens and Jahren, 2002). However, in the Hell Creek sections where the carbon isotope excursion has been studied to date, carbon isotope values generally return to pre-impact levels within fewer than 20 cm above the iridium- and shocked mineral–bearing boundary clay (Arens and Jahren, 2000, 2002). The fact that the anomaly is present, but at lower magnitude than is typical of sections with an Ir anomaly, suggests that a minimal section is missing at Russell Basin.

METHODS

The most stratigraphically detailed and geographically extensive data on the vegetation of the Maastrichtian and Cretaceous-Paleogene boundary come from the palynological record (Nichols and Johnson, 2008, and references therein). Consequently, we have chosen to use this record to begin to examine the press-pulse model prediction that ecosystems experienced extirpation and relative abundance change prior to the terminal Cretaceous bolide impact (Table 1).

For this preliminary test, we measured a small stratigraphic section at centimeter scale and sampled sediment at ~30 cm intervals through the uppermost 3.5 m of the Hell Creek Formation, and in each of the lithologically distinct beds of the first 2 m of the Fort Union Formation (Fig. 2). Fieldwork was conducted in August 1997. Sandstones were not sampled because they preserved few palynomorphs and little other terrestrial organic material. Samples were split for carbon isotope and palynological analysis. Carbon isotope analysis followed the method detailed in Arens and Jahren (2000), including separate analyses of bulk sedimentary organic carbon and isolated plant cuticle. All samples were analyzed in triplicate, resulting in an analytical uncertainty of less than 0.1‰, reported against the Peedee belemnite (PDB) standard. Because we wished to assess the concentration of palynomorphs within sediment as a control for one type of preservational bias, we followed the protocol for calculating absolute palynomorph frequency (Traverse, 1988). For palynological analysis, 1 g of sediment was demineralized (HCl and HF) and oxidized in room-temperature Schulze's solution (1:1 HNO_3:K_2ClO_3). Palynomorphs were well preserved with low thermal maturation, i.e., 1–2 on the scale defined by Batten (1981), and thus only gentle oxidation was needed to remove excess sedimentary organic material. Slides and residue were weighed to permit calculation of the number of palynomorphs per gram sample following the method outlined by Traverse (1988). For each sample, an entire slide was scanned at 1000× magnification, and all grains, including damaged and poorly preserved grains, were counted. Because the absolute palynomorph frequency (grains per gram sediment) differed among samples, counting only grains on a single slide unavoidably resulted in an uneven, and sometimes small, sample size of identifiable grains (Appendix). For palynospecies richness data, only identifiable grains were included (Appendix). Approximately 300 grains per sample are generally counted to reduce the standard deviation of relative abundance values for any given species (Traverse, 1988). Since secular change in species richness as a whole, rather than relative abundance of particular species, was important to this study, we compensated for uneven sample size using rarefaction (Gotelli and Colwell, 2001). Rarefaction estimates for each sample and the associated 99% confidence interval were calculated using Analytic Rarefaction software (S.M. Holland, http://strata.uga.edu/software/index.html, accessed September 2011).

The reconstruction of extinction patterns is vulnerable to uncertainty in the relationship between extinction and the last appearance datum (LAD) of rare species, the so-called Signor-Lipps effect (Signor and Lipps, 1982). Signor and Lipps (1982) postulated that the LAD of rare taxa—those with low stratigraphic abundance—would not accurately represent their time of extinction. In contrast, the LAD of commonly sampled taxa would more precisely and accurately correspond to the stratigraphic position of their extinction. They postulated that even an instantaneous mass extinction would produce a gradual or step-wise pattern of LADs in the stratigraphic record, with rare species appearing to become extinct before the extinction horizon (Signor and Lipps, 1982). This pattern is often invoked at the Cretaceous-Paleogene boundary when patterns of LADs appear gradual or stepwise. Nichols and Johnson (2008) argued that even palynological data were vulnerable to Signor-Lipps artifacts despite the observation that palynomorphs are abundant and ubiquitous in the sediments of the Hell Creek and Fort Union Formations. In contrast to Signor and Lipps (1982), who studied the effect of rare species, Payne (2003) concluded that the stratigraphic distribution of species appeared less continuous as abundance in a sample increased. Since continuous sampling is required of most statistical methods that distinguish among gradual, step-wise, and single horizon extinction patterns, he concluded that most actual data sets were not appropriate to the statistical tests used to distinguish between gradual and instantaneous mass extinction models.

Other workers have addressed the question of uncertainty in stratigraphic distributions by calculating confidence intervals for the LADs of individual taxa (e.g., Strauss and Sadler, 1989; Marshall, 1994, 1997; Marshall and Ward, 1996; Holland, 2003). This approach is particularly useful in the visual representation of individual stratigraphic range data and is an improvement over the absence of such estimates (e.g., Labandeira et al., 2002; Wilf et al., 2003; Wilf and Johnson, 2004; Wilson, 2005), but it is less applicable to aggregate extinction data. Meldahl (1990) examined the pattern of LADs from an actual stratigraphic record with a known point of universal last appearances and developed a rubric for evaluating last appearance data. He noted that the LAD of species with stratigraphic abundance of less than 15% (those species found in fewer than 15% of stratigraphic samples) did not accurately record the time of actual disappearance, while those with greater stratigraphic abundance did. Meldahl (1990) recommended removing these rare species and plotting the frequency of LADs of the remaining common species to evaluate the stratigraphic distribution of LADs within a stratigraphic section. While still short of a formal test for the Signor-Lipps effect, this does offer a more objective way to evaluate stratigraphic extinction patterns. We have followed Meldahl's (1990) approach but have applied a more conservative standard by removing all taxa with a stratigraphic abundance lower than 20% (present in fewer than three samples in this study) before calculating extinction proportion and plotting extinction frequency.

Data reduction, statistical analysis, and visualization were performed in Microsoft Excel 11.1.1 and Aabel 1.5.8.9 for Macintosh.

RESULTS

Between 53 and 1068 identifiable grains were encountered per slide (Appendix). Absolute pollen frequency ranged from 4428 to 1,100,380 grains/g sediment (Appendix), showing that palynomorphs were indeed abundant throughout the sampled section. We distinguished 165 distinct palynomorph forms (Appendix). Ninety-five of those occurred in multiple samples, while 70 were found in only one sample. Sixty appeared in three or more samples and were thus considered stratigraphically abundant. Figures 2B–2D plot changing palynospecies richness against stratigraphic position; sample positions are noted both in Figure 2 and the Appendix. Figure 2B plots palynospecies richness of the full data set, for which sample size varied among samples (see Appendix). Figure 2C presents rarefaction estimates of species richness (and associated 99% confidence interval of estimation) for resampling of 50 palynomorphs from each underlying distribution. This small sample size was chosen because it is lower than the smallest actual sample size obtained in this study (Appendix). Fifty grains is a very small sample size for palynological analysis, and thus the rarefaction estimate constitutes a very conservative analysis. Approximately 30% of the palynomorphs that we recognized as morphologically distinct in this study could not be assigned to genera or species based on the literature we had at hand. Figure 2D plots rarefaction estimates of species richness (and associated 99% confidence interval of estimation) for resampling of 50 palynomorphs from each underlying distribution of only those morphologically distinct forms that could be identified to genus or species.

