

Land plant extinction at the end of the Cretaceous: a quantitative analysis of the North Dakota megafloral record

Peter Wilf and Kirk R. Johnson

Abstract.—We present a quantitative analysis of megafloral turnover across the Cretaceous/Paleogene boundary (K/T) based on the most complete record, which comes from the Williston Basin in southwestern North Dakota. More than 22,000 specimens of 353 species have been recovered from 161 localities in a stratigraphic section that is continuous across and temporally calibrated to the K/T and two paleomagnetic reversals. Floral composition changes dynamically during the Cretaceous, shifts sharply at the K/T, and is virtually static during the Paleocene. The K/T is associated with the loss of nearly all dominant species, a significant drop in species richness, and no subsequent recovery. Only 29 of 130 Cretaceous species that appear in more than one stratigraphic level (non-singletons) cross the K/T. Only 11 non-singletons appear first during the Paleocene. The survivors, most of which were minor elements of Cretaceous floras, dominate the impoverished Paleocene floras. Confidence intervals show that the range terminations of most Cretaceous plant taxa are well sampled. We infer that nearly all species with last appearances more than about 5 m below (approximately 70 Kyr before) the K/T truly disappeared before the boundary because of normal turnover dynamics and climate changes; these species should not be counted as K/T victims. Maxima of last appearances occur from 5 to 3 m below the K/T. Interpretation of these last appearances at a fine stratigraphic scale is problematic because of local facies changes, and megafloral data alone, even with confidence intervals, are not sufficient for precise location of an extinction horizon. For this purpose, we rely on high-resolution palynological data previously recovered from continuous facies in the same sections; these place a major plant extinction event precisely at the K/T impact horizon. Accordingly, we interpret the significant cluster of last appearances less than 5 m below the K/T as the signal of a real extinction at the K/T that is recorded slightly down section. A maximum estimate of plant extinction, based on species lost that were present in the uppermost 5 m of Cretaceous strata, is 57%. Palynological data, with higher stratigraphic but lower taxonomic resolution than the megafloral results, provide a minimum estimate of a 30% extinction. The 57% estimate is significantly lower than previous megafloral observations, but these were based on a larger thickness of latest Cretaceous strata, including most of a globally warm interval, and were less sensitive to turnover before the K/T. The loss of one-third to three-fifths of plant species supports a scenario of sudden ecosystem collapse, presumably caused by the Chicxulub impact.

Peter Wilf. *Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802 and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109. E-mail: pwilf@psu.edu*

Kirk R. Johnson. *Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado 80205. E-mail: KJohnson@dmns.org*

Accepted: 12 December 2003

Introduction

Since Alvarez et al. (1980) proposed an extraterrestrial cause for the end-Cretaceous extinctions, the Chicxulub structure in the Yucatán peninsula of Mexico has been identified as an impact crater (Hildebrand et al. 1991) of terminal Cretaceous age (Izett et al. 1991; Swisher et al. 1992), its distal ejecta isotopically fingerprinted (Krogh et al. 1993; Blum et al. 1993), its structure mapped in detail (Christeson et al. 2001), and possible killing mechanisms investigated (Toon et al. 1997; Pope 2002). Paleontologists have taken up the task of assessing the end-Cretaceous extinctions,

which appear to have been sudden and severe for many major groups of organisms (Sheehan et al. 1991, 2000; Marshall and Ward 1996; Norris et al. 1999; Pearson et al. 2001, 2002; Labandeira et al. 2002a,b).

Land plants are the trophic and structural basis of terrestrial ecosystems. Accordingly, their fates at the Cretaceous/Paleogene boundary (we use the historic abbreviation, "K/T," because it is widely recognized) are of primary interest to extinction studies because a decimation of land plants would suggest a simultaneous catastrophe for dependent animal life (Labandeira et al. 2002b). Palynological data show a significant plant extinction

precisely at the K/T impact horizon, at a stratigraphic resolution not available from megafossils (Tschudy 1970; Leffingwell 1970; Orth et al. 1981; Tschudy et al. 1984; Nichols et al. 1986; Johnson et al. 1989; Sweet and Braman 2001; Hotton 2002; Nichols and Johnson 2002). Palynology also provides the only reliable evidence for a K/T plant extinction outside North America (Saito et al. 1986; Vajda et al. 2001; Vajda and Raine 2003). However, palynomorphs are relatively limited in taxonomic resolution and underrepresent many insect-pollinated taxa (Johnson and Hickey 1990). Megafloral data allow species-level resolution of extinction, origination, richness, relative abundance, and compositional change, as well as quantitative inference of paleoclimates (Wing et al. 2000). Unlike palynomorphs, many types of plant megafossils, such as leaves, cannot be reworked into younger strata. The taxonomic resolution of megafossils, combined with the stratigraphic resolution of palynomorphs, offers the best opportunity for improved understanding of plant turnover at the K/T (e.g., Pearson et al. 2001).

Early reports after the Alvarez et al. (1980) paper found no evidence for an abrupt megafloral extinction at the K/T (Hickey 1981, 1984). Significant floral turnover was observed but attributed to relatively gradual processes such as climate change, as it was before 1980 (Dorf 1940; Brown 1962; Krassilov 1975, 1978). At this time sample sizes were relatively low, stratigraphic and taxonomic resolution were coarse, Cretaceous floras were much less sampled than Paleocene floras, and correlations of megafloras to the K/T impact layer were not yet achieved, as discussed by Johnson (2002).

The discovery of a coeval iridium anomaly and palynological extinction in the Raton Basin of New Mexico and Colorado (Orth et al. 1981) set the stage for a megafloral study by Wolfe and Upchurch (1987). These authors reported a loss from the latest Cretaceous to the Paleocene of 84% of species interpreted as evergreen dicots and 33% of deciduous dicots, followed by a recovery of richness into the early Paleocene. Sample size was not taken into account in these estimates. To date, apart from the K/T impact horizon, there are no high-resolution stratigraphic data reported, such as

paleomagnetic reversals, that constrain the ages of the Raton sections. Interpretations of floral recovery rates in the Raton Basin (Beerling et al. 2001) are therefore premature in our view. Wolfe and Upchurch (1986) also examined other, more coarsely sampled, latest Cretaceous and early Paleocene floras throughout the Western Interior of the United States and found corroboration of the mass extinction pattern from the Raton Basin.

Johnson and colleagues increased the resolution of the K/T megafloral record with their study of the Williston Basin in the vicinity of Marmarth, in southwestern North Dakota (Johnson et al. 1989; Johnson and Hickey 1990; Johnson 1992, 1996, 2002). These workers first recognized the K/T from the simultaneous occurrence of an iridium anomaly and shocked minerals (Johnson et al. 1989), which are associated locally with the loss of vertebrate species (Sheehan et al. 1991, 2000; Pearson et al. 2001, 2002). The iridium anomaly coincides with the loss of approximately 30% of palynomorphs (Johnson et al. 1989; Nichols and Johnson 2002; Nichols 2002). The first syntheses of megafloral change in the Marmarth area were based on over 11,000 megafloral specimens from approximately 90 localities, representing about 250 species (Johnson et al. 1989; Johnson and Hickey 1990). Turnover events were recognized both before and at the K/T, and a biozonation was developed to recognize these changes. The largest turnover was at the K/T: 79% of species present in the uppermost Cretaceous biozone (zone HCIII, found in the uppermost 24 m of Cretaceous strata), including nearly all dominant species, were not found in Paleocene strata (Johnson et al. 1989; Johnson 1992). The homogeneous, low-diversity "disaster" flora from the basal Paleocene of the Marmarth area was found to be widespread in correlative strata of Colorado, Wyoming, Montana, and the Dakotas, corroborating a mass extinction scenario over a large area (Johnson and Hickey 1990; Barclay et al. 2003), as suggested by Wolfe and Upchurch (1986).

More recently, Johnson (2002) greatly increased sample size and provided extensive documentation of the floras from the Marmarth area, including information on the tax-

onomy and stratigraphic ranges of species, updated descriptions of localities and biozones, and possible effects of facies changes on recovered floral composition. Labandeira et al. (2002a,b) investigated insect damage on the Marmarth floras and found the first evidence for a mass extinction of insects at the K/T. In a companion paper to this contribution, Wilf et al. (2003) analyzed paleotemperatures for the Marmarth section, their relationship to species richness, and their correlation to marine climates.

Despite the scientific importance of the K/T and a rich history of investigations, there are no detailed quantitative analyses of megafloral change. The sections from the vicinity of Marmarth, North Dakota are the most intensively sampled, and, because of recent work, they are well understood with regard to stratigraphy, sedimentology, paleobotany, and paleoclimate. Here, we present a suite of analyses that are made possible by the improved North Dakota record. We examine floral turnover, richness, and composition and attempt to distinguish events at the Cretaceous/Paleogene boundary from those that occurred during the Cretaceous and Paleocene.

Sampling

Stratigraphy.—The recent revision of the stratigraphy, sedimentology, geochronology, and paleobotany of K/T strata from the Marmarth area is the framework for this contribution (Johnson 2002; Hicks et al. 2002; other papers in Hartman et al. 2002). The Marmarth record is correlated using a composite stratigraphic section that contains all of the Cretaceous Hell Creek Formation and most of the Ludlow Member of the Fort Union Formation, in a total of 103 m of Cretaceous and 80 m of Paleocene strata collected over a north-south distance of 70 km (Fig. 1). Most of the Fort Union Formation is Paleocene in the study area, but in some local sections about 2 m of its most basal strata are Cretaceous (Johnson et al. 1989; Pearson et al. 2001; Nichols and Johnson 2002). Megafloral localities are predominantly derived from a variety of Cretaceous channels (78% of Cretaceous localities) and Paleocene floodplain ponds and mires (79%), as detailed by Johnson (2002). Megaf-

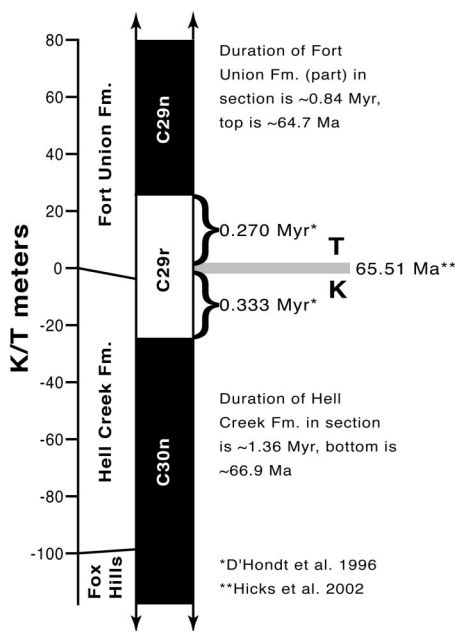


FIGURE 1. Stratigraphic summary and age model, redrawn from Hicks et al. (2002). The composite section contains three temporal reference points, the K/T and the base and top of C29r. After Hicks et al. (2002) and D'Hondt et al. (1996), we use 65.51 ± 0.10 Ma as the age of the K/T and 0.333 Myr and 0.270 Myr as the durations of the Cretaceous and Paleocene portions of C29r, respectively. The Hicks et al. (2002) estimate that the section represents approximately 1.36 Myr of Cretaceous and 0.84 Myr of Paleocene time is based on two linear stratigraphic extrapolations. The Cretaceous estimate is extrapolated from the K/T and the average stratigraphic position of the bottom of C29r; the Paleocene estimate is likewise extrapolated from the K/T and the top of C29r. The two extrapolations are used to generate an interpolated, modeled age for every stratigraphic level. A complete list of the modeled ages for each 1-m bin is presented in the online supplement of Wilf et al. (2003).

loras occur within all of these environments on both sides of the K/T, although Cretaceous mires are restricted to the basal Fort Union Formation. The K/T palynological extinction has been identified in 17 local sections, coincident with the iridium anomaly in the two sections where the latter is known and used as a proxy for the boundary where it is not (Johnson 2002; Nichols and Johnson 2002). Stratigraphic positions of megafloral localities are calibrated to the K/T (Johnson 2002), a major improvement over previous calibrations to the Hell Creek/Fort Union contact. Another significant development is the introduction of paleomagnetic stratigraphy: the lower and upper bounds of magnetic polarity subchron

TABLE 1. Morphospecies sampling by taxonomic category, calculated from the minimum abundance matrix (Table 2, data set 4). See Johnson (2002) for detailed taxonomic information.

