

Plants, a Yardstick for Measuring the Environmental Consequences of the Cretaceous-Tertiary Boundary Event

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Résumé de l'article

Les répercussions sur les peuplements de végétaux enregistrées dans les couches rocheuses lors de l'impact météoritique de la limite Crétacé-Tertiaire (K-T) vont de l'extinction d'espèces, à l'annihilation de masse, aux fluctuations dans l'abondance relative des taxons et, pour certains taxons, à l'apparente insensibilité face aux contraintes ambiantes. Autant de façon de mesurer l'étendue des répercussions de perturbations environnementales engendrées par des impacts : les extinctions d'espèces, par leurs étendues et leurs sélectivités, les annihilations de masse par leurs étendues géographiques et, les survivants, par la variation de leur sensibilité spécifique à l'événement limite, tel qu'il est reflété dans leur tendance, leur abondance et leur distribution relatives. Des données recueillies dans différentes localités de l'Ouest canadien et de l'état du Montana indiquent que la plupart des extinctions de végétaux ont affecté des espèces d'angiospermes probablement zoophiles (pollinisés par des animaux); que les espèces du sous-étage forestier ont pu survivre à l'événement; qu'il y aurait eu destruction massive du couvert forestier à l'échelle du continent, et; que les réactions à l'événement de la limite K-T des angiospermes pollinisés par le vent ont été variées.



Plants, a Yardstick for Measuring the Environmental Consequences of the Cretaceous-Tertiary Boundary Event

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SUMMARY

Reactions registered by plant communities to the Cretaceous-Tertiary (K-T) boundary cometary impact event include extinctions, killing events, shifts in the relative number and abundances of taxa, and, for some taxa, an apparent insensitivity to imposed stresses. All these provide yardsticks to measure the extent of impact-generated environmental perturbations: extinctions by their magnitude and selectiveness, killing events by their geographic extent, and the survivors by their varying sensitivities to the boundary event as reflected in trends in their relative abundances and distribution. Information has been assembled from localities in western Canada and Montana that suggests: most plant extinctions involved what were likely zoophilous (animal-pollinated) angiosperms; understory vegetation may have survived the event; there was extensive destruction of the forest canopy on a continental scale; and there was a variable response to the K-T boundary event by what were likely wind-pollinated angiosperms.

RÉSUMÉ

Les répercussions sur les peuplements de végétaux enregistrées dans les couches rocheuses lors de l'impact météoritique de

la limite Crétacé-Tertiaire (K-T) vont de l'extinction d'espèces, à l'annihilation de masse, aux fluctuations dans l'abondance relative des taxons et, pour certains taxons, à l'apparente insensibilité face aux contraintes ambiantes. Autant de façon de mesurer l'étendue des répercussions des perturbations environnementales engendrées par des impacts : les extinctions d'espèces, par leurs étendues et leurs sélectivités, les annihilations de masse par leurs étendues géographiques et, les survivants, par la variation de leur sensibilité spécifique à l'événement limite, tel qu'il est reflété dans leur tendance, leur abondance et leur distribution relatives. Des données recueillies dans différentes localités de l'Ouest canadien et de l'état du Montana indiquent que la plupart des extinctions de végétaux ont affecté des espèces d'angiospermes probablement zoophiles (pollinisés par des animaux); que les espèces du sous-étage forestier ont pu survivre à l'événement; qu'il y aurait eu destruction massive du couvert forestier à l'échelle du continent, et; que les réactions à l'événement de la limite K-T des angiospermes pollinisés par le vent ont été variées.

INTRODUCTION TO THE IMPACT SCENARIO

Leaving an echo that has projected through time, the collision of a comet with the Yucatan Peninsula of Mexico 65 million years ago ejected molten impact debris over much of North America. In a geological instant, millimetre-sized solidified beads of the formerly molten debris formed a thin layer, which was preserved in low-energy sedimentary environments. The swamps and ponds that spread throughout mid-continental North America toward the end of the Cretaceous Period provided such environments, as tectonic loading from the rising Cordillera to the west translated into subsidence and accommodation space in the adjacent foreland basin. The kaolinization of this layer of beads yielded a pinkish to brownish white hackly claystone, up to 1.5 cm thick (Fig. 1A).