The method followed for absolute pollen frequency calculations produced varied sample sizes, and variation in the number of grains counted in a sample might drive species richness patterns. However, an analysis of variance (ANOVA) demonstrated that palynological species richness was not correlated with the number of identifiable grains counted per sample ($p = 0.24$). Similarly, the number of identifiable grains counted per sample was not correlated with species richness in any of the major taxonomic groups identified: spores, including pteridophytes and bryophytes ($p = 0.11$); gymnosperms, including conifers, cycads, and ephedroid pollen ($p = 0.24$); monosulcate angiosperm pollen produced primarily by monocot angiosperms ($p = 0.93$); and triaperturate angiosperm pollen produced primarily by dicot angiosperms ($p = 0.28$). This shows that species richness patterns are not driven primarily by sampling effort. This result is counter to conventional wisdom. Nonetheless, rarefaction estimates of species richness that mitigate sample size, rather than actual counts, are discussed in the following.

Beginning with the most basal samples, we recorded declining palynological species richness (Figs. 2B–2D) from −3.5 m to −2.5 m. Between −1.4 m and −1.0 m, palynospecies richness dropped to very low levels in a flora dominated (> 60% relative abundance) by an unidentified small, heavily sculptured grain (unknown 50; Fig. 3AE). Most of the species present in this low-species-richness interval were present at high stratigraphic confidence (they occurred in three or more samples). Interpretation

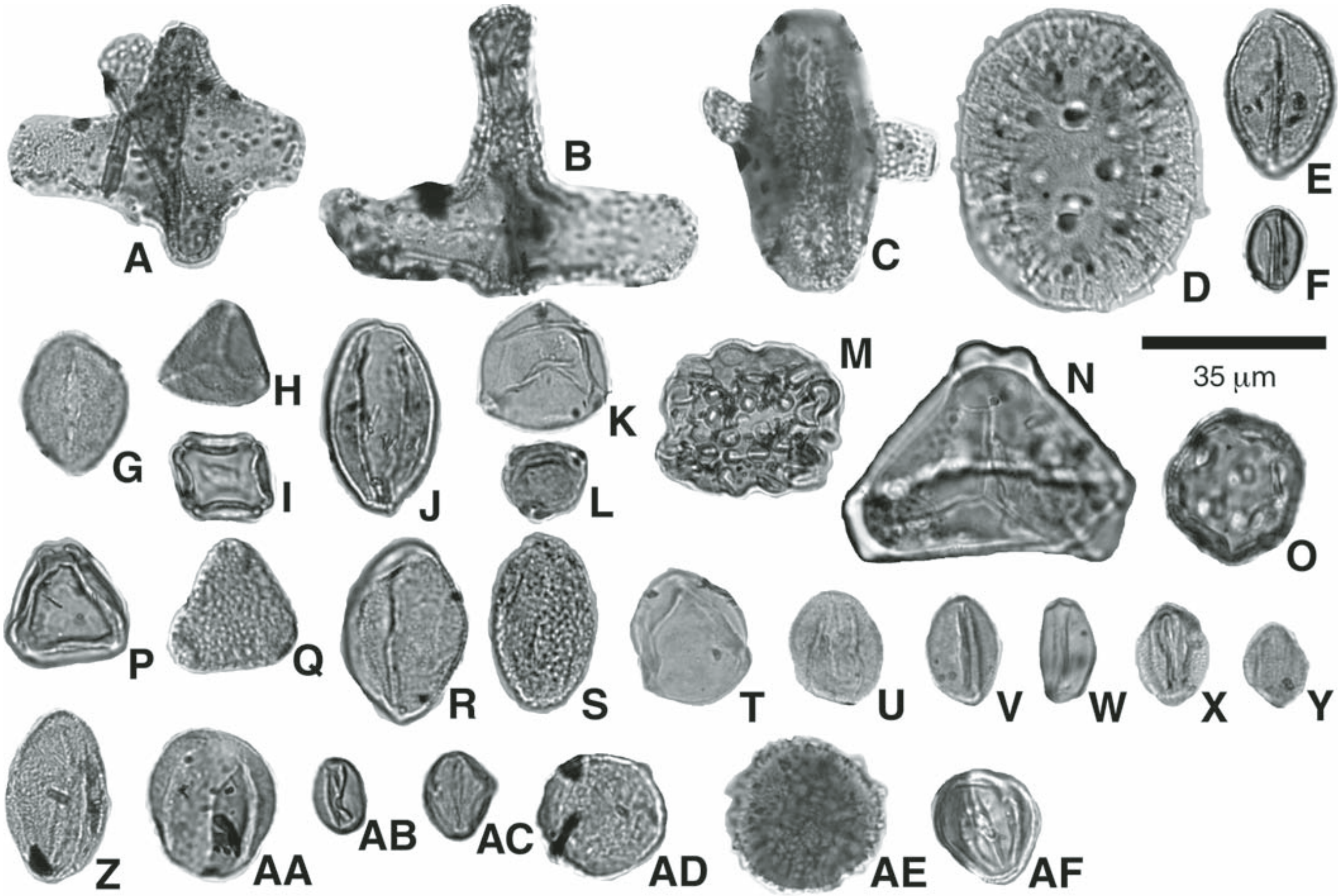

Figure 3. Some angiosperm pollen recovered from the Russell Basin samples. (A) *Aquilapollenites amplus*, (B) *Aquilapollenites collaris*, (C) *Aquilapollenites reductus*, (D) *Wodehouseia spinata*, (E) *Arecipites* cf. *columellus*, (F) unknown monosulcate 5, (G) unknown monosulcate 12, (H) *Cupanieidites reticularis*, (I) *Alnipollenites* sp., (J) *Cupuliferoidaepollenites* sp. 3, (K) *Kurtzipites trispissatus*, (L) *Momipites* cf. *sanjuanensis*, (M) *Marsypiletes cretacea*, (N) *Normapoles* sp. 1, (O) *Polyporina cribraria*, (P) *Triporopollenites triplicatus*, (Q) *Tschudypollis retusus*, (R) *Rousea* sp. 1, (S) *Rousea* sp. 3, (T) *Triatriopollenites bituitus*, (U) unknown tricolpate 18, (V) unknown tricolpate 19, (W) unknown tricolpate 22, (X) *Tricolpites hians*, (Y) *Tricolpites micromunus*, (Z) *Tricolpites* sp., (AA) *Fraxinoipollenites variabilis*, (AB) *Tricolporites traversei*, (AC) *Tricolporopollenites* cf. *cingulum*, (AD) *Ulmipollenites* sp., (AE) unknown 50, (AF) cf. *Wilsonipites* sp.

of this pattern in raw data (Fig. 2B) must be tempered by smaller sample sizes between −3.0 m and −1.0 m (Appendix). To compensate for uneven sample size, Figure 2C plots rarefaction estimates of species richness. Although absolute values from rarefaction analysis were predictably lower, the pattern of declining species richness between −3.5 m and −1.0 m was reproduced, and the magnitude of this change is outside of the 99% confidence interval of estimation, showing that this pattern is not a sampling artifact. The pattern of species richness decline was reproduced again when only those palynomorph forms that could be identified to genus or species were subsampled by rarefaction (Fig. 2D), showing that the pattern was probably not a taxonomic artifact. Species richness recovered above the interval of low species richness (−1.4 m to −1.0 m) but remained relatively low in the uppermost 1.0 m of the Hell Creek Formation compared to samples below −2.5 m (Fig. 2).