Higher taxon and organ	Morphospecies	Specimens	% Morphospecies	% Specimens
Bryophyta, vegetative	2	41	0.5	0.2
Sphenopsida, reproductive	1	6	0.3	<0.1
Lycopsida, vegetative	1	2	0.3	<0.1
Filicopsida				
leaves	20	182	5.2	0.8
reproductive	1	1	0.3	<0.1
Cycadales, leaves	1	175	0.3	0.8
Ginkgoales, leaves	1	114	0.3	0.5
Coniferales				
leaves	10	2207	2.6	9.9
cones	4	22	1.0	0.1
seeds	4	37	1.0	0.2
Unknown affinity, fruit	1	1	0.3	<0.1
Liliopsida				
leaves	9	751	2.3	3.4
reproductive	1	12	0.3	0.1
Magnoliopsida				
leaves	309	18,126	80.1	81.6
fruits	18	361	4.7	1.6
seeds	3	167	0.8	0.8
Total, nonreproductive	353	21,598		
Total, all	386	22,205		

C29r, which straddles the K/T, have been found in several local sections, allowing the calculation of a modeled age for each locality (Hicks et al. 2002) (Fig. 1). The modeled ages are most accurate within C29r, where they are bounded by more than one datum point, and are inferred to decrease in accuracy with increasing stratigraphic distance from C29r (Hicks et al. 2002). The modeled ages are not critical to the arguments of this paper, but we refer to them occasionally to provide temporal context.

Paleobotany.—We describe here our use of the terms “morphotype,” “morphospecies,” and “species.” Morphotypes are morphologically discrete populations of plant organs with no formal taxonomic status, although in practice they are taxonomic works in progress (Johnson et al. 1989; Ash et al. 1999). Some morphotypes are usually equivalent to known, described species, whereas most, usually the majority in angiosperm paleobotany because of an intrinsically high discovery rate, represent undescribed species. Morphotypes are used, sometimes in combination, to develop proxy species, known as morphospecies,

when formal species descriptions are lacking or inadequate. Morphospecies plus formally described species, all referred to here as “morphospecies” for convenience, are our fundamental units of analysis.

Johnson (2002) listed, illustrated, and updated the stratigraphic distribution and systematic standing of 380 megafloral morphotypes from the study area. Johnson also listed dominant taxa characteristic of megafloral zones and described the methodology for circumscribing leaf morphotypes, in particular, using diagnostic combinations of architectural characters (Hickey 1979; Ash et al. 1999). Some minor additions and adjustments to these morphotypes and notes regarding their conversion to morphospecies for this paper are described in the Appendix. With all adjustments, our primary data contain 386 morphospecies (Table 1, Appendix). More than 80% of the morphospecies are leaves of dicotyledonous angiosperms, 6% are dicot fruits and seeds, and 6%, 5%, and 3% are various organs of ferns, conifers, and monocots, respectively (Table 1). The remaining morphospecies are organs of cycads, ginkgophytes, lycophytes,

TABLE 2. Summary of data sets and derived analyses. See text for details. Data sets (1) and (2), from which all the other data sets are derived, as well as data set (4), are available in electronic format as described in text.

Data set	Derived from	Analyses
(1) Museum vouchers: 12,589 specimens	Primary, museum inventory	
(2) Field census: 13,914 specimens	Primary, field tallies	
(3) Dicot leaf census: 8591 specimens	(2), 16 quarries \geq 250 dicot specimens each	rarefaction: Fig. 3C, closed symbols; Fig. 4
(3A) Dicot leaf census minus species that occur in only one of 16 quarries	(3)	ordination: Fig. 5, "census"
(4) Minimum abundance: 22,205 specimens	(1) and (2), binned by meter	sample size: Fig. 2; Table 1
(4A) Minimum abundance with only dicot leaves: 18,126 specimens	(4), bins \geq 350 specimens each	supplemental rarefaction: Fig. 3C, open symbols
(4B) Minimum abundance minus singletons and reproductive morphospecies: 141 species, 20,642 specimens	(4)	ranges and confidence intervals: Figs. 8, 9
(5) Presence-absence	(4), minus reproductive morphospecies	raw richness: Fig. 3A
(5A) Presence-absence minus herbs and nondicots	(5)	leaf-margin analysis: Fig. 3D, open symbols
(5B) 5A plus range-through occurrences	(5A)	leaf-margin analysis: Fig. 3D, line
(5C) Presence-absence minus singletons: 141 species	(5), or equivalently from (4B)	ordination: Fig. 5, open symbols
(5D) 5C plus range-through occurrences	(5C)	first and last appearances: Fig. 6
		standing richness: Fig. 3B
		ordination: Fig. 5, line
		per capita rates: Fig. 7
		extinction percentages: Table 3

sphenopsids, and bryophytes. Of the 386 morphospecies, 353 are nonreproductive, of which 350 are leaves and three represent photosynthetic portions of bryophytes and herbaceous lycopods. Nonreproductive morphospecies provide the best estimate of minimum species richness by eliminating the possibility of counting the reproductive and nonreproductive organs of the same original plant as more than one species. For simplification of text and discussion, we use "species" hereafter to denote the 353 nonreproductive morphospecies.

Collections.—The 161 megafloral localities analyzed here, from 128 distinct stratigraphic horizons, are mostly identical to the 158 quarries reported by Johnson (2002), with some minor revisions (Appendix). All of the collections were made by K.R.J. using described field methods (Johnson 2002), and vouchers are housed at the Denver Museum of Nature & Science (DMNH) and the Yale Peabody Museum.

Fossil plant specimens were collected both selectively and quantitatively, resulting in two, partially overlapping data sets. We will reference these as the "voucher" and "census"

data sets (Table 2, data sets 1 and 2, respectively). Selective collecting involves the discarding of some identifiable field specimens without any record kept of these specimens. In quantitative collecting (Chaney and Sanborn 1933; MacGinitie 1941), also known as censusing or bulk collecting, the investigator tallies all specimens found in the field, keeping some fraction of these specimens as vouchers. In our case, the museum vouchers from censuses were until recently mixed in museum drawers with selectively collected vouchers from the same localities. The first data set is the total of 12,589 identified museum voucher specimens (Table 2). The total tally of identified, censused specimens, tabulated from field notebooks and analyzed here for the first time, is 13,914 (Table 2), an unknown number of which are also included in the voucher set. Material that could not be identified to a species or morphospecies, comprising several thousand additional specimens, was excluded from all of our working data sets and analyses.

The complete data set used in this article is available as a single electronic file for unrestricted download from the Paleobiology Da-

tabase, www.paleodb.org (under "major data sets deposited") or by request from either author. Detailed locality data, most of which are provided by Johnson (2002), are also archived without access restriction in the Paleobiology Database (search under the locality names in the electronic file or under "Authorizer = Johnson").

Facies and Climate Changes.—Facies and climate issues are addressed elsewhere in detail, as cited below, but an abbreviated discussion is presented here because of their relevance for interpreting megafloral samples. In summary, both local facies and global climate changes occurred during the terminal Cretaceous, complicating interpretation of extinction. Palynological data from continuous facies sampled at high resolution provide the only direct evidence that a major extinction of land plants occurred precisely at the K/T (Johnson et al. 1989), and thus we rely on palynology to interpret megafloral results from problematic facies near the K/T (Pearson et al. 2001; Nichols and Johnson 2002).

In some local sections, the uppermost 2 m or so (approximately 30 Kyr) of Cretaceous strata are fossiliferous mire deposits of the Cretaceous portion of the Fort Union Formation, whereas in others, barren, possibly leached strata of the uppermost Hell Creek Formation reach the K/T (Pearson et al. 2001; Johnson 2002; Nichols and Johnson 2002). Mire deposits that contain plant fossils have not been found within the Hell Creek Formation (Johnson 2002). The dinosaur-bearing, Cretaceous mires of the basal Fort Union Formation contain megafloras that are compositionally similar to Paleocene floras, with minor differences (Pearson et al. 2001; Johnson 2002). We follow Johnson (2002) in the use of the term "FU0" to denote this megafloral biozone associated with terminal Cretaceous mire deposits. Diagnostically Cretaceous palynomorphs, derived from the same source vegetation as the megafloras, show the survival of typical Cretaceous plants within FU0 and their extinction at the K/T impact layer (Johnson et al. 1989; Pearson et al. 2001; Nichols and Johnson 2002). The productive Hell Creek strata just below the mires offer the last glimpse of most of the Cretaceous megaflora,

which does not appear in any facies above the K/T. Therefore, any analysis of megafloral extinction in this area must include Hell Creek strata. Many of the figures in this contribution show a major drop in diversity, spike in last appearances, or change in composition at about 2 m below the K/T, which, in accord with the work discussed above, we interpret as an artifact of facies change that smears a true extinction at the K/T a short distance down section (see Signor and Lipps 1982).

At a larger scale, facies change from the Hell Creek Formation to the Fort Union Formation is also germane because the majority of Hell Creek megafloral localities are from channel deposits and the majority from the Fort Union Formation are from floodplain deposits. Johnson (2002) recognized this and sampled floras from rare Hell Creek floodplain and Fort Union channel deposits. Although sample sizes are not yet sufficient for a detailed, facies-controlled study, we provide some preliminary analyses here: significantly, uppermost Cretaceous floodplain and channel deposits contain megafloras that are very different from their Paleocene counterparts. For example, the highest Cretaceous pond flora, at -6 m, has 17 species but only two that are found above the K/T. Similarly, only 19 of 112 species from channel deposits in the uppermost 15 m of Cretaceous strata have been found in Paleocene channel deposits. The best-sampled flora from a Paleocene channel, at +7 m, contains 11 species, seven of which are Cretaceous survivors, and all Paleocene channels combined contain 19 species, of which 13 are Cretaceous survivors, 15 occur in Paleocene floodplain deposits, 14 occur in Paleocene ponds (the dominant floodplain subenvironment), and 11 occur in Paleocene mires. The fact that most Paleocene channel species can be found in pond and other types of floodplain deposits indicates their broad original distribution across environments and mitigates the problem with the general shift in dominant facies near the K/T. Also, the observations above are consistent with the lack of origination in the basal Paleocene such that the majority of Paleocene species are Cretaceous survivors, as discussed further below.

Climate change near the K/T is analyzed in

a companion paper (Wilf et al. 2003). Temperature is a strong correlate of plant diversity, both today and in the past (Crane and Lidgard 1989; Wing et al. 2000; Phillips and Miller 2002), and a drop in temperatures just before the K/T could be associated with a loss of richness before impact. Wilf et al. (2003) analyzed paleotemperatures from the Marmarth megafloras by using leaf-margin analysis, a method that estimates mean annual temperature from the percentage of woody dicot species with untoothed leaf margins by using the strong positive correlation between these variables observed in living forests (Bailey and Sinnott 1915; Wolfe 1979; Wilf 1997). The megafloral results were correlated using paleomagnetic stratigraphy to four marine temperature records from oxygen isotope ratios of foraminifera (Li and Keller 1998; Barrera and Savin 1999; Olsson et al. 2001), supplemented by records of latitudinal range shifts for plants and foraminifera. Both plants and foraminifera indicated a global warming beginning about 0.5 Myr before the K/T, a peak of warming lasting from 0.3 to 0.1 Myr before the K/T, cooling to pre-warming values within the final 0.1 Myr of the Cretaceous coinciding in part with the deposition of the FU0 floras, and the continuation of cool temperatures during the earliest Paleocene. The warming peak corresponded to maximum plant diversity in the Marmarth section and poleward range expansions of thermophilic foraminifera. Wilf et al. (2003) observed that similarly cool temperatures were associated with rich Cretaceous but poor Paleocene floras. On the basis of this and other evidence, they concluded that climate changes were not the cause of plant extinction at the K/T, but that extinction percentages based on the number of species lost since the warming peak were probably inflated because of nearly synchronous global cooling and local facies changes just prior to the K/T.