The deposition of glass beads was followed by a more gradual settling of dust and aerosols created by the impact. The coarsest of this material is estimated to have settled out of the atmosphere over a period of up to three months to form a layer 0.8-1 cm thick that altered into a

macroscopically homogeneous, satiny-textured, smectitic black layer with a conchoidal fracture, the satiny claystone. This layer was overlain by about 10 organic-rich, clay laminae that formed a laminated shale 0.3-1.0 cm thick. Assuming the laminae have annual significance, deposition presumably occurred over about a decade. Coal usually occurs above the laminated shale, signalling either an increase in the rate of production of organic material and/or increased isolation of the sites of deposition from clastic input. Hence, in the K-T boundary exposures of western Canada (Figs. 1B, C), the composite boundary claystone can be seen in the preservational embrace of coals and coaly shales.

The resulting thin white layer is distributed across the mid-continental United States, and northward into southern Saskatchewan and Alberta. It is amazing to contemplate that by using this layer as a datum, 65-million-year-old fossil communities can be tracked at time intervals within the range of human experience across the mid-continental area. It is also a layer left to captivate the human mind with both its innocuous appearance in outcrop and its enormous implications to the biological development of the earth.

ASPECTS OF K-T BOUNDARY INVESTIGATIONS

The focus of this review is on floral responses to end-Cretaceous events and the limits these place on impact-generated environmental disturbances. The information presented is based on studies integrating palynology (the study of pollen and spores), geochemistry, and magnetostratigraphy. The primary references for this account are *Lerbekmo et al.* (1987), *Lerbekmo et al.* (1996), *Sweet* (1994), *Sweet and Braman* (1992, 2001), and *Sweet et al.* (1999). In these publications, D.R. Braman (Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta), J.F. Lerbekmo (University of Alberta, Edmonton, Alberta), and the author have detailed the physical and paleofloral characteristics of the K-T boundary interval in the world-class exposures of western Canada and Montana, including those now within Grasslands National Park, south-central Saskatchewan. Fortunately, this is the region of North America where there is

evidence of an apparent attenuation in the energy released by the impact event. Hence, it is possible to document the more subtle changes in affected ecosystems, both those directly dependent upon the cometary impact, and ongoing changes initiated prior to the impact that carried through into the Tertiary.

Starting up to 6 million years prior to the K-T boundary event, the last pulse of the great Cretaceous epicontinental seas began to withdraw southeastward from Alberta and southern Saskatchewan. A record of the succeeding latest Cretaceous and earliest Tertiary terrestrial ecosystems occurs in an elongated region more or less perpendicular to paleolatitudes in mid-continental North America (Fig. 2). Of the potential non-marine

fossils, only pollen and spores (microscopic plant reproductive structures) are abundant and durable enough to provide a nearly continuous and impeccably precise record of ecological events across the K-T boundary. Thousands of pollen and spores, whose size permits up to 50 to fit across the head of a pin (megaspores excluded), can be obtained from a few grams of rock. Hence, pollen and spores can be recovered in large numbers from stratigraphic intervals only a few millimetres thick, and therefore can be used to tell the terrestrial environmental story with a precision not possible if larger fossils, such as dinosaurs and other animals with less continuous and time-sensitive records, are used.

There are three main aspects of K-

T boundary investigations: the recognition and definition of the causal event; understanding the environmental consequences of the causal event for the earliest Tertiary world; and consideration of biological responses to abrupt and profound disturbances. Over the last 20 years, evidence for a K-T impact, the most probable site of the impact (Fig. 2), and the physical characteristics of the impact site have been successfully documented (Alvarez *et al.*, 1980; Hildebrand *et al.*, 1991, 1998). Modelling the environmental consequences of a 16.5-km diameter cometary impact (Hildebrand *et al.* 1998) in the Yucatan's carbonate and anhydrite platform is continuing, although the likely sequence of events has been detailed (Fig. 3). Still open to debate is the severity and duration of changes in the environment, and the extent to which these changes were directly responsible for animal and plant extinctions. These are in part addressed by detailing the nature and timing of changes in plant communities and, by implication, environmental perturbations in the early Tertiary.