Sixty palynospecies were ranked stratigraphically abundant, meaning that they occurred in three (>20%) or more samples (some of which are plotted in Fig. 2E). Fifty-seven of these occurred in Cretaceous-age sediments below the low-species-richness interval (−1.4 m to −1.0 m). Of these, only six made last appearances below the low-species-richness interval. The remainder reappeared above the low-species-richness interval, illustrating that it did not constitute an extinction event but rather a local extirpation. Figure 2E presents stratigraphic distributions of the 40 most regionally common and stratigraphically abundant palynomorph species. In this subset, the low-diversity interval between −1.4 m and −1.0 m is apparent, as is the pattern showing that most species reoccur in stratigraphically higher samples.

To assess last appearances within this stratigraphic interval, we calculated LAD frequency for the 60 stratigraphically abundant taxa (Fig. 4). LAD frequency was generally low throughout the sample interval. Average background LAD frequency was two palynospecies per sample (±2). Given this background level, mass extinction (sensu Raup and Sepkoski [1982], where mass extinction was defined as >2 standard deviations above the mean) would be recognized at more than eight LADs per sample. By this definition, no single sample meets the criterion for a mass extinction. However, the highest frequency of LADs—a cluster of three samples above the Cretaceous-Paleogene boundary—meets the criterion for a major extinction (Fig. 4). At Russell Basin, the extinction is not simultaneous with the boundary but is spread over three samples within 60 cm of the boundary, and some taxa (e.g., *M. cretacea* and *T. microreticulatus*) persist to the top of the section measured in this study. For taxa present with high stratigraphic confidence, the local extinction proportion across the Cretaceous-Paleogene boundary was ~21%. This value is commensurate with other sections in the Hell Creek type area (Hotton, 2002) and throughout the western interior (Nichols and Fleming, 1990; Nichols, 2002), where extinction proportions for individual sites range from 15% to 30%. When rare taxa are added, the extinction proportion rose to 29%.

To evaluate the plant groups involved in the latest Cretaceous species richness decline, we placed each palynospecies into broad categories: gymnosperms (including conifers, cycads, and ephedroid pollen; Fig. 5), triaperturate pollen (dicot angiosperms; Fig. 3), monosulcate pollen (primarily monocot angiosperms), and spores (primarily pteridophytes and bryophytes; Fig. 5; Appendix). These groupings have some phylogenetic meaning (eudicot angiosperms are monophyletic, although gymnosperms and spores are not), and some ecological meaning (pteridophytes and bryophytes generally prefer moist habitats). Figure 6A, which plots relative abundances of these major groups using rarefaction estimates of species abundance, shows that most of the species lost below the Cretaceous-Paleogene boundary were dicot angiosperms (represented by triaperturate pollen). Gymnosperms and monosulcate pollen maintained relatively low species richness over the interval sampled. Spores tracked dicot trends but at lower species richness. In contrast, relative abundance counts (Fig. 6B; Appendix) showed a postimpact palynoflora somewhat enriched in fern spores (25% in the uppermost Cretaceous sample to 36% to 52% in the lowermost Paleocene samples), and angiosperms. These results are qualitatively similar to those described at other North American localities (Tschudy et al., 1984; Nichols and Fleming, 1990; Sweet et al., 1990; Hotton, 2002; Nichols, 2002), as would be expected immediately following the Cretaceous-Paleogene boundary impact (Bercovici et al., 2009). Gymnosperms were not important components of the Russell Basin flora except in two samples: one at approximately −3.0 m and a second from a Fort Union lignite bed at ~2.0 m (Fig. 2).

Variation in depositional environment as reflected in lithology can influence palynological count data (Sweet, 1994; Kroeger, 2002; Bercovici et al., 2009). To evaluate the effect of facies variation on species richness, we regressed the number of palynospecies recovered in each sample onto weight-

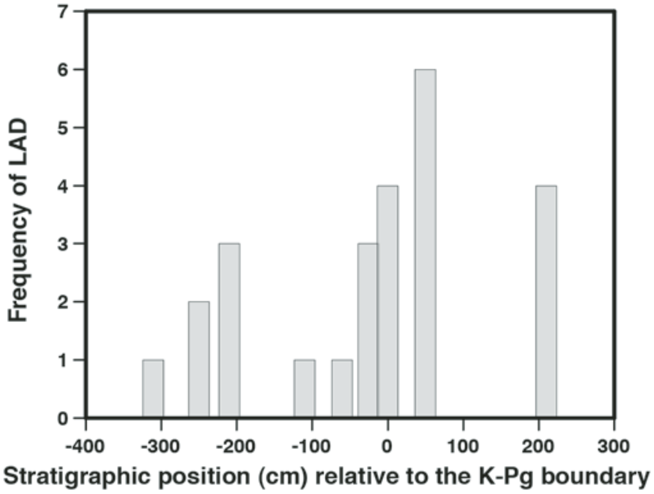

Figure 4. Frequency distributions of last occurrence datum (LAD) for Russell Basin palynomorph forms ($N = 60$) with greater than 20% stratigraphic abundance (a conservative interpretation of the recommendation of Meldahl, 1990) plotted relative to the Cretaceous-Paleogene (K-Pg) boundary at 0 cm.