Data Analysis

Several different subsets of the primary data were needed in order to quantify sampling (Table 1, Fig. 2), diversity (Figs. 3, 4), composition (Fig. 5), and first and last appearances (Figs. 6–9). The data sets used are listed and numbered in Table 2. Our methodology is de-

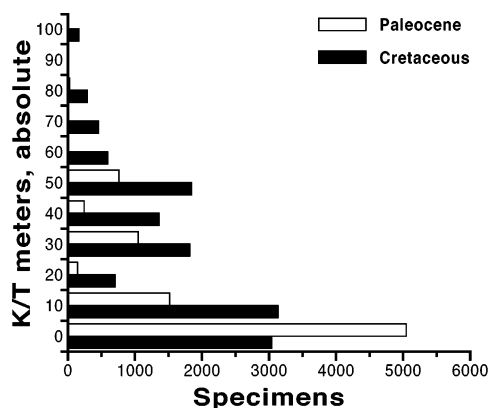


FIGURE 2. Summary of megafloral sampling in 10-m intervals from the K/T, based on the minimum abundance matrix of 22,205 specimens (Table 2, data set 4), 13,420 Cretaceous and 8785 Paleocene. Sampling intensity is greatest near the K/T, especially for the first 10 m of Paleocene strata.

tailed below in procedural order, but several of our figures combine results from more than one data set and major analysis.

In summary (details below), the primary data are the museum vouchers (Table 2, data set 1) and field census tallies (data set 2). First, we examined the census data for 8591 dicot-leaf specimens from 16 localities with more than 250 specimens each (data set 3), in order to obtain the best possible, site-specific information. Second, we placed all of the voucher and census data independently, into 184 stratigraphic bins of 1 m each, then combined the two data sets into a single, minimum abundance matrix containing the minimum number of specimens of each morphospecies in each bin (data set 4). Third, we converted the minimum abundance matrix into a presence-absence matrix (data set 5). Most of the data conversions and analyses were executed by using code written for the purpose by P.W. in Mathematica® (Wolfram 2003). The code for calculating confidence intervals on stratigraphic ranges from a stratigraphically ordered abundance matrix, using the technique described below, is available from the Paleobiology Source Code Archive, www.paleodb.org/paleosource. Other software used is referenced below.

Dicot Census Data.—Counts of 300 or more specimens are considered to produce the best approximation of original relative abundance

and richness at individual sites (Burnham et al. 1992). This signal is probably compromised by the allochthonous setting of many Hell Creek floras (Johnson 2002). Nevertheless, leaf counts offer a valuable complement to presence-absence data, which have no abundance information. From the complete set of census data (data set 2), we analyzed the 16 quarries with more than 250 specimens of dicot leaves each (269 to 1298 specimens; data set 3). Census sites are referenced here by their precise meter level. Richness was standardized for sample size by using rarefaction analyses (Figs. 3C, 4), which were evaluated with 95% confidence intervals by using Analytic Rarefaction 1.3 by S. M. Holland, www.uga.edu/~strata/software. To quantify compositional change, we used detrended correspondence analysis (DCA; see Wing and Harrington 2001), after first removing species that only occurred at one locality of the 16 to avoid distortion effects (data set 3A) (Fig. 5, census data). The software package MVSP® (Kovach 2000) was used for the DCA analyses.

Binning, Minimum Abundance Matrix, and Sample Distribution.—To make possible our remaining analyses from two, partially overlapping data sets, we streamlined the process by binning the data. All localities and corresponding occurrence data for plant species were lumped into 184 bins of 1 m thickness each, according to their position in the composite section. Binning was done separately for the vouchers (data set 1) and censused specimens (data set 2). The bins are referenced by their lowest stratigraphic level relative to the K/T, e.g., “-3 m” contains all localities and constituent specimens from stratigraphic position L such that $-3 \text{ m} \leq L < -2 \text{ m}$.

Use of a composite section greatly increases sample size, statistical power, and stratigraphic coverage. However, a composite section inevitably introduces some temporal mixing of floras because localities are combined from the same meter level in different local sections, which do not have uniform sedimentation rates. Construction of the composite section caused negligible vertical mixing of megafloreal biozones (Johnson 2002), and most bins are dominated by a single locality or several localities from the same bed in a single local sec-

tion, so that mixing problems are minimal. Another effect of constructing a single composite section is the loss of information about original spatial heterogeneity in floral composition, so that apparent temporal change in floral composition may reflect original variation on the landscape more than true turnover. We assume that this problem is significant only over the shortest stratigraphic distances, such as comparisons from one bin to the next.

From the binned voucher and census data, we generated a single, minimum abundance matrix (data set 4), containing for each of the 184 bins the minimum number of specimens of each morphospecies occurring in that bin. This number was calculated by comparing, for each morphospecies in each bin, the number of voucher versus the number of census specimens and retaining the greater number. The minimum abundance matrix partly solves the problem of the unknown overlap between the voucher and census data by generating a conservative working estimate of specimen counts. The numbers of specimens would be slightly greater if comparisons were made for localities instead of bins, but this route is much more computationally intensive, and the improvement would only be of marginal use here.

The minimum abundance matrix produced 22,205 specimens (Table 1). This sample size is more than double that of previous studies in the area, which included unidentified specimens and did not include census data (Johnson et al. 1989; Johnson 1992, 2002). We use the minimum abundance matrix to evaluate the sample sizes of bins (Fig. 2) and relative abundances of morphospecies (Table 1). Dicot leaves dominate the percentages of total specimens (82%) and species richness (80%). Some other organ types show more disparity between abundance and richness, such as conifer leaves (10% vs. 3%, respectively). The 353 non-reproductive morphospecies, which we use as operational species as described above, constitute 97.3% of the total specimens.

Historically, Maastrichtian floras were undersampled in comparison to Paleocene floras (Johnson 2002). The stratigraphic distribution of sampling (Fig. 2) shows that the reverse is now true in the study area, with 13,420 Cre-

taceous and 8785 Paleocene specimens. At face value, this sampling inequity creates bias in favor of a higher observed extinction. However, the critical lowest 10 m of Paleocene strata is about 60% better sampled than the highest 10 m of the Cretaceous (Fig. 2), which counteracts the bias. The sampling distribution also shows a heavy concentration of collections close to the K/T, where they are most needed to evaluate extinction rates. However, increased sampling at greater stratigraphic distance is necessary, especially in the Paleocene, to improve quantification of turnover above the boundary.

In order to extend the stratigraphic range of the dicot census data (data set 3), supplemental rarefactions (Fig. 3C, open symbols) were calculated from the minimum abundance matrix for bins with at least 350 specimens of dicot leaves (data set 4A).

Confidence Intervals on Stratigraphic Ranges.—The placement of confidence intervals on the endpoints of stratigraphic ranges is, at best, a probability exercise that is always made imperfect by the unpredictable nature of the fossil record (e.g., Marshall and Ward 1996; Payne 2003; Holland 2003). Nevertheless, confidence intervals give at least a rough idea of how well the true range of a taxon is sampled, and ranges with confidence intervals are a major improvement over “raw” ranges. Strauss and Sadler (1989; see also Marshall 1990) presented a simple formula for deriving the desired confidence interval as a range extension r , calculated as a fraction α of the observed range R of a taxon, where r and R can be denoted in any units of stratigraphic thickness or time; we use meters of stratigraphic thickness here. The Strauss and Sadler formula uses the simplifying assumption that fossil recovery potential is uniform through a sampled section. First, α is calculated as a function of the desired confidence level C , $0 \leq C \leq 1$, and the number of distinct horizons H in which the taxon of interest is found:

$$\alpha = (1 - C)^{1/H} - 1 \quad (1)$$

Second, r is calculated from α :

$$r = \alpha R \quad (2)$$

In practice, fossil recovery potential is never

uniform, because sampling, preservational quality, and facies are variable even in the most ideal study areas. One solution is to use equation (1) as an approximation, which is an improvement over the lack of any confidence intervals when recovery potential is not thought to vary greatly within an interval (e.g., Marshall and Ward 1996). However, sampling data (Fig. 2) show clearly that recovery potential is not uniform in the Marmarth section. Instead, the potential for finding a given taxon is much greater near the K/T, where sampling is most intensive.

To mitigate unevenness, we have adapted Marshall's (1997) recent method, which allows recovery potential to vary stratigraphically (Figs. 8, 9). Our approach is nearly identical to that of Labandeira et al. (2002b), but we provide a more detailed explanation here.

Following Marshall's (1997) method, we evaluate the confidence interval r by using integration, with respect to the area under a curve $f(h)$ that expresses the relative recovery potential with respect to stratigraphic height h :

$$\int_b^{b+r} f(h) dh = \alpha \int_a^b f(h) dh \quad (3)$$

where a is the stratigraphic level of first appearance, b is the level of last appearance, and the proportionality factor α is calculated from equation (1). Marshall (1997) showed that equation (1) is a special case of equation (3) in which recovery potential does not vary stratigraphically, and therefore $f(h)$ is equal to a constant.

Marshall (1997) left to the investigator the practical problem of assigning a recovery curve $f(h)$ to a particular fossiliferous section. In a section such as ours with specimen counts for each stratigraphic level, the number of specimens examined within a bin is a good approximation for the potential of recovering a given taxon within that interval because the specimen count directly reflects the effort expended in search of the taxon. Equation (3) is therefore not solved analytically but graphically: the area under the curve at the level of a particular bin is simply the number of specimens in that bin, so that the recovery curve

$f(h)$, if drawn, would have the appearance of a stacked bar graph (see Fig. 9, right side).

Prior to analysis, all species appearing in only one bin, hereafter termed "singletons" (sensu Foote 2000), were removed because they have undefined confidence intervals, along with the 33 reproductive morphospecies, leaving 141 non-singleton species represented by 20,642 specimens (data set 4B). For each species, the total number of specimens in this culled data set within the range of that species, inclusive, was summed. The sum was multiplied by the proportionality factor α (eq. 1), with H set equal to the number of bins of occurrence, to derive a scaled potential equivalent to the right side of equation (3). The remaining task was to calculate r so that the left side of equation (3) equaled the scaled potential of the right side. Starting with the first bin above the range top of the species, specimen counts in each bin were summed through successively higher bins until a number greater than or equal to the scaled potential was reached. The midpoint of the highest bin summed was the top of the confidence interval, with r equal to the total range extension. The procedure above can be modified easily for range bottoms by reversing direction.

The ranges of the 141 non-singleton species are shown first with 50% confidence intervals (Fig. 8A). For illustrative purposes, the confidence intervals are placed on the ranges of all species, including survivors of the K/T, and are applied separately both to range tops and range bottoms by using the same derivation, to show the dependence of confidence interval length on sampling distribution. Note that a different calculation for the range bottom versus top extensions would be required in a true two-tailed case (Strauss and Sadler 1989), but the lower range extensions in Figure 8A are simply a second, reversed application of the one-tailed case for the sake of direct pictorial comparison. Confidence intervals near the K/T are considerably shorter than confidence intervals far from the K/T, many of which do not terminate within the section. This difference reflects the higher sampling intensity near the K/T (Fig. 2), such that the calculation of the range extensions requires the summa-

tion of relatively few bins in order to balance equation (3).

Intensive sampling near the K/T made possible the calculation of 99% confidence intervals, most of which remained within the bounds of our section; we place these on the range tops of the 101 species with Cretaceous last appearances (Fig. 8B). We also extract a detailed view of the 57 species with last appearances within the uppermost 15 m of Cretaceous strata (Fig. 9).