At the end of the Cretaceous, the world's terrestrial floras were divided into several floristically distinctive regions, with most of North America falling within the mid- to high-latitude *Aquila-pollenites* Phytogeographic Province (Fig.

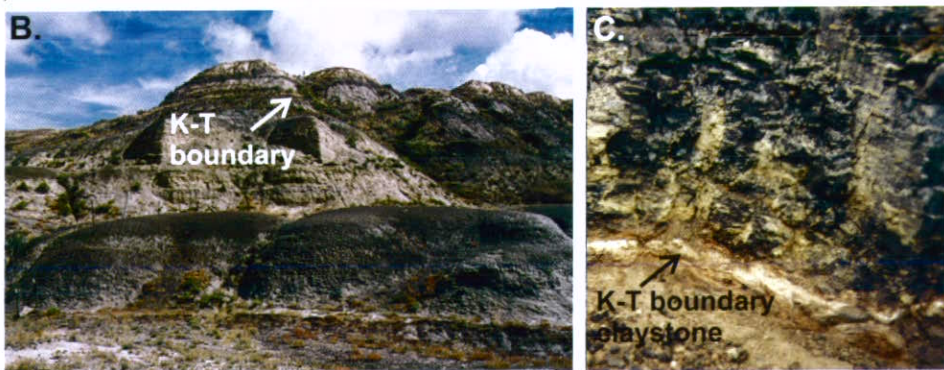
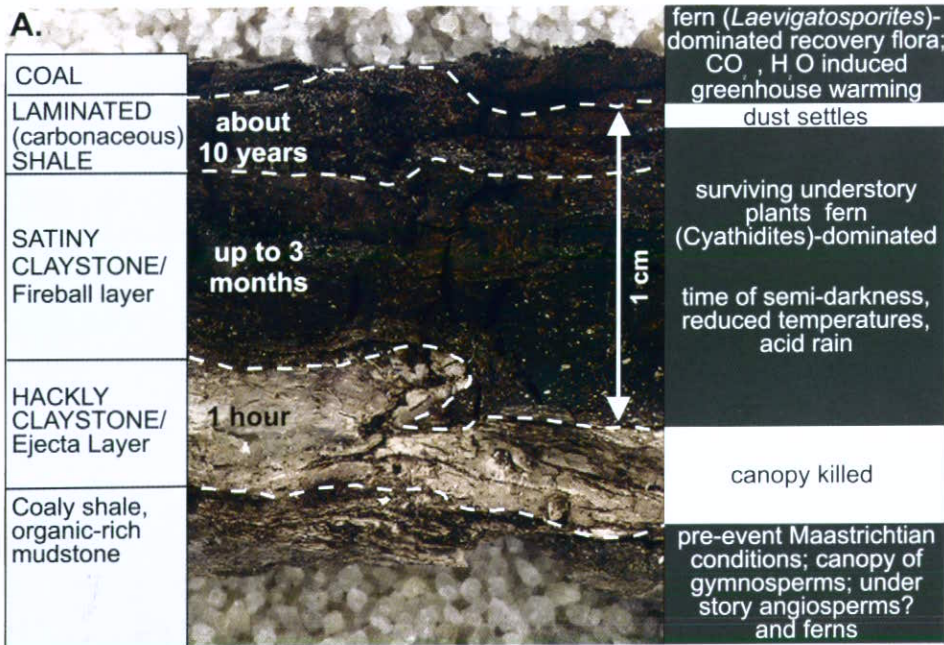


Figure 1(A) Layering in a composite boundary claystone sample from central Saskatchewan, an interpretation of their time significance, and the associated floral state (modified after Sweet *et al.*, 2000). (B) Zahurksi's Point, Grasslands National Park, Wood Mountain area, with position of K-T boundary indicated by arrow. (C) Photograph showing hackly claystone (thin white layer) at Zahurksi's Point.