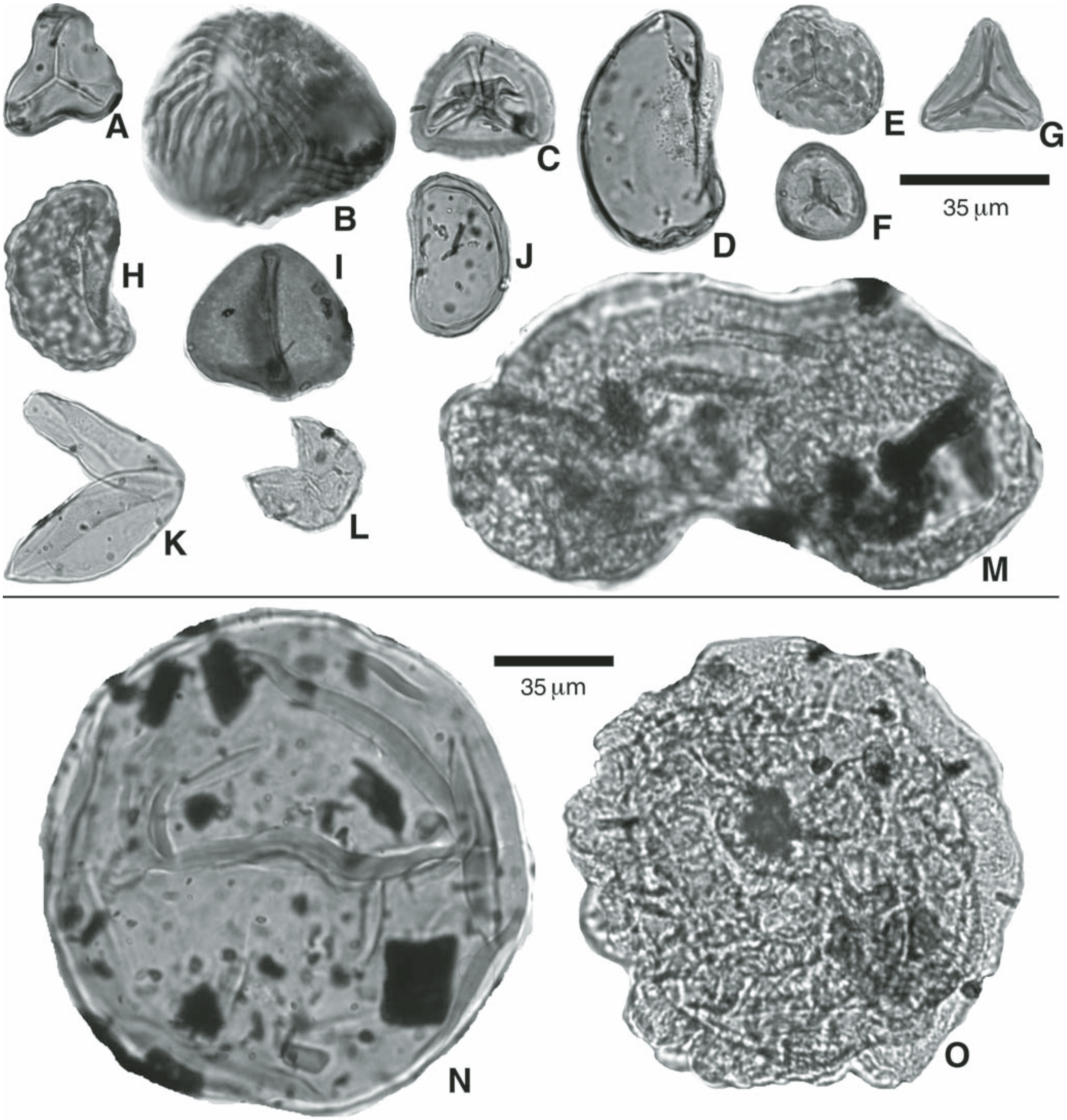

Figure 5. Some pteridophyte and bryophyte spores, and gymnosperm pollen recovered from the Russell Basin samples. (A) *Cyathidites minor*, (B) *Cicatricosisporites* sp. 2, (C) *Cingulatisporites radiatus*, (D) *Laevigatosporites haardtii*, (E) *Sphagnum regium*, (F) *Stereigranisporis* sp. 3, (G) unknown spore 9, (H) *Verrucatosporites favus*, (I) *Triplanosporites sinuosus*, (J) *Laevigatosporites* sp. 1, (K) *Cycadopites scabratus*, (L) *Taxodiaceaepollenites hiatus*, (M) *Abietipites* sp., (N) *Laricoidites magnus*, (O) *Tsugaepollenites mesozoicus*.

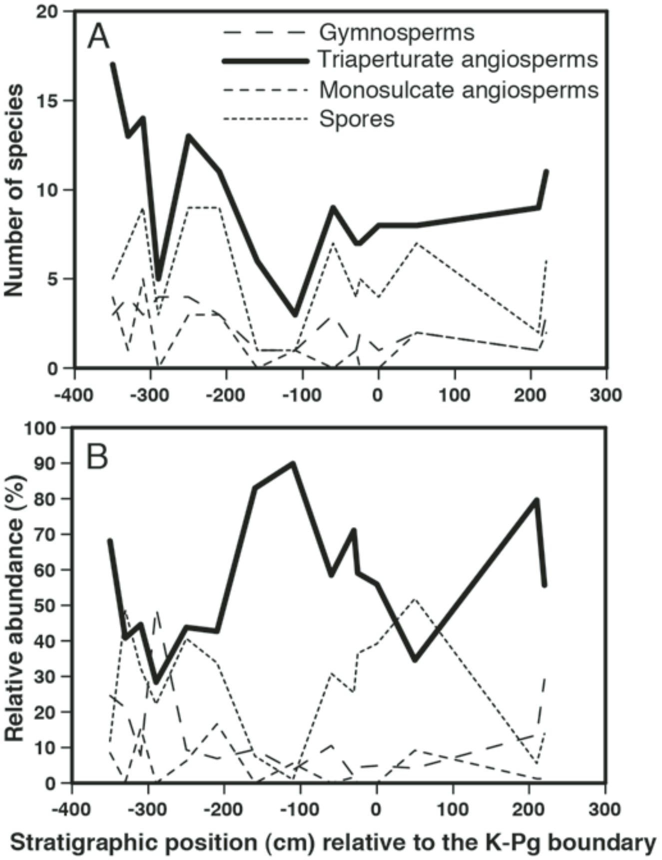

Figure 6. (A) Estimated species richness within major taxonomic groups based on rarefaction analysis and (B) relative abundance of grains per sample for each major group. Rarefaction and relative abundance calculations were used to remove the effect of variable sample sizes. Species were aggregated into one of four major groups plotted against stratigraphic position relative to the Cretaceous-Paleogene (K-Pg) boundary at 0 cm. Gymnosperms include conifers, cycads, and ephedroid pollen. Triaperturate grains represent dicot angiosperms. Monoaperturate grains probably represent monocot angiosperms. Spores include pteridophyte and bryophyte spores.

percent organic-carbon content of the sediment (Appendix). Weight-percent organic-carbon content is a useful if crude proxy for depositional environment: Carbon-poor samples (<15% by weight) correspond to floodplain siltstone facies as described in the field, while carbon-rich samples (40% to 65%) represent carbonaceous mudstone and lignite characteristic of wetland environments (Arens and Jahren, 2000). However, for this analysis, we preferred the continuous data offered by quantitative measure of organic-carbon content over a more subjective field classification of depositional facies. We avoided sampling well-developed paleosol horizons, where both palynological composition and carbon isotope values may be altered by physical or biogeochemical alteration during soil formation (Arens and Jahren, 2000). There was no significant correlation between species richness and weight-percent organic-carbon content of sediment ($p = 0.36$), showing that the palynospecies richness pattern was not driven primarily by facies change in this section. A similar result was obtained when considering richness within the four taxonomic groups: spores ($p = 0.35$), gymnosperms ($p = 0.75$), monosulcate angiosperm grains ($p = 0.95$), and triaperturate angiosperm grains ($p = 0.17$). To test the effects of facies on the number of grains recovered, we regressed the number of identifiable grains recorded in each sample onto weight-percent organic-carbon content. There was no significant correlation ($p = 0.12$), showing that abundance data were not significantly influenced by lithological variation in this section. We obtained similar nonsignificant results when regressing relative-abundance values for each taxonomic group onto weight-percent organic-carbon content of sediment: spores ($p = 0.37$), gymnosperms ($p = 0.23$), monosulcate angiosperm pollen ($p = 0.53$), and triaperturate angiosperm pollen ($p = 0.69$). We chose relative abundance data for this analysis to normalize grain counts for variable sample sizes. Our results contrasted with many localities in Canada, where conifers dominated the organic-rich substrates of the latest Cretaceous and early Paleocene (Sweet et al., 1990; McIver, 1999; Sweet and Braman, 2001). This difference may be related to latitude. To evaluate the effects of variable sedimentation rate or pollen rain on species richness data (sample size effect on species richness), we regressed the number of palynospecies recovered from each sample onto the estimated number of grains preserved in each gram of sediment ($p = 0.26$). Again, palynospecies richness was independent of palynomorph concentration, as was richness within taxonomic groups: spores ($p = 0.06$), gymnosperms ($p = 0.28$), monosulcate angiosperm pollen ($p = 0.35$), and triaperturate angiosperm pollen ($p = 0.50$). Together, these results strongly suggest that sample size, facies variation, and preservation do not appear to have driven the underlying pattern of palynospecies richness. Of course, some other aspect of depositional or preservation variation for which we cannot test may be at work.