Presence-Absence Data.—The original minimum abundance matrix (data set 4) exclusive of the reproductive morphospecies was converted to a presence-absence matrix (data set 5). Raw richness was calculated from simple tallies of the number of species in each stratigraphic bin (Fig. 3A). The presence-absence matrix minus all occurrences of non-dicots and herbaceous dicots (data set 5A), which are conventionally excluded from leaf-margin analysis (Wolfe 1979), was used to generate paleotemperature estimates (Fig. 3D, open symbols), as described in the companion paper (Wilf et al. 2003). The presence-absence matrix with singletons removed (data set 5C), was subjected to DCA (Fig. 5, "raw").

Range-through occurrences were added to data sets 5A and 5C (generating data sets 5B and 5D, respectively), so that a species was considered to be present in a bin if it either occurred in that bin or if it occurred both above and below the bin but not in it. The addition of range-through occurrences makes the assumption that a species did not leave the area and return, as a literal reading of the record would suggest, but instead existed in the area undetected as a recovered fossil. This assumption undoubtedly is not always valid and may be especially problematic for taxa with relatively long absences. However, the range-through approach has several benefits, including the smoothing of outliers from raw data (Figs. 3B, 5), the generation of estimates for more bins, the use of more species in calculations, and the fact that more localities and therefore more facies are involved in each estimate, thus helping to reduce taphonomic overprints on richness and composition (e.g., Burnham 1994). Data set 5B was used for a second, range-through leaf-margin analysis in

the companion paper (Wilf et al. 2003), redrawn here (Fig. 3D, solid line). Data set 5D was used for additional DCA (Fig. 5, “range-through”), estimation of standing richness per bin (Fig. 3B, “total minus singletons”), derivation of the number of first and last appearances per bin (Fig. 6), and estimation of extinction percentages (Table 3).

For further analysis of richness and turnover rates, we used the recent methodological revision presented by Foote (2000). Using the presence-absence matrix with range-through occurrences (data set 5D), the three classes of taxa present in a stratigraphic interval (our bins) and in at least one adjacent interval (i.e., non-singletons) were calculated for each bin as defined by Foote (2000). These are (1) taxa that cross only the lower boundary of an interval, which are our species with a last appearance in a bin (Fig. 6B); (2) taxa that cross only the upper boundary of an interval, which are our species with a first appearance in a bin (Fig. 6A); and (3) taxa that cross both boundaries of an interval, which are our species that range through a bin but do not begin or end their ranges there. Variables that represent the number of species in these categories for a particular bin are N_{bL} , N_{Ft} , and N_{bt} , respectively, after Foote (2000). We also use two derived variables, the total number of taxa that cross the lower boundary of an interval, or “bottom crossers,” $N_b (= N_{bL} + N_{bt})$ and the total number that cross the upper boundary, or “top crossers,” $N_t (= N_{Ft} + N_{bt})$. The quantity $N_{bL} + N_{Ft} + N_{bt}$ is equal to total richness minus singletons (Fig. 3B). All of these variables by definition exclude singletons, which have many undesirable characteristics when used to estimate richness or turnover rates (Foote 2000).

For estimating standing richness, the counting of bottom crossers or top crossers has several theoretical advantages over counting total richness minus singletons (Foote 2000). In our data, the difference between total richness minus singletons and bottom or top crossers is mostly inconsequential (Fig. 3B). However, both bottom- and top-crossing data smooth the largest spike in species richness, at -15 m, a small increase in richness just above the K/T, and several other transient peaks (Fig. 3B).

These peaks are therefore better attributed to preservation and sampling than to actual increases in richness. All three richness measures show edge effects near the bottom and top of the section because the number of overlapping ranges drops artifactually near the bounds of the sampled interval.

Foote (2000) advocated the quantification of origination and extinction by using estimated per capita rates, which we apply here (Fig. 7). These rates for a particular bin are logarithmic ratios of the number of non-singleton taxa having first or last appearances in a bin to the number of non-singleton taxa that range across the bin. Practically, our use of “origination rates” and “extinction rates” is best understood in the local context. Calculation of rates is based on first and last appearances and makes no explicit distinction between immigration and speciation as the cause of local origination, nor between emigration and true extinction as the cause of local extinction.

Specifically, the per capita rate of origination per time unit t is (Foote 2000: eq. 22):

$$\hat{p} = \ln(N_t/N_{bt})/\Delta t \quad (4)$$

and the per capita rate of extinction is (Foote 2000: eq. 23):

$$\hat{q} = \ln(N_b/N_{bt})/\Delta t. \quad (5)$$

We present per capita rates (Fig. 7), setting $t = 1$ for the Cretaceous and scaling t for the Paleocene by the calculated relative rate of sedimentation (30% higher for Paleocene [Hicks et al. 2002]). Analysis of the entire section shows edge distortions at the top of the section for extinction and the bottom for origination (Fig. 7A), and so we detail the portion of the section without edge effects (Fig. 7B).

Diversity

All measures of species richness show a significant drop from the latest Cretaceous to the Paleocene (Figs. 3, 4), and no analysis of Paleocene floras produces diversity comparable to that of Cretaceous floras. Many Cretaceous floras have more species than any Paleocene flora. All analyses show a peak in richness at -15 m (~ 200 Kyr before K/T), at the same time as maximum temperatures (Wilf et al. 2003), and the continuing presence of rich flo-

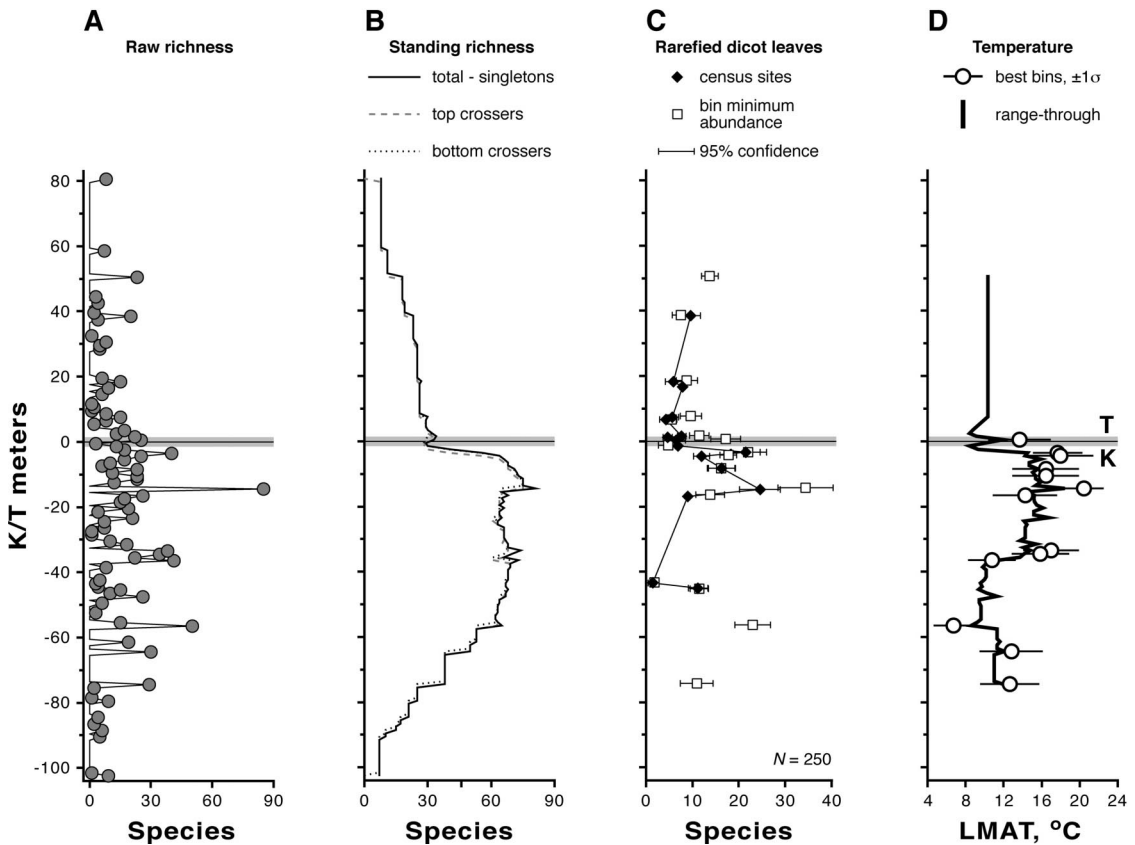


FIGURE 3. Megafloral richness (A–C) and estimated temperature (D). A, Raw richness, equal to the total number of nonreproductive morphospecies per 1-meter bin (Table 2, data set 5), shown when greater than zero. B, Standing richness, estimated using three metrics discussed in text (data set 5D). C, Rarefied number of dicot species at 250 specimens, for census sites with at least 250 specimens (closed symbols, data set 3) and from the minimum abundance matrix for bins with at least 350 specimens (open symbols, data set 4A). An unusual site at -16.4 m with 500 specimens and only one species is not plotted here or in Figure 4, and it is not used in DCA (Fig. 5) because of distortion effects. D, Estimated mean annual temperatures from leaf margin analysis (LMAT), redrawn from the companion paper by Wilf et al. (2003). Circles are estimates from bins with at least 20 dicot species each (data set 5A). Solid line shows estimates from bins with at least 20 dicot species each when range-through occurrences are included (data set 5B).

ras to -4 m (~ 60 Kyr before K/T), the highest level of the Hell Creek Formation with good sampling and preservation (Figs. 3, 4).

Raw richness data (Fig. 3A) show that 10 Cretaceous bins, ranging from -75 to -4 m and from 26 to 85 species, are more diverse than the richest Paleocene bin at 0 m, which has 25 species. With range-through occurrences included and singletons discarded (Fig. 3B), Cretaceous bins are continuously more diverse than any Paleocene bin over the interval from -75 to -3 m (approximately 1000 to 40 Kyr before K/T), with 38 to 75 bottom crossers per bin. The largest number of bottom crossers for the Paleocene, 30, occurs

at $+1$ m (Fig. 3B). Similarly cool temperatures are associated with rich Cretaceous floras in the lower part of the Hell Creek Formation but with poor Paleocene floras (Fig. 3D), suggesting that terminal Cretaceous cooling was unrelated to the major drop in plant diversity across the K/T (Wilf et al. 2003).

Rarefaction of dicot census data corroborates the presence of rich Cretaceous floras that were lost by the Paleocene (Figs. 3C, 4). This trend is evident at a coarse scale in a comparison of the combined rarefaction curves for sites from the uppermost 15 m of the Cretaceous against all Paleocene sites (Fig. 4A). Examination of separate rarefaction curves for

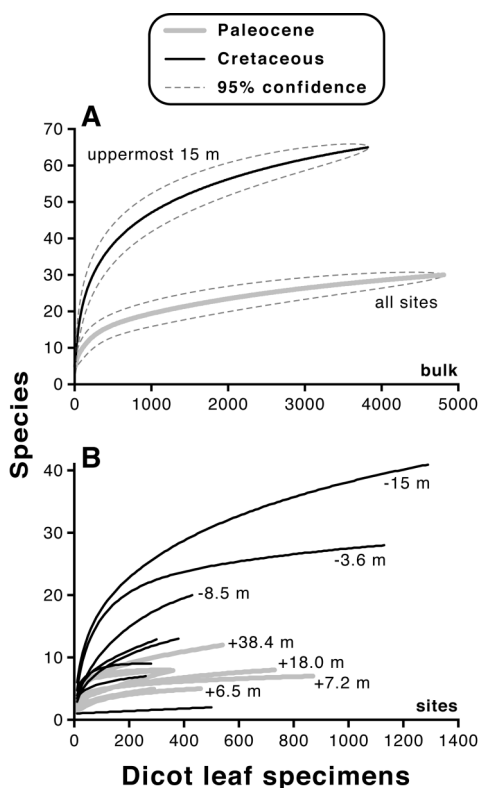


FIGURE 4. Rarefaction curves from dicot census data, 16 quarries with at least 250 specimens each (Table 2, data set 3; plotted at $n = 250$ specimens in Fig. 3C). A, Bulk rarefactions of all Paleocene sites and of sites from the uppermost 15 m of Cretaceous strata. B, Results from individual quarries, meters to K/T marked for the best-sampled localities. Complete list of meter levels used, ordered by expected number of species at 250 specimens (as plotted in Fig. 3C): -43.7 m (1.5 species), $+6.5$ (4.3), $+1.1$ (4.7), $+7.2$ (5.7), $+0.2$ (6.6), -1.7 (6.9), $+1.3$ (7.7), $+16.5$ (7.9), -17.1 (9), -45.2 m (11.3), -4.8 (12), -8.5 (16.4), -3.6 (21.6), -15.0 (24.6), $+18.0$ (6), $+38.4$ (9.6). The site at $+38.4$ m has the greatest rarefied richness for the Paleocene, but 95% confidence intervals (not shown) overlap with several other Paleocene sites at most sample sizes.