DISCUSSION

Data from Russell Basin show a 21% local extinction of stratigraphically abundant species in association with the Cretaceous-Paleogene boundary (Fig. 4). The extinction percentage calculated for Russell Basin increases to 29% when rare species are included. This result is consistent with a 15% to 30% extinction at individual localities reported in a larger study of the Hell Creek type area (Hotton, 2002) and is similar to rates reported elsewhere in the western interior (Nichols, 1990; Nichols and Johnson, 2002). An extinction rate above background is consistent with the predictions of both the press-pulse and catastrophic models (Table 1), and this pattern is generally interpreted in support of the catastrophic model (Schulte et al., 2010).

In addition to extinction, we also observe a significant decline in palynological species richness at −1.5 m in Russell Basin (Fig. 2). Most of the species lost during this interval were dicot angiosperms (Fig. 6). However, the species richness decline did not represent extinction of these forms. Having eliminated significant bias due to sampling, preservation, and facies variation as potential drivers of this pattern, our results suggest a local and temporary extirpation that may indicate reorganization of local vegetation or response to some environmental change that did not leave a discernible signal in the sedimentological record. This result is consistent with the prediction of the press-pulse ecological model, but it does not conform to the catastrophic model, which predicts little or no change in community composition or relative abundance before the catastrophic disturbance. However, the Russell Basin section constitutes few samples from a single section. Have similar patterns been observed elsewhere?

Although latitudinal variations in palynofloras have been noted, stratigraphic variation in the Hell Creek Formation flora had not been reported in the United States (Nichols and Fleming, 1990). However, Nichols (2002) proposed a preliminary and informal palynological subzonation for the Hell Creek Formation based on detailed sampling in North Dakota. This scheme represented subdivision of the *Wodehouseia spinata* zone of Braman and Sweet (1999) following Srivastava (1970). Nichols' (2002) subzone E, approximately the top 5 m of the formation, was defined on the last appearance of a single taxon: *Liliacidites altimurus*. Although this result suggests vegetation change in the upper meters of the Hell Creek Formation, it is not directly commensurate with the Russell Basin data.

Using a large data set that included 14 sections from across the Hell Creek type area, including the Bug Creek drainage where the Russell Basin section is located, Hotton (2002) noted a decline in average species richness of typical Cretaceous forms from 34 species in the lower Hell Creek to 27.6 species in the interval –3.50 m to –0.04 m to 20 species in the interval –0.04 m to the Cretaceous-Paleogene boundary. However, this pattern was not statistically significant across the full range of localities sampled, probably because of considerable variation in lithology among sites. Hotton (2002) proposed poor preservation in clays immediately below lignite beds and regional facies change as important additional sources of this variation.

Similarly, Bercovici et al. (2009) performed quantitative analyses of several well-studied localities in southwestern North Dakota. They found a significant decrease in dicot angiosperm species richness that occurred between –1.5 m and –0.5 m. At Mud Buttes, section 171, section 168, and section 166 dicot species richness declined and did not recover before the Cretaceous-Paleogene boundary. In the composite section 170 and 156, dicot species richness decreased at about –1.0 m, recovered to levels similar to those seen below this horizon, and dropped again in association with the Cretaceous-Paleogene boundary impact (Bercovici et al., 2009).

Declines in angiosperm species richness similar to that observed at Russell Basin were also documented in detailed sampling of the uppermost 3 m of Terry's Fort Union Dinosaur section and Dean's High Dinosaur section in southwestern North Dakota (data from Pearson et al., 2001; Nichols and Johnson, 2002). Although these data sets reported only presence/absence of key indicator taxa, they appear to show a similar pattern of species richness decline in the uppermost 3 m of Cretaceous time (Fig. 7). Pearson et al. (2001) reported the stratigraphic distribution of the 44 most common angiosperm pollen taxa in the Terry's Fort Union Dinosaur section where the Cretaceous-Paleogene boundary was recognized biostratigraphically and with carbon isotope data (Arens and Jahren, 2002). The Cretaceous-Paleogene boundary occurred at 2.6 m in this section (Pearson et al., 2001; Nichols and Johnson, 2002). The highest frequency of LADs is concentrated at the Cretaceous-Paleogene boundary, as expected (Fig. 7A). In this section, angiosperm species richness declined

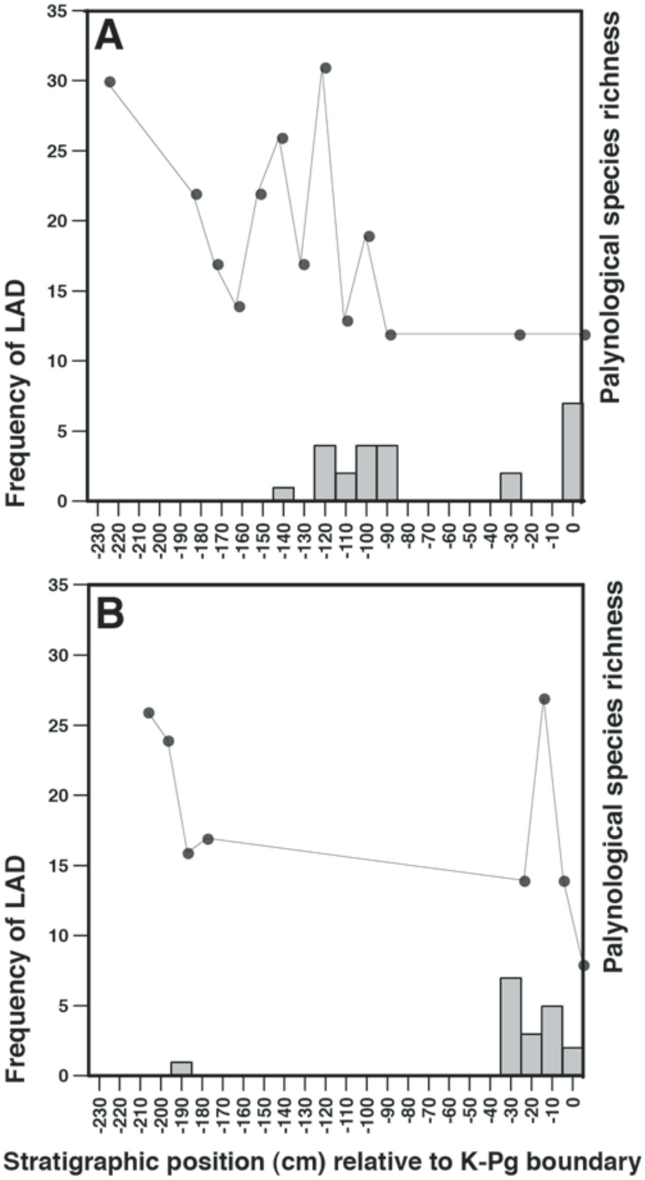

Figure 7. Palynological species richness (curve) and frequency distribution of last occurrence datums (LAD, bars) of species with stratigraphic abundance greater than 20% at (A) Terry's Fort Union Dinosaur locality (Pearson et al., 2001; Nichols and Johnson, 2002) and (B) Dean's High Dinosaur locality (Nichols and Johnson, 2002), both in southwestern North Dakota, plotted against stratigraphic position relative to the Cretaceous-Paleogene (K-Pg) boundary at 0 cm.

from 30 species (at approximately –2.2 m; Fig. 7A) to 12 species in the uppermost Cretaceous samples (data from Pearson et al., 2001; Nichols and Johnson, 2002). The decrease is stochastic, with significant variation in species richness observed in the uppermost meters of the Cretaceous (Fig. 7A), a pattern similar to that seen at Russell Basin. However, it is important to note that the authors of the original studies did not note this as a significant pattern and did not interpret it.

In the Dean's High Dinosaur section, where the Cretaceous-Paleogene boundary (recognized biostratigraphically and with carbon isotope data; Arens and Jahren, 2002; Nichols and Johnson, 2002) occurred at ~2.1 m, Nichols and Johnson (2002) reported the stratigraphic distribution of 45 of the most common palynospecies. The highest frequency of LADs was again concentrated at or just below the Cretaceous-Paleogene boundary. Species richness declined from 26 species (at approximately –2.2 m and –0.2 m; Fig. 7B) to eight species immediately below the boundary (Nichols and Johnson, 2002). Again, the authors of the original study did not note this as a significant pattern and did not interpret it.

Sweet and Braman (1992) reported similar species richness declines in morphologically complex dicot pollen at approximately –2 m from the Cretaceous-Paleogene boundary at a series of localities in the western interior of Canada. The geographic perspective offered by this data set allowed them to conclude that most of the species lost in a given site persisted elsewhere (Sweet and Braman, 1992), which is consistent with our conclusion that species richness loss before the Cretaceous-Paleogene boundary represented local extirpation and rearrangement of terrestrial vegetation rather than extinction. Data from Russell Basin support their conclusion that vegetation was changing and the distribution of species was becoming more regionally patchy prior to the terminal Cretaceous impact.

In a later analysis, Sweet and Braman (2001) attributed species richness losses at one of the Canadian sections, Police Island, to changes in depositional environment (clastic vs. organic sedimentation). At Police Island, substrate change coupled with the edaphic specificity of some angiosperms (press stress) might account for the loss of diversity. Changing depositional environment cannot explain species richness decline at Russell Basin because the number of palynospecies decreased in the apparently sedimentologically homogeneous upper Hell Creek siltstone beds, not coincident with changes in depositional style at the Hell Creek–Fort Union formational contact. This observation also holds for the Terry's Fort Union Dinosaur locality in southwestern North Dakota (Fig. 5A; Pearson et al., 2001; Nichols and Johnson, 2002).

Neither the Russell Basin data, nor those from the other localities discussed earlier point toward a cause of the latest Cretaceous palynospecies richness declines. However, a hypothesis has emerged from order-of-magnitude estimates of sedimentation rate. In northeastern Montana, the top ~15 m section of the Hell Creek Formation was deposited during the C29r magnetochron (Archibald et al., 1982; Swisher et al., 1993). Using precessional chronometry, D'Hondt et al. (1996) calculated that this interval represented ~333 k.y. This suggests an average sedimentation rate of ~45 cm/10 k.y. Detailed field observation of the Hell Creek portion of the Russell Basin section did not reveal erosional unconformities, and paleosol analysis did not indicate depositional hiatuses greater than ~30 k.y. (Retallack, 1994). Applying this average sedimentation rate reveals that the 3.5 m of Hell Creek sediment in which angiosperm species richness declined probably represents less than 78,000 yr. Adding a conservative approximation for the "missing time" associated with the development of the two paleosol horizons observed in the measured interval (Fig. 2), we estimate that the decline occurred over the last 100,000–110,000 yr of the Cretaceous. Although this approach is imprecise because terrestrial sedimentation rates are notoriously variable (see Arens et al., this volume), this temporal magnitude suggests a possible driver of plant community change. The last 450,000 yr of the Cretaceous were warm (Li and Keller, 1999), with cooling beginning ~100,000 yr before the Cretaceous-Paleogene boundary (Wilf et al., 2003). Warming during the last half million years of the Cretaceous may have been associated with CO_2 emissions from the first Deccan Trap "megapulse" that began near the C30r-C30n transition, while subsequent latest Cretaceous cooling may have been linked to SO_4 and particulate emissions associated with initiation of the second and largest pulse that began during the C29r magnetochron (Self et al., 2006; Chenet et al., 2007, 2008, 2009; Keller et al., 2009, 2011). Although the temporal precision of our study and the others discussed herein does not allow for definitive correlation of these climate events with the Russell Basin palynospecies richness decline, it does suggest volcanically mediated climatic cooling—a press disturbance—as a hypothesized driver of changes in plant community structure observed between –1.4 m and –1.0 m.

It is important to emphasize that we currently lack important context in which to interpret these palynological data. The observed changes in palynospecies richness appear robust for this locality and small swath of geological time. However, the current data set lacks a geographic perspective, opening the possibility that the pattern recorded in Russell Basin is only local environmental stochasticity, rather than the result of a regional or global press disturbance. Data from other sections discussed earlier herein are suggestive of a regional or continental pattern, but this hypothesis must await an analysis applying similar quantitative methods at sites across the region. In addition, no studies to date have taken a detailed or quantitative look at palynospecies richness and compositional variation throughout the Hell Creek Formation as a whole. Without this temporal perspective, we cannot reject the null hypothesis that the low-species-richness interval is part of the normal variation in palynospecies richness that occurred in the absence of press stress. This test will require quantitative analysis of a detailed section spanning the full stratigraphic thickness of the Hell Creek Formation.