individual sites (Fig. 4B) shows that three of the Cretaceous census sites from the uppermost 15 m, including one at -3.6 m, are more rich than any other sites. A site from -1.7 m, within the FU0 zone, is depauperate (Fig. 4B). Even the total richness of all Paleocene censuses combined (Fig. 4A) does not approach several single sites from the Cretaceous (Fig. 4B). For example, at 1000 specimens, all Paleocene sites combined have an estimated 19.4 ± 3.5 species (at 95% confidence), but the comparable figures for the censuses at -15 m and

-3.6 m are 38.1 ± 3.0 and 27.5 ± 1.3 species, respectively. Moreover, the trajectories of rarefaction curves indicate that new Cretaceous species are significantly more likely to be found with further sampling than are Paleocene species. The highest census site, at $+38.4$ m, also has the highest rarefied richness of the Paleocene sites. Although this is the only possible indication of floral recovery in our analyses, it is not significant because the 95% confidence intervals (not shown) of the $+38.4$ m rarefaction curve overlap those of several other Paleocene sites at most sample sizes. Supplemental rarefactions derived from the minimum abundance matrix (data set 4A in Table 2), which includes voucher data, are concordant with those based entirely on census counts; however, the predicted and observed tendency is for rarefied richness to increase with the inclusion of the selectively collected vouchers (Fig. 3C). The supplemental rarefactions show high richness below the lowest census sites, in agreement with the other analyses (Fig. 3) and before the onset of significant warming (Fig. 3D).

Composition

Detrended correspondence analyses indicate significant differences between Cretaceous and Paleocene floras, whether quantified from presence-absence data or relative abundance data from field censuses (Fig. 5). Presence-absence data with range-throughs trend in a negative direction along the first axis to a minimum at -57 m, followed by a weak positive trend to -37 m and a stronger positive trend from -36 m to -16 m. At -15 m there is a sharp increase, followed by a resumed positive trend and step increases at -3 and -2 m, the latter corresponding to FU0. Samples from FU0 cluster on the first axis with Paleocene floras, quantifying the "Paleocene" composition attributed to these samples (Pearson et al. 2001; Johnson 2002; Nichols and Johnson 2002). The first two meters of the Paleocene continue the positive trend, after which the most noteworthy pattern is the near lack of any change. The DCA results thus support the existence of ongoing changes in floral composition during the Cretaceous. Inflection points in floral composition occur at -57 ,

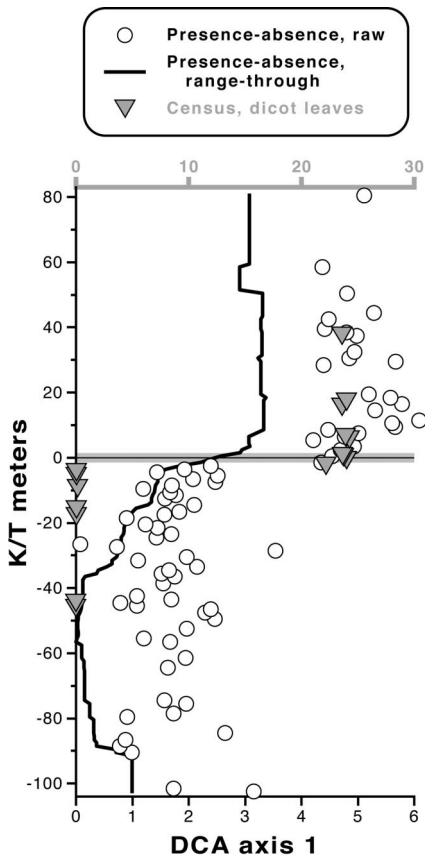


FIGURE 5. Detrended correspondence analyses (DCA, first axis) of presence-absence (Table 2, data sets 5C for raw and 5D for range-through data) and dicot census data (gray axis; data set 3A), plotted against stratigraphic height.

–36, and –15 m, with a major shift at –2 m that we interpret as the K/T extinction smeared down-section as discussed above. The second DCA axis gave noisy results (not shown) that generally corroborate these shifts and show differences between lower and upper Hell Creek censused floras. The horizons listed, unsurprisingly, all are associated either with exceptionally rich samples (–57, –36, and –15 m) or with the taphonomic loss of the typical Hell Creek floras in FU0 (–2 m). In contrast, the Paleocene shows no evidence for compositional change.

For the census data, the relatively large scaling of the first DCA axis, which is marked in standard deviation units, and the major shift along this axis across the K/T quantify the loss of nearly all Cretaceous dominant taxa, recognized since early investigations in the

Marmarth area (Johnson et al. 1989); the affected dominant species were recently tabulated elsewhere (Johnson 2002). The turnover of relative abundance structure at the K/T and the lack of correlation between abundance and survivorship underscore the ecological severity of the extinction, which is also manifest in the coincident loss of specialized insect damage (Labandeira et al. 2002b). The lack of correlation appears similar to results from the marine record across the K/T (McKinney et al. 1998; Lockwood 2003).

The megafloreal zonation of Johnson and others (Johnson et al. 1989; Johnson 2002) is supported by the DCA results. These authors place all floras below –57 m in zone HC1a, and the lowest floras of zone HC1b appear at –57 m. The –36 m level corresponds to a significant and presumably taphonomic loss of herbaceous taxa characteristic of zone HC1b (Johnson 2002). Diverse, thermophilic Hell Creek floras from –15 m and above belong entirely to zone HCIII, with the richest sample of the entire study at –15 m (Fig. 3A). Nearly all floras from –2 m and higher belong to the Fort Union Formation and zones FU0 and FU1. Even though they overlap somewhat in the stratigraphic column because of facies controls, the megafloreal zones are recognizable in a quantitative analysis based solely on lithostratigraphic order, and they should continue to be used and evaluated (e.g., Johnson 2002).

Turnover

First and Last Appearances.—Several pulses of first appearances are apparent within the Cretaceous but virtually none during the Paleocene (Fig. 6A). Spikes near the bottom of the section can be attributed to edge effects because many occurrences are also first appearances. There are 12 first appearances each at –65 and –57 m, 20 cumulatively from –37 to –34 m, and 16 at –15 m. In the first two meters of Paleocene strata there are eight first appearances, but only three follow for the remainder of the Paleocene section, for a total of 11 Paleocene first appearances. Trends in the per capita rates of origination (Fig. 7) are quite similar to simple first appearances (Fig. 6A). There are high origination rates at –57 m, from –37 to –34 m, and especially at –15 m.

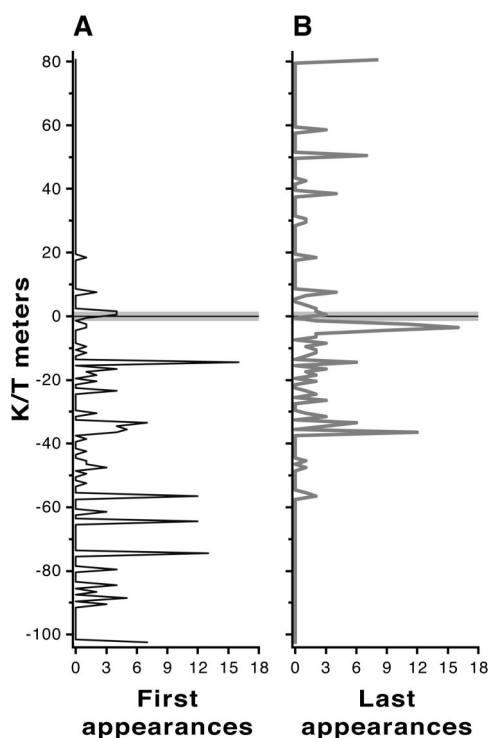


FIGURE 6. Raw numbers of first (A) and last (B) appearances per 1-m stratigraphic bin, based on 141 non-reproductive morphospecies that each appear in more than one bin (Table 2, data set 5C). The uppermost 5 m of Cretaceous strata contains a total of 38 last appearances.

Paleocene origination rates are highest in the first two meters and then drop sharply.

All of the measures of first and last appearances indicate an extraordinary loss of species from -5 m to the K/T (interpretation below). In total, there are 101 non-singleton species restricted to the Cretaceous, 29 survivors, and only 11 species with first appearances during the Paleocene (Table 3). The uppermost 5 meters of Cretaceous strata contains 38 last appearances (Figs. 6B, 8, 9; Table 3). The second-largest spike, at -37 m, represents the taphonomic loss of zone HC1b floras (Johnson 2002). There are 12 last appearances at -37 m, and 21 cumulatively from -37 to -34 m. Subsequently, the Paleocene data show a steady accumulation of last appearances as ranges terminate and sampling decreases (Fig. 2). Similarly, per capita rates of extinction are high at -37 m and then peak just below FU0, from -5 to -3 m; extinction rates at -4 m and -3 m are each more than three standard de-

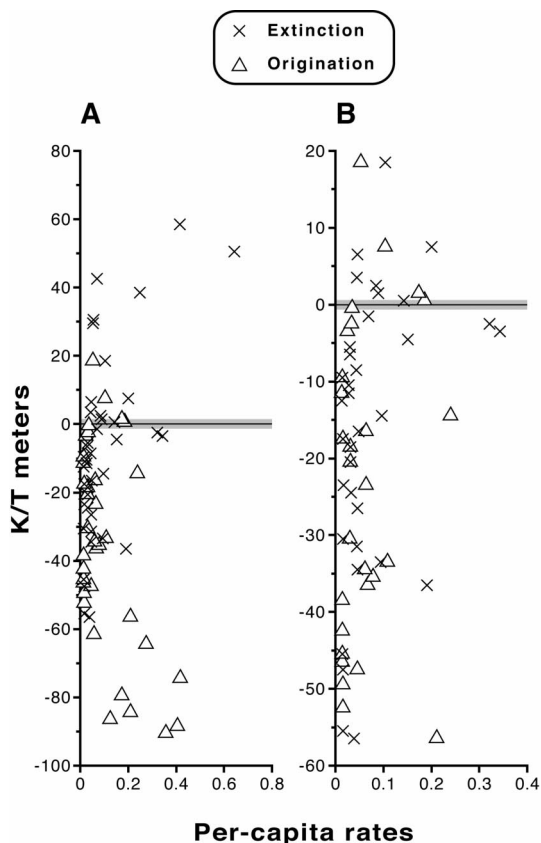


FIGURE 7. A, Per capita rates of origination (or immigration) and extinction (or emigration), based on 141 nonreproductive morphospecies that each appear in more than one bin and including range-through occurrences (Table 2, data set 5D; see text). Edge effects distort origination rates at the bottom and extinction rates at the top of (A). B, Axes rescaled to remove intervals with large edge effects. Paleocene rates are scaled for a faster sedimentation rate relative to the Cretaceous (Fig. 1), i.e., a proportionately lower value of t for equations (4) and (5).

viations above the mean. Given the facies problems associated with FU0, it is noteworthy that this zone nevertheless include the last appearances of two taxa found in the Hell Creek Formation, including the most abundant and long-ranging species of the formation, "*Dryophyllum*" *subfalcatum*.