In conclusion, the single section at Russell Basin provides evidence that changes in local palynological species richness were under way before the extinction at the Cretaceous-Paleogene boundary. A review and reanalysis of previously published data from the region shows that similar declines have been observed in some other areas, but that the pattern varies from place to place,

APPENDIX. PALYNOLOGICAL DATA

Stratigraphic position (cm) Khc/PGFtu = 0		–340	–305	–275	–245	–225	–185	–135	–85	–35	–5	0	+10	+65	+225	+235
Taxon		MT97-117	MT97-118	MT97-119	MT97-120	MT97-121	MT97-122	MT97-123	MT97-124	MT97-125	MT97-126	MT97-127	MT97-128	MT97-129	MT97-130	MT97-131
Cicatricosisporites sp.	S	1	4	1												1
Cingulatisporites dakotaensis	S													16		
Cingulatisporites radiatus	S										7					
Concavisporites jurienensis	S	1														
Cyathidites minor	S	1	4	1	7		1					35	22	6		8
Cyathidites sp.	S	7				7	1			5		55	58		5	15
Foveasporis triangulus	S						3									
Gleicheniidites sp.	S			1												
Goshispora cf. *bella*	S	1														
Hymenophyllumsporites furcosus	S											7				
Laevigatosporites haardtii	S	12	29	4		7			1	3		17	16	23		38
Laevigatosporites sp. 1	S		9			1	9			9		13		25		2
Laevigatosporites sp. 2	S		10				23	4			40	36	77	83	4	53
Laevigatosporites sp. 3	S						1							36		
Leptolepidites tenuis	S															1
Pluricellaesporites psilatus	S									1						
Reticulatisporites sp.	S	1														
Retitriletes austroclavatidites	S	2	40											2		13
Rugulatisporites sp.	S									2						
cf. *Schizosporis laevigatus*	S						4									6
Spore unknown 4	S		2	2		2	6									
Spore unknown 5	S			1						4						
Spore unknown 6	S		11											1		
Spore unknown 7	S	1	4													
Spore unknown 8	S		2													
Spore unknown 9	S		1	2			2			3		59	13	108	4	
Spore unknown 10	S		2													
Spore unknown 11	S		25		5	1	2			11			135			
Spore unknown 15	S					1				19		40		116		1
Spore unknown 16	S					1										
Spore unknown 17	S											1				
Spore unknown 18	S													14		6
Spore unknown 19	S					1										
Spore unknown 20	S	1														
Stereigranisporis regius	S				2									1		1
Stereigranisporis sp. 1	S	1														
Stereigranisporis sp. 2	S			3												
Stereigranisporis sp. 3	S						1			6	1			8		
Tetrad sp. 3	S						16									
Tetrad sp. 4	S						1							1		
Triplanosporites cf. *sinuosus*	S	7	3	4	7	2	6				17			36		3

(*Continued*)

APPENDIX. PALYNOLOGICAL DATA (*Continued*)

Stratigraphic position (cm) Khc/PGFtu = 0		–340	–305	–275	–245	–225	–185	–135	–85	–35	–5	0	+10	+65	+225	+235
Taxon		MT97-117	MT97-118	MT97-119	MT97-120	MT97-121	MT97-122	MT97-123	MT97-124	MT97-125	MT97-126	MT97-127	MT97-128	MT97-129	MT97-130	MT97-131
Verrucatosporites cf. *alienus*	S					2										
Verrucatosporites favus	S						3			4		6		12		
Abietipites sp.	C	2			1	1										26
Cycadopites scabratus	C	9	8	2		2	2			3	4	5		1		9
Ephedripites sp.	C		3													
Inaperturopollenites sp.	C	1	5	1	12	1	9		4	2				7		11
Laricoidites magnus	C	1			1		2							3		
Pinuspollenites elongatus	C	1	3							4						
Pinuspollenites semicircularis	C	1					1			1		11	11	11	4	36
cf. *Pityosporites labdacus*	C			2												
Podocarpidites maximus	C							5								
Podocarpidites sellowiformis	C		6				2							4		16
Podocarpidites sp. 1	C											1				
cf. *Podocarpidites* sp. 2	C			2	31	1										35
Taxodiaceaepollenites hiatus	C	20	5		2					13	1	16	29	14	28	179
Tsugaepollenites mesozoicus	C	1	1													
Zonalapollenites sp.	C					1										
Arecipites cf. *columellus*	M						2									
Arecipites sp.	M						5							1		
Echimonocolpites sp. 1	M	1		3			21							27	2	3
Echimonocolpites sp. 2	M			2			9									
Echimonocolpites sp. 3	M					1										
Liliacidites complexus	M		1	1												
Liliacidites sp. 1	M			2												
Liliacidites sp. 3	M	1														
Liliacidites sp. 4	M	1														
cf. *Monocolpopollenites areolatus*	M			1												
Monocolpopollenites sp. 1	M															1
Monocolpopollenites sp. 2	M					1	1				4			48		8
Monosulcate unknown 1	M								5							
Monosulcate unknown 2	M	4												5		
Monosulcate unknown 3	M	3														
Monosulcate unknown 5	M	5					1									
Monosulcate unknown 6	M	4														
Monosulcate unknown 7	M	6														
Monosulcate unknown 12	M	1												6	1	
Monosulcate unknown 15	M			1												
Monosulcate unknown 16	M					1										
Monosulcate unknown 17	M															1
Monosulcate unknown 18	M								1							
Monosulcate unknown 19	M					1										
Alnipollenites sp.	T	10	2	2		1	1			4	4	4		7		
Aquilapollenites attenuatus	T	1				1	4									3
Aquilapollenites collaris	T		4													

(*Continued*)

APPENDIX. PALYNOLOGICAL DATA (*Continued*)

Stratigraphic position (cm) Khc/PGFtu = 0		–340	–305	–275	–245	–225	–185	–135	–85	–35	–5	0	+10	+65	+225	+235
Taxon		MT97-117	MT97-118	MT97-119	MT97-120	MT97-121	MT97-122	MT97-123	MT97-124	MT97-125	MT97-126	MT97-127	MT97-128	MT97-129	MT97-130	MT97-131
Aquilapollenites reductus	T	2	9	3												
Aquilapollenites sp.	T			1												
Cupanieidites reductus	T	2									2					
Cupuliferoidaepollenites sp. 1	T	3	8				1					14			24	75
Cupuliferoidaepollenites sp. 2	T	5	1	2			9		3	2		13		59	3	41
Cupuliferoidaepollenites sp. 3	T						1									16
Dicolpate unknown 1	T		1	1												
Erdtmanipollis cretaceus	T						10	4		5			1			
Foveotricolpites sp.	T	3	4	1								1				
Fraxinoipollenites variabilis	T	3			2	4				1			4	2		
Kurtzipites trispissatus	T											1			24	
cf. *Leptopecopites pocockii*	T		1													
Marsypiletes cretacea	T		1				9									2
Momipites cf. *sanjuanensis*	T												2	4		
cf. *Momipites* sp. 1	T											4				
cf. *Momipites* sp. 3	T						2									
Myrtipites cf. *scabratus*	T	1														
Normapolles sp. 1	T									1						
Normapolles sp. 2	T													3		7
Nudopolles sp.	T		1													
Polyporina cribraria	T	1		1												21
Rhoipites cf. *pisinnus*	T	1														
Rousea sp. 1	T									1		8	17			
Rousea sp. 3	T		6				1			5				6	1	
“*Salix*” sp. 2	T					1										7
Santalacites minor	T	5				4	2	1	1	34	29			38	6	1
cf. *Satisha* sp. 1	T	1										1				
Tetraporate sp. 1	T			1									1			33
Triatriopollenites bituitus	T	7									21	3	48	2		1
Tricolpate unknown 10	T		11			5	4									
Tricolpate unknown 11	T		5													8
Tricolpate unknown 12	T		4			1	2								2	6
Tricolpate unknown 13	T				11		3					4				
Tricolpate unknown 15	T						5								15	
Tricolpate unknown 16	T												6	2		
Tricolpate unknown 17	T													10		
Tricolpate unknown 18	T													3	53	77
Tricolpate unknown 19	T													23	3	25
Tricolpate unknown 20	T	1												19	19	
Tricolpate unknown 21	T														7	11
Tricolpate unknown 22	T			3		2					5			1		34
Tricolpate unknown 23	T															9
Tricolpate unknown 24	T														10	
Tricolpites hians	T	26	4			1				3	14	9	34			
Tricolpites micromunus	T	11	10	3		2										

(*Continued*)

APPENDIX. PALYNOLOGICAL DATA (*Continued*)

Stratigraphic position (cm) Khc/PGFtu = 0		–340	–305	–275	–245	–225	–185	–135	–85	–35	–5	0	+10	+65	+225	+235
Taxon		MT97-117	MT97-118	MT97-119	MT97-120	MT97-121	MT97-122	MT97-123	MT97-124	MT97-125	MT97-126	MT97-127	MT97-128	MT97-129	MT97-130	MT97-131
Tricolpites microreticulatus	T	1				1									8	1
Tricolpites sp. 1	T	9	16	2		1	15									
Tricolpites sp. 2	T	7														15
Tricolpites sp. 3	T	8	2	1			6			15		14	40	1		
Tricolpites sp. 6	T	40	10		5		14	2		19	71	358	296	129	9	101
Tricolpites sp. 7	T						1									
Tricolpites sp. 8	T	1														
Tricolpites sp. 9	T	1												1		
“Tricolpites” parvistratus	T	3	6		4	1	6	1							3	18
Tricolporate unknown 1	T	3		2												
Tricolporate unknown 8	T	3														
Tricolporate unknown 9	T	1														
Tricolporate unknown 12	T	1									1					
Tricolporites sp.	T	2														
Tricolporites traversei	T	18								4	27					45
Tricolporopollenites cf. *cingulum*	T	8	1					2	1							
Tricolporopollenites cf. *steinensis*	T			1												
Triporate unknown 3	T				1											
Triporate unknown 6	T			3									6	11		38
Triporate unknown 7	T						2									
Triporate unknown 8	T													3		
Triporopollenites granilabratus	T												4			
Triporopollenites plektosus	T	1												1		
Triporopollenites triplicatus	T		1		4											
Tschudypollis retusus	T	2														
Ulmipollenites krempii	T		1													
cf. *Ulmipollenites* sp.	T	9		2		2										
Unknown 1	T	1														
Unknown 29	T		8													
Unknown 36	T									1						
Unknown 46	T	1														
Unknown 50	T					1	2	34	92	32		1				
cf. *Wilsonipites* sp.	T	5									8					
Wodehouseia fimbriata	T		6													
Wodehouseia spinata	T														1	
Totals																
Total grains counted*		306	301	65	95	63	234	53	108	217	256	737	820	940	236	1068
Total taxa		67	47	35	15	34	47	8	8	30	17	28	20	47	23	48
Gymnosperm taxa		8	7	3	5	5	5	1	1	5	2	4	2	6	2	7
Triaperturate taxa		41	25	16	6	15	21	6	4	14	10	14	13	20	16	24
Monosulcate taxa		9	1	6	0	4	6	0	2	0	1	0	0	5	2	4
Spore taxa		12	14	10	4	11	16	1	1	11	5	10	6	17	3	13

(*Continued*)

APPENDIX. PALYNOLOGICAL DATA (*Continued*)

Stratigraphic position (cm) Khc/PGFtu = 0	–340	–305	–275	–245	–225	–185	–135	–85	–35	–5	0	+10	+65	+225	+235
Taxon	MT97-117	MT97-118	MT97-119	MT97-120	MT97-121	MT97-122	MT97-123	MT97-124	MT97-125	MT97-126	MT97-127	MT97-128	MT97-129	MT97-130	MT97-131
Relative abundance															
Gymnosperm grains	11.8	10.3	10.8	49.5	9.5	6.8	9.4	3.7	10.6	2.0	4.5	4.9	4.3	13.6	29.2
Triaperturate grains	68.0	40.9	44.6	28.4	44.4	42.7	83.0	89.8	58.5	71.1	59.0	56.0	34.6	79.7	55.7
Monoaperturate grains	8.5	0.3	15.4	0.0	6.3	16.7	0.0	5.6	0.0	1.6	0.0	0.0	9.3	1.3	1.2
Spores	11.8	48.5	29.2	22.1	39.7	33.8	7.5	0.9	30.9	25.4	36.5	39.1	51.9	5.5	13.9
Gymnosperm taxa	11.9	14.9	8.6	33.3	14.7	10.6	12.5	12.5	16.7	11.8	14.3	10	12.8	8.7	14.6
Triaperturate taxa	61.2	53.2	45.7	40	44.1	44.7	75	50	46.7	58.8	50	65	42.6	69.6	50
Monosulcate taxa	13.4	2.1	17.1	0	11.8	12.8	0	25	0	5.9	0	0	10.6	8.7	8.3
Spore taxa	17.9	29.8	28.6	26.7	32.4	34.0	12.5	12.5	36.7	29.4	35.7	30	36.2	13.0	27.1
Grains/g sediment	67,984	45,664	21,038	13,837	8234	55,952	4428	4526	53,789	29,455	55,377	46,185	1,100,380	33,062	163,020
δ^{13}C bulk organic carbon (‰)	–24.101	NA	–24.135	–24.165	–24.09	–23.912	NA	–24.075	–24.468	–24.481	–24.577	–26.319	–23.752	–24.302	–23.811
δ^{13}C isolated plant cuticle (‰)	–23.705	–24.315	–23.962	–23.999	–24.448	–24.77	–24.456	–24.523	–24.724	–24.636	–24.879	–26.059	–23.989	–23.738	–23.765
Organic-carbon content (wt%)	21.326	12.872	56.085	61.75	40.497	22.059	23.268	51.732	37.893	31.707	14.151	2.961	3.776	1.317	28.638

Note: Table shows number of grains counted for each taxon for each sample. Each taxon is coded as a pteridophyte or bryophyte spore (S); gymnosperm, including conifer, cycad, and ephedroid pollen (C = conifer/cycad); monosulcate angiosperm pollen, primarily representing monocotyledons (M); or triaperturate angiosperm pollen representing dicotyledons (T). These broad taxonomic categories are plotted and discussed in the text. Stratigraphic position is given relative to the Cretaceous Hell Creek–Paleogene Fort Union (Khc/PGFtu) contact.

*Undamaged, well-preserved grains with the potential for identification.

suggesting a strong regional signal and increasing heterogeneity of the latest Cretaceous vegetation. This is consistent with the predictions of the press-pulse model in which organisms were responding to hypothesized press disturbance by changing relative abundance and range. A more detailed spatial-temporal analysis will be required to further test this hypothesis. These data are inconsistent with a model that predicts no biotic change prior to the Cretaceous-Paleogene boundary.

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