There is ongoing turnover within the Cretaceous and virtually none during the Paleocene, a pattern that mirrors the ordination analyses (Fig. 5). In comparison to the Cretaceous, the Paleocene floras seem to have no capacity for "normal" turnover dynamics, and few of their species survive beyond the basal

Paleocene anywhere in North America (Johnson and Hickey 1990; Barclay et al. 2003). These floras are compositionally static, depauperate, and short lived beyond the extinction horizon, a general pattern similar to observations of surviving marine lineages after the K/T and other mass extinctions. The 29 Cretaceous survivors, most of which were minor elements of Cretaceous floras, dominate the depauperate Paleocene floras, constituting 71% of Paleocene species and 88% of specimens. In the uppermost 5 m of Cretaceous strata, the same 29 species constituted only 19% of specimens.

Confidence intervals show that the great majority of range tops are well sampled (Fig. 8B), and we infer observed last appearances to be very close to true last appearances. The probability that species with Cretaceous range tops will be found eventually in Paleocene strata is extremely low. Of species with range tops more than 5 m below the K/T, only two have 99% confidence intervals that cross the boundary (Fig. 8B), suggesting that much of the turnover observed before the K/T is real and stratigraphically well-constrained. Few of these species can be considered to be K/T victims.

Confidence intervals that terminate in or close to the FU0 zone (Fig. 9, uppermost 2 m of Cretaceous strata) show the difficulties in attempting to use this method at high resolution in proximity to a major facies change (Marshall 1990; Holland 2003), especially in a composite stratigraphic section. Confidence intervals that intersect the FU0 zone are problematic because most typical Cretaceous species cannot be found there at any sample size, and the confidence intervals depend on sample size. Also of interest are species with last appearances at the -5 and -4 m levels whose confidence intervals terminate below -2 m. Although it is possible that these species went extinct before the K/T, this seems unlikely because they are part of a highly significant step of last appearances that occurs in close proximity to the impact horizon and associated palynological extinction (Figs. 6–8). It seems more probable, at this fine scale, that the short confidence intervals reflect the lack of sensitivity in the composite section to original flo-

ral and environmental heterogeneity on the landscape. For example, the specimens from the -5 m and -4 m bins are, respectively, 86% and >99% derived from two localities 3.5 km apart (Johnson 2002: localities 61 and 63, respectively, in his Figs. 1 and 2). The flora from -4 m is the highest large Cretaceous sample from a channel environment (Fig. 9). Because our confidence interval method uses sample size as a proxy for preservation potential, the -4 m bin consumes all of the preservation potential for the species that occur in the -5 m bin so that all of the confidence intervals for the latter terminate at -4 m (Fig. 9). The confidence interval lengths are too short to the extent that the compositional differences between these two floras reflect original heterogeneity and not extinction or emigration. This type of problem is significant only in the case of a last well-sampled occurrence of a major facies type, in this example the channel flora from -4 m.

Measuring the Extinction.—The maximum concentration of last appearances occurs at -5 m and closer to the K/T (Fig. 6B). We suggest that these 38 species, of 67 non-singletons present, are those most likely to have suffered actual extinction at the K/T, an estimated 57% species extinction. Two less conservative analyses would include all 130 Cretaceous non-singleton species, of which 78% are not found in the Paleocene, or the 86 species present in the uppermost 15 m of the Cretaceous, 66% (Table 3). The last 15 m correspond to most of the specimens from the HCIII floral zone, on which the first estimates, of 79% extinction, were based (Johnson et al. 1989). The 79% estimate included singletons, which are more common in Cretaceous strata, thus inflating the estimate (Johnson 1992). Also, the HCIII zone correlates to an interval of globally warm temperatures, so a direct comparison with the cooler basal Paleocene probably overestimates extinction as discussed elsewhere (Wilf et al. 2003).

The 57% figure should be regarded as a maximum estimate for several reasons. First, the formational contact near the K/T is assumed to decrease observed survivorship and to increase observed extinction by unknown amounts, although observations of Paleocene

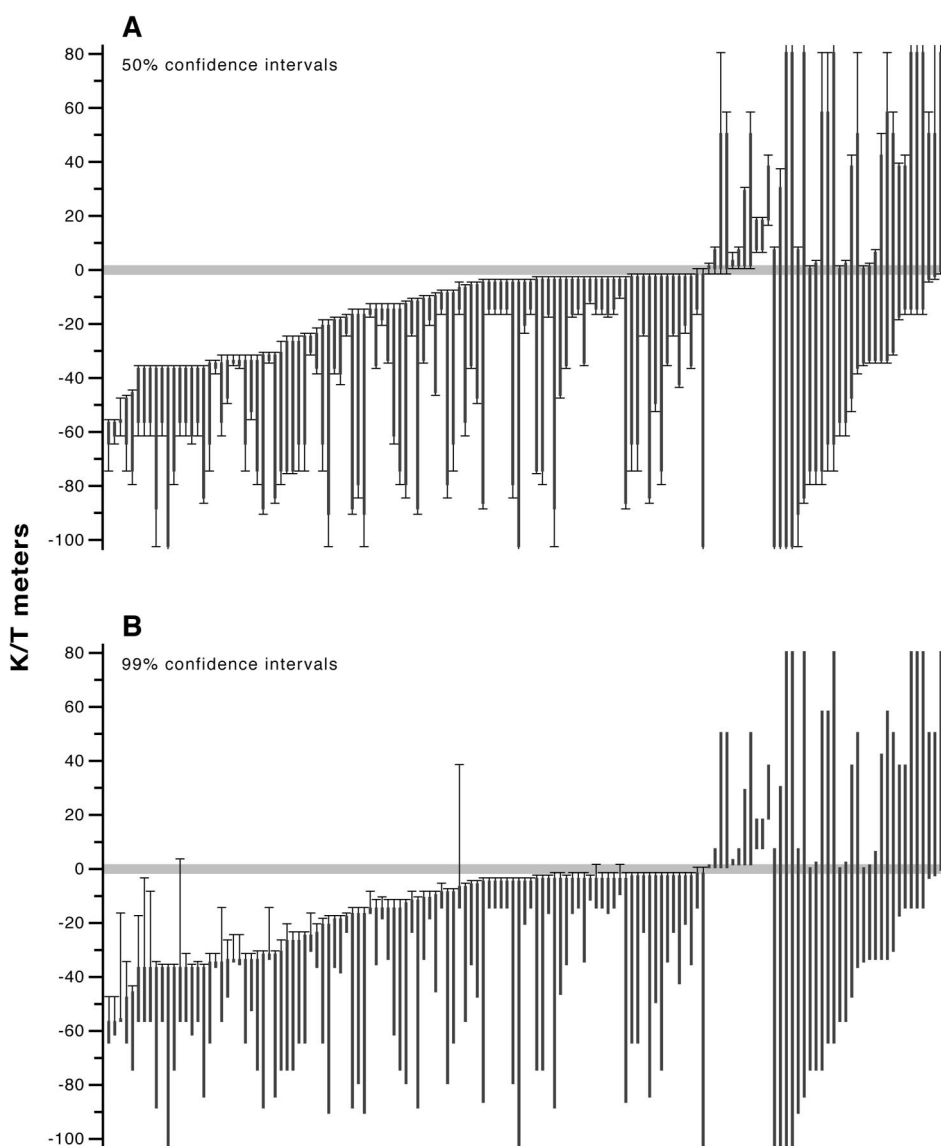


FIGURE 8. Ranges of the 141 nonreproductive morphospecies that each occur in more than one stratigraphic bin (Table 2, data set 4B). There are 130 Cretaceous-only species arranged by last appearance, 11 Paleocene-only species arranged by first appearance, and 29 survivors arranged by first appearance. A, Confidence intervals of 50% are applied to both the bottoms and tops of ranges to illustrate the dependence of interval length on sampling intensity, using the methods described in the text. Note that a different calculation for the range bottom vs. top extensions would be required in a rigorous two-tailed case (Strauss and Sadler 1989), but the lower range extensions here are a second, reversed application of the one-tailed case solely for the purpose of direct pictorial comparison: if sampling were uniform, confidence intervals for a given species would be the same length in either direction. Sampling is heaviest near the K/T (Fig. 2); accordingly, confidence intervals generally shorten with increasing proximity to the K/T. B, Confidence intervals of 99% are applied to the tops of ranges with Cretaceous terminations.

channel floras, discussed above, suggest that this is not a major problem. Second, the local facies change associated with FU0 coincides with global cooling just prior to the K/T, which reversed a preceding warming that lasted about 400 Kyr (Wilf et al. 2003). The

57% estimate, from the uppermost 5 m of the Cretaceous, avoids much of the globally warm interval but still includes some Cretaceous floras from climates warmer than those of basal Paleocene floras. Palynological data from the same strata, at lower taxonomic but higher

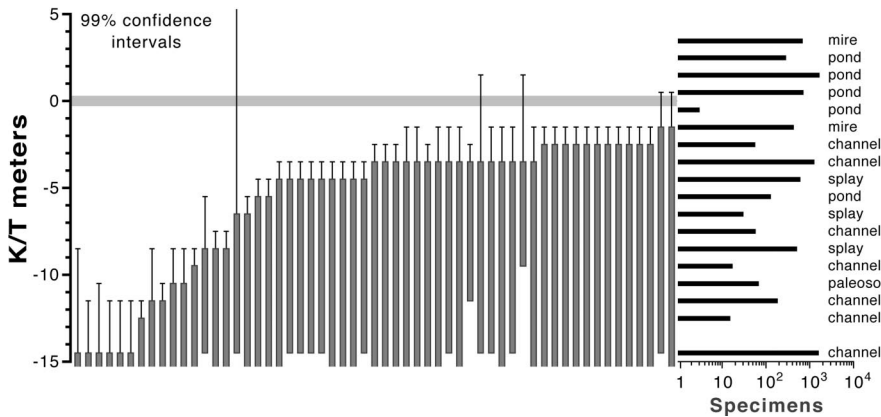


FIGURE 9. Expansion from Figure 8B for the 57 non-singleton species with range terminations in the uppermost 15 m of Cretaceous strata. Numbers of specimens are shown at right (note log scale; data from minimum abundance matrix, data set 4 of Table 2), and the depositional environment for the majority of fossils analyzed is indicated for each 1-m bin. The FU0 megafloral zone (see text) occurs primarily in mire deposits within the uppermost 2 m of Cretaceous strata. Paleocene floras from channel deposits (not including abandoned channels) occur at +1.0 m (2 voucher specimens), +2.4 m (31 vouchers), +5.0 m (1 voucher), +7.4 m (116 voucher, 212 census specimens), +18.4 m (22 vouchers, 68 census), +19.9 m (22 vouchers), +50.0 m (3 vouchers), and +58.0 m (29 vouchers).

stratigraphic resolution than the megafloral data, provide a minimum estimate of about a 30% extinction (Johnson et al. 1989; Nichols and Johnson 2002; Nichols 2002). This amount of extinction is seen at a stratigraphic resolution of a few centimeters on either side of the K/T, in continuous facies and after the latest Cretaceous climate shifts occurred (Nichols and Johnson 2002), and it is similar to percentages reported from throughout western North America (e.g., Hotton 2002 and references therein). Palynology still provides the most direct linkage of the K/T event to plant extinctions.

Recovery

No floral recovery during the basal Paleocene is evident in the Marmarth section. In the northern Rockies and Great Plains of the United States and Canada, floral diversity is low until the early Eocene climatic optimum, more than 10 Myr after the K/T (Hickey 1977; Crane

et al. 1990; McIver and Basinger 1993; Wing et al. 1995, 2000; Gemmill and Johnson 1997; Hoffman and Stockey 1999; Wilf 2000). Systematic studies show that the taxonomic diversity of Paleocene floras is low above the species level and is mostly attributable to a few higher taxa such as Cornales (Manchester et al. 1999; Manchester 2002) and Hamamelidae, including Betulaceae, Juglandaceae, Platanaceae, and Trochodendrales (Crane and Stockey 1985; Pigg and Stockey 1991; Manchester and Dilcher 1997; Manchester and Chen 1998). This scenario of a delayed recovery appears to be in accord with marine data from intervals following mass extinctions, including the K/T (Sepkoski 1978; Patzkowsky 1995; Kirchner and Weil 2000). However, the marine record shows significant spatial variation in recovery from mass extinctions (Erwin 2001; Jablonski 2002), and a more complete picture of land-plant rebound will emerge with data from other areas. Most Paleocene floras found to date were deposited in basin centers. New discoveries from the Denver Basin, more than 700 km south of Marmarth, reveal that humid rainforest vegetation with extremely high diversity existed near the foothills of the Paleocene Front Range during a warming event less than 2 Myr after the K/T (Johnson and Ellis 2002; Ellis et al. 2003; Johnson et al. 2003). Patterns of plant survival

TABLE 3. Extinction estimates, based on range-through counts of Cretaceous non-singleton species (Table 2, data set 5D) that survive into the Paleocene.

Present in	Species	Survivors	% Extinct
Upper 5 m of Cretaceous	67	29	57
Upper 15 m of Cretaceous	86	29	66
All Cretaceous	130	29	78

and recovery may have varied significantly with latitude, climate, and altitude.

Conclusions

The most complete record of megafloral turnover across the Cretaceous/Paleogene boundary comes from the Williston Basin in southwestern North Dakota. Floral diversity drops sharply across the K/T from a maximum only 15 m below (about 200 Kyr before) the boundary and does not recover in the approximately 0.8 Myr sampled interval of the Paleocene. There are several shifts in floral composition during the Cretaceous, with major differences between lower and upper Hell Creek floras. Paleocene floras have sharp compositional differences from Cretaceous floras, including a major turnover of dominant species, but there is no evidence for significant compositional change within the Paleocene. Similarly, there are several pulses of first appearances during the Cretaceous but none of significance during the Paleocene. The largest cluster of last appearances is seen between 5 m and 3 m below (about 70 to 40 Kyr before) the K/T, which we interpret, relying on the major palynological extinction that occurs precisely at the impact horizon, as the signal of a K/T extinction that is smeared slightly down-section. Of the 130 Cretaceous species found at more than one stratigraphic level, only 29 are found in the Paleocene, and only 11 species first appear during the Paleocene. A conservative, maximum estimate of the K/T plant extinction comes from the 57% loss of the species present within the final 5 m of the Cretaceous; these taxa do not reappear in the Paleocene, locally or elsewhere. Palynological data provide a minimum estimate of a 30% extinction.

Confidence intervals that use specimen counts as a proxy for preservation potential were applied to the range tops of the 130 species that last appear during the Cretaceous. Intensive sampling allowed the placement of 99% confidence intervals, which show that nearly all of the range terminations within the Cretaceous are well sampled. The floral turnover within the Cretaceous therefore appears to be a real pattern; correspondingly, it is unlikely that many of the 130 Cretaceous species

will ever be found in the Paleocene. Confidence intervals are problematic at the meter-level resolution needed to interpret range terminations less than about 5 m below the K/T because of facies changes in that interval.

Basal Paleocene floras, which appear to be composed of survivors from Cretaceous peat swamps, are impoverished and static by comparison to preceding Cretaceous floras. There is virtually no origination or change in floral composition, and much of the survival flora does not last beyond the earliest Paleocene. Most studies to date indicate no regional recovery of floral diversity until the early Eocene. However, investigations have focused on a restricted geographic area, and the available data from other regions suggest spatial, climatic, and topographic variation in patterns of floral survival and recovery.

Acknowledgments

We thank R. Horwitt, M. Patzkowsky, D. Royer, and an anonymous reviewer for helpful comments on previous versions of this paper. P.W. received support from the Petroleum Research Fund and the Michigan Society of Fellows; K.R.J. was funded by National Science Foundation (NSF) grant EAR-9805474 and the Denver Museum of Nature & Science. Archiving of primary locality data in the Paleobiology Database was supported by NSF grant DEB-0129208 to H. J. Sims, P. G. Gensel, and S. L. Wing. This is Contribution No. 21 of the Paleobiology Database.

Literature Cited

- Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction: experimental results and theoretical interpretation. *Science* 208: 1095–1108.
- Ash, A. W., B. Ellis, L. J. Hickey, K. R. Johnson, P. Wilf, and S. L. Wing. 1999. *Manual of leaf architecture: morphological description and categorization of dicotyledonous and netveined monocotyledonous angiosperms*. Smithsonian Institution, Washington, D.C.
- Bailey, I. W., and E. W. Sinnott. 1915. A botanical index of Cretaceous and Tertiary climates. *Science* 41:831–834.
- Barclay, R. S., K. R. Johnson, W. J. Betterton, and D. L. Dilcher. 2003. Stratigraphy, megaflora, and the K-T boundary in the eastern Denver Basin, Colorado. *Rocky Mountain Geology* 38: 45–71.
- Barrera, E., and S. M. Savin. 1999. Evolution of late Campanian-Maastrichtian marine climates and oceans. Pp. 245–282 *in* E. Barrera and S. M. Savin, eds. *Evolution of the Cretaceous ocean-climate system*. Geological Society of America Special Paper 332.

- Beerling, D. J., B. H. Lomax, G. R. Upchurch, D. J. Nichols, C. L. Pillmore, L. L. Handley, and C. M. Scrimgeour. 2001. Evidence for the recovery of terrestrial ecosystems ahead of marine primary production following a biotic crisis at the Cretaceous-Tertiary boundary. *Journal of the Geological Society* 158:737–740.
- Blum, J. D., C. P. Chamberlain, M. P. Hingston, C. Koeberl, L. E. Marin, B. C. Schuraytz, and V. L. Sharpston. 1993. Isotopic comparison of K/T boundary impact glass with melt rock from the Chicxulub and Manson impact structures. *Nature* 364:325–327.
- Brown, R. W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U.S. Geological Survey Professional Paper 375: 1–119.
- Burnham, R. J. 1994. Paleocological and floristic heterogeneity in the plant-fossil record: an analysis based on the Eocene of Washington. U.S. Geological Survey Bulletin 2085-B:1–36.
- Burnham, R. J., S. L. Wing, and G. G. Parker. 1992. The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. *Paleobiology* 18:30–49.
- Chaney, R. W., and E. I. Sanborn. 1933. The Goshen flora of west central Oregon. Carnegie Institution of Washington Publication 439.
- Christeson, G. L., Y. Nakamura, R. T. Buffler, J. Morgan, and M. Warner. 2001. Deep crustal structure of the Chicxulub impact crater. *Journal of Geophysical Research* 106:21751–21769.
- Crane, P. R., and S. Lidgard. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* 246:675–678.
- Crane, P. R., and R. A. Stockey. 1985. Growth and reproductive biology of *Joffrea speirsii* gen. et sp. nov., a *Cercidiphyllum*-like plant from the Late Paleocene of Alberta, Canada. *Canadian Journal of Botany* 63:340–364.
- Crane, P. R., S. R. Manchester, and D. L. Dilcher. 1990. A preliminary survey of fossil leaves and well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene) near Almont, North Dakota. *Fieldiana (Geology)* 20:1–63.
- D'Hondt, S., T. D. Herbert, J. King, and C. Gibson. 1996. Planktic foraminifera, asteroids and marine production: death and recovery at the Cretaceous-Tertiary boundary. Pp. 303–317 in G. Ryder, D. Fastovsky, and S. Gartner, eds. *The Cretaceous-Tertiary event and other catastrophes in Earth history*. Geological Society of America Special Paper 307.
- Dorf, E. 1940. Relationship between floras of the type Lance and Fort Union Formations. *Geological Society of America Bulletin* 51:213–236.
- Ellis, B., K. R. Johnson, and R. E. Dunn. 2003. Evidence for an *in situ* early Paleocene rainforest from Castle Rock, Colorado. *Rocky Mountain Geology* 38:73–100.
- Erwin, D. H. 2001. Lessons from the past: biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences USA* 98:5399–5403.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: general problems. *Paleobiology* 26S:74–102.
- Gemmill, C. E. C., and K. R. Johnson. 1997. Paleocology of a late Paleocene (Tiffanian) megafloora from the northern Great Divide Basin. *Palaio* 12:439–448.
- Hartman, J. H., K. R. Johnson, and D. J. Nichols, eds. 2002. *The Hell Creek Formation and the Cretaceous-Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous*. Geological Society of America Special Paper 361.
- Hickey, L. J. 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. *Geological Society of America Memoir* 150:1–183.
- . 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 in C. R. Metcalfe and L. Chalk, eds. *Anatomy of the dicotyledons*, (2d ed). Clarendon, Oxford.
- . 1981. Land plant evidence compatible with gradual, not catastrophic change at the end of the Cretaceous. *Nature* 292: 529–531.
- . 1984. Changes in the angiosperm flora across the Cretaceous-Tertiary boundary. Pp. 279–313 in W. A. Berggren and J. A. Van Couvering, eds. *Catastrophes in Earth history: the new uniformitarianism*. Princeton University Press, Princeton, NJ.
- Hicks, J. F., K. R. Johnson, J. D. Obradovich, L. Tauxe, and D. Clark. 2002. Magnetostratigraphy and geochronology of the Hell Creek and basal Fort Union Formations of southwestern North Dakota and a recalibration of the age of the Cretaceous-Tertiary boundary. Pp. 35–55 in Hartman et al. 2002.
- Hildebrand, A. R., G. T. Penfield, D. A. Kring, M. Pilkington, A. Camargo, S. B. Jacobsen, and W. V. Boynton. 1991. Chicxulub crater: a possible Cretaceous-Tertiary boundary impact crater on the Yucatan Peninsula, Mexico. *Geology* 19:867–871.
- Hoffman, G. L., and R. A. Stockey. 1999. Geological setting and paleobotany of the Joffre Bridge Roadcut fossil locality (Late Paleocene), Red Deer Valley, Alberta. *Canadian Journal of Earth Sciences* 36:2073–2084.
- Holland, S. M. 2003. Confidence limits on fossil ranges that account for facies changes. *Paleobiology* 29:468–479.
- Hotton, C. L. 2002. Palynology of the Cretaceous-Tertiary boundary in central Montana: evidence for extraterrestrial impact as a cause of the terminal Cretaceous extinctions. Pp. 473–501 in Hartman et al. 2002.
- Izett, G. A., G. B. Dalrymple, and L. W. Sneek. 1991. ⁴⁰Ar/³⁹Ar age of Cretaceous-Tertiary boundary tektites from Haiti. *Science* 252:1539–1542.
- Jablonski, D. 2002. Survival without recovery after mass extinctions. *Proceedings of the National Academy of Sciences USA* 99:8139–8144.
- Johnson, K. R. 1992. Leaf-fossil evidence for extensive floral extinction at the Cretaceous/Tertiary boundary, North Dakota, USA. *Cretaceous Research* 13:91–117.
- . 1996. Description of seven common plant megafossils from the Hell Creek Formation (Late Cretaceous: late Maastriichtian), North Dakota, South Dakota, and Montana. *Proceedings of the Denver Museum of Natural History*, series 3,3: 1–48.
- . 2002. The megafloora 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. Pp. 329–391 in Hartman et al. 2002.
- Johnson, K. R., and B. Ellis. 2002. A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary boundary. *Science* 296:2379–2383.
- Johnson, K. R., and L. J. Hickey. 1990. Megafloreal change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A. Pp. 433–444 in V. L. Sharpston and P. D. Ward, eds. *Global catastrophes in Earth history: an interdisciplinary conference on impacts, volcanism, and mass mortality*. Geological Society of America Special Paper 247.
- Johnson, K. R., D. J. Nichols, M. Attrep Jr., and C. J. Orth. 1989. High-resolution leaf-fossil record spanning the Cretaceous-Tertiary boundary. *Nature* 340:708–711.
- Johnson, K. R., M. L. Reynolds, K. W. Werth, and J. R. Thomasson. 2003. Overview of the Late Cretaceous, early Paleocene, and early Eocene megaflooras of the Denver Basin, Colorado. *Rocky Mountain Geology* 38:101–120.
- Kirchner, J. W., and A. Weil. 2000. Delayed biological recovery from extinctions throughout the fossil record. *Nature* 404: 177–180.

- Kovach, W. L. 2000. MVSP—a multivariate statistical package for Windows, Version 3.12c. Kovach Computing Services, Pe-traeth, Wales.
- Krasilov, V. A. 1975. Climatic changes in eastern Asia as indicated by fossil floras. II. Late Cretaceous and Danian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 17:157–172.
- . 1978. Late Cretaceous gymnosperms from Sakhalin, U.S.S.R., and the terminal Cretaceous event. *Palaeontology* 21:893–905.
- Krogh, T. E., S. L. Kamo, V. L. Sharpton, L. E. Marin, and A. R. Hildebrand. 1993. U-Pb ages of single shocked zircons linking distal K/T ejecta to the Chicxulub crater. *Nature* 366:731–734.
- Labandeira, C. C., K. R. Johnson, and P. Lang. 2002a. Preliminary assessment of insect herbivory across the Cretaceous-Tertiary boundary: major extinction and minimum rebound. Pp. 297–327 in Hartman et al. 2002.
- Labandeira, C. C., K. R. Johnson, and P. Wilf. 2002b. Impact of the terminal Cretaceous event on plant-insect associations. *Proceedings of the National Academy of Sciences USA* 99: 2061–2066.
- Leffingwell, H. A. 1970. Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) formations of the type Lance area, Wyoming. Pp. 1–64 in R. M. Kosanke and A. T. Cross, eds. *Symposium on palynology of the Late Cretaceous and Tertiary*. Geological Society of America Special Paper 127.
- Li, L. Q., and G. Keller. 1998. Abrupt deep-sea warming at the end of the Cretaceous. *Geology* 26:995–998.
- Lockwood, R. 2003. Abundance not linked to survival across the end-Cretaceous mass extinction: patterns in North American bivalves. *Proceedings of the National Academy of Sciences USA* 100:2478–2482.
- MacGinitie, H. D. 1941. A middle Eocene flora from the central Sierra Nevada. Carnegie Institution of Washington Publication 534.
- Manchester, S. R. 2002. Leaves and fruits of *Davidia* (Cornales) from the Paleocene of North America. *Systematic Botany* 27: 368–382.
- Manchester, S. R., and Z. D. Chen. 1998. A new genus of Coryloideae (Betulaceae) from the Paleocene of North America. *International Journal of Plant Sciences* 159:522–532.
- Manchester, S. R., and D. L. Dilcher. 1997. Reproductive and vegetative morphology of *Polyptera* (Juglandaceae) from the Paleocene of Wyoming and Montana. *American Journal of Botany* 84:649–663.
- Manchester, S. R., P. R. Crane, and L. B. Golovneva. 1999. An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the Paleocene of North America and eastern Asia. *International Journal of Plant Sciences* 160:188–207.
- Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.
- . 1997. Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. *Paleobiology* 23: 165–173.
- Marshall, C. R., and P. D. Ward. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of western European Tethys. *Science* 274:1360–1363.
- McIver, E. E., and J. F. Basinger. 1993. Flora of the Ravenscrag Formation (Paleocene), southwestern Saskatchewan, Canada. *Palaeontographica Canadiana* 10:1–167.
- McKinney, F. K., S. Lidgard, J. J. Sepkoski Jr., and P. D. Taylor. 1998. Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades. *Science* 281:807–809.
- Nichols, D. J. 2002. Palynology and palynostratigraphy of the Hell Creek Formation in North Dakota: a microfossil record of plants at the end of Cretaceous time. Pp. 393–456 in Hartman et al. 2002.
- Nichols, D. J., and K. R. Johnson. 2002. Palynology and microstratigraphy of Cretaceous-Tertiary boundary sections in southwestern North Dakota. Pp. 95–143 in Hartman et al. 2002.
- Nichols, D. J., D. M. Jarzen, C. J. Orth, and P. Q. Oliver. 1986. Palynological and iridium anomalies at Cretaceous-Tertiary boundary, south-central Saskatchewan. *Science* 231:714–717.
- Norris, R. D., B. T. Huber, and J. Self-Trail. 1999. Synchronicity of the K-T oceanic mass extinction and meteorite impact: Blake Nose, western North Atlantic. *Geology* 27:419–422.
- Olsson, R. K., J. D. Wright, and K. G. Miller. 2001. Paleobiogeography of *Pseudotextularia elegans* during the latest Maastrichtian global warming event. *Journal of Foraminiferal Research* 31:275–282.
- Orth, C. J., J. S. Gilmore, J. D. Knight, C. L. Pillmore, R. H. Tschudy, and J. E. Fassett. 1981. An iridium abundance anomaly at the palynological Cretaceous-Tertiary boundary in northern New Mexico. *Science* 214:1341–1342.
- Patzkowsky, M. E. 1995. A hierarchical branching model of evolutionary radiations. *Paleobiology* 21:440–460.
- Payne, J. L. 2003. Applicability and resolving power of statistical tests for simultaneous extinction events in the fossil record. *Paleobiology* 29:37–51.
- Pearson, D. A., T. Schaefer, K. R. Johnson, and D. J. Nichols. 2001. Palynologically calibrated vertebrate record from North Dakota consistent with abrupt dinosaur extinction at the Cretaceous-Tertiary boundary. *Geology* 29:39–42.
- Pearson, D. A., T. Schaefer, K. R. Johnson, D. J. Nichols, and J. P. Hunter. 2002. Vertebrate biostratigraphy of the Hell Creek Formation in southwestern North Dakota and northwestern South Dakota. Pp. 145–167 in Hartman et al. 2002.
- Phillips, O. L., and J. S. Miller. 2002. Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set. Missouri Botanical Garden Press, St. Louis.
- Pigg, K. B., and R. A. Stockey. 1991. Platanaceous plants from the Paleocene of Alberta, Canada. *Review of Palaeobotany and Palynology* 70:125–146.
- Pope, K. O. 2002. Impact dust not the cause of the Cretaceous-Tertiary mass extinction. *Geology* 30:99–102.
- Saito, T., T. Yamanoi, and K. Kaiho. 1986. End-Cretaceous devastation of terrestrial flora in the boreal Far East. *Nature* 323: 253–255.
- Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology* 4:223–251.
- Sheehan, P. M., D. E. Fastovsky, R. G. Hoffmann, C. B. Berghaus, and D. L. Gabriel. 1991. Sudden extinction of the dinosaurs: latest Cretaceous, upper Great Plains, USA. *Science* 254:835–839.
- Sheehan, P. M., D. E. Fastovsky, C. Barreto, and R. G. Hoffmann. 2000. Dinosaur abundance was not declining in a “3 m gap” at the top of the Hell Creek Formation, Montana and North Dakota. *Geology* 28:523–526.
- Signor, P. W., and J. H. Lipps. 1982. Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. Pp. 291–296 in L. T. Silver and P. H. Schultz, eds. *Geological implications of impacts of large asteroids and comets on the Earth*. Geological Society of America Special Paper 190.
- Strauss, D., and P. M. Sadler. 1989. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Mathematical Geology* 21:411–421.
- Sweet, A. R., and D. R. Braman. 2001. Cretaceous-Tertiary palynofloral perturbations and extinctions within the *Aquillapol-lenites* Phytogeographic Province. *Canadian Journal of Earth Sciences* 38:249–269.
- Swisher, C. C., J. M. Grajales-Nishimura, A. Montanari, S. V. Margolis, P. Claeys, W. Alvarez, P. Renne, E. Cedillo-Pardo, F. J. M. R. Maurrasse, G. H. Curtis, J. Smit, and M. O. McWilliams. 1992. Coeval $^{40}\text{Ar}/^{39}\text{Ar}$ ages of 65.0 million years

- ago from Chicxulub crater melt rock and Cretaceous-Tertiary boundary tektites. *Science* 257:954–958.
- Toon, O. B., K. Zahnle, D. Morrison, R. P. Turco, and C. Covey. 1997. Environmental perturbations caused by the impacts of asteroids and comets. *Reviews of Geophysics* 35:41–78.
- Tschudy, R. H. 1970. Palynology of the Cretaceous-Tertiary boundary in the northern Rocky Mountains and Mississippi Embayment regions. Pp. 65–111 in R. M. Kosanke and A. T. Cross, eds. *Symposium on palynology of the Late Cretaceous and early Tertiary*. Geological Society of America Special Paper 127.
- Tschudy, R. H., C. L. Pillmore, C. J. Orth, J. S. Gilmore, and J. D. Knight. 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous-Tertiary boundary, Western Interior. *Science* 225:1030–1032.
- Vajda, V., and J. I. Raine. 2003. Pollen and spores in marine Cretaceous/Tertiary boundary sediments at mid-Waipara River, North Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics* 46:255–273.
- Vajda, V., J. I. Raine, and C. J. Hollis. 2001. Indication of global deforestation at the Cretaceous-Tertiary boundary by New Zealand fern spike. *Science* 294:1700–1702.
- Wilf, P. 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. *Paleobiology* 23:373–390.
- . 2000. Late Paleocene-early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. *Geological Society of America Bulletin* 112:292–307.
- , K. R. Johnson, and B. T. Huber. 2003. Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous-Paleogene boundary. *Proceedings of the National Academy of Sciences USA* 100:599–604.
- Wing, S. L., and G. J. Harrington. 2001. Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change. *Paleobiology* 27:539–563.
- Wing, S. L., J. Alroy, and L. J. Hickey. 1995. Plant and mammal diversity in the Paleocene to early Eocene of the Bighorn Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115: 117–155.
- Wing, S. L., H. Bao, and P. L. Koch. 2000. An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic. Pp. 197–237 in B. T. Huber, K. MacLeod, and S. L. Wing, eds. *Warm climates in Earth history*. Cambridge University Press, Cambridge.
- Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. U.S. Geological Survey Professional Paper 1106.
- Wolfe, J. A., and G. R. Upchurch. 1986. Vegetation, climatic and floral changes at the Cretaceous-Tertiary boundary. *Nature* 324:148–152.
- . 1987. Leaf assemblages across the Cretaceous-Tertiary boundary in the Raton Basin, New Mexico and Colorado. *Proceedings of the National Academy of Sciences USA* 84:5096–5100.
- Wolfram, S. 2003. *The Mathematica book*, 5th ed. Wolfram Media, Champaign, Ill.

Appendix

Additions and Adjustments to Localities and Plant Morphotypes of Johnson 2002

Two additional field seasons are included here, 2000 and 2001, providing four new localities and new specimens from several previously collected quarries. Emphasis was placed on increasing the sampling of FU0 and of Paleocene floras more than 10 m above the K/T. The new quarries are DMNH localities 2412, 2514, 2612, 2613, with stratigraphic positions relative to the K/T and paleoenvironments (after Johnson 2002) of +3.4 m (pond), +6.5 m (pond), +16.5 m (pond), and +38.4 m (carbonaceous shale/mire), respectively. These collections added seven dicot leaf morphotypes (FU99, FU104–109), three pteridophyte leaf morphotypes (FU100, FU102, FU103), and one lycopod axis morphotype (FU101). We removed from the analysis a single locality of uncertain stratigraphic position, DMNH locality 569 (see Johnson 2002), which resulted in the elimination of three morphotypes, HC237, HC238, and HC239, that only occur at that locality. Five localities are from adjacent Harding County, South Dakota, and the two lowest localities are from the uppermost Fox Hills Formation (Johnson 2002). Attached lateral and terminal leaflets have been found in organic attachment in the case of two described species in the Marmarth section, *Erlingdorfia montana* and *Platanites marginata*, both in the Platanaceae (Johnson 1996), so the four leaf morphotypes, two lateral and two terminal, are combined in analysis here as two morphospecies (equivalent to the two formal entities *E. montana* and *P. marginata*). Aside from these two examples of attachment, all of Johnson's (2002) morphotypes (388 total, as adjusted above) are equivalent here to morphospecies (386).