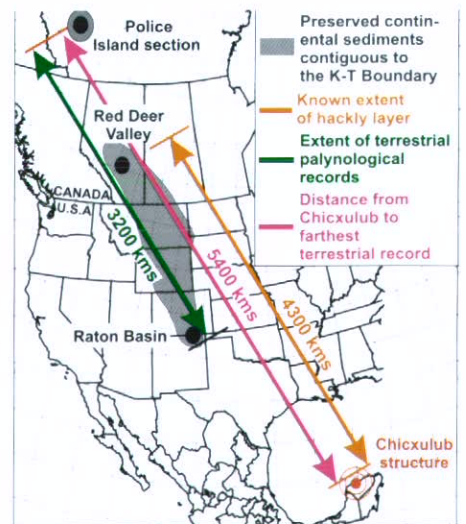


Figure 2 Map showing distances from the Chicxulub impact structure, Yucatan Peninsula, Mexico, for which there is a palynological record and a preserved K-T boundary claystone (modified after Sweet and Braman, 2001, fig. 2).

4). Data from throughout this province provide a record of Cretaceous to Tertiary paleofloral events. However, only in mid-continental North America is there a detailed record of paleofloral changes set against the precise datums provided by the K-T claystone and polarity chron boundaries. These allow contemporaneous floras to be examined on a continental scale (Fig. 2). Consequently we recognize that the substance of the paleofloral story from lower latitude localities in

Montana, Wyoming, Colorado, and New Mexico is somewhat different from that in western Canada. In the latest Cretaceous and early Paleocene, angiosperms — flowering plants — are dominant in southern pollen and spore assemblages, whereas gymnosperms — conifers and other, mostly cone-bearing plants — often dominate northern assemblages, except for the immediate post-impact interval in which fern spores dominate throughout the mid-continental region.

BIOLOGICAL RESPONSES AND INFERRED ENVIRONMENTAL CAUSES

Three types of biological responses are recorded across the K-T boundary: 1) extinctions, 2) fluctuations in composition and taxon abundance within communities, and 3) no detectable change (Fig. 5). Extinctions involve the total elimination of species from throughout their geographic range, and thus reflect equally extensive environmental or other perturbations. It is the universal components of the K-T impact scenario (e.g., dust-related cooling, ozone depletion, and acid rain) that are usually invoked as the cause of extinctions in both marine and continental realms. In the sea, both microscopic and macroscopic life was severely depleted. The adaptive advantages of the dinosaurs, which dominated the land for 130 million years, failed them in the post-impact world. Selected mammals and plants also became extinct. Such extinctions are recorded in the pollen and spore record within the *Aquilapollenites* Province and therefore must reflected environmental perturbations that are at least close to hemispheric in extent.

Fluctuations in plant communities in mid-continental North America point to a killing event, coincident with the deposition of K-T boundary impact ejecta and therefore possibly caused by a thermal pulse, which was geographically

AGENT OF ENVIRONMENTAL CHANGE	TIME SCALE
Fireball irradiance	Minutes
Thermal pulse from ejecta (fires)	Hour+
Winds (500 km/hr), giant waves	Hours
Dust veil (cold, darkness)	Months
Acid rain (nitric and sulphuric)	Year
Stratospheric aerosols (cold)	Decades
Ozone depletion (UV exposure)	Decades
H ₂ O greenhouse effect	Decades
Poisons and mutagens	Years-millenia
CO ₂ greenhouse effect	Millenia
Impact-triggered volcanism	Millenia?
Disrupted climate	Million years

Figure 3 Summary of environmental consequences suggested to have resulted from the impact of a comet ~15 km in diameter into the Yucatan Peninsula, Mexico (after a listing presented in Hildebrand *et al.*, 1998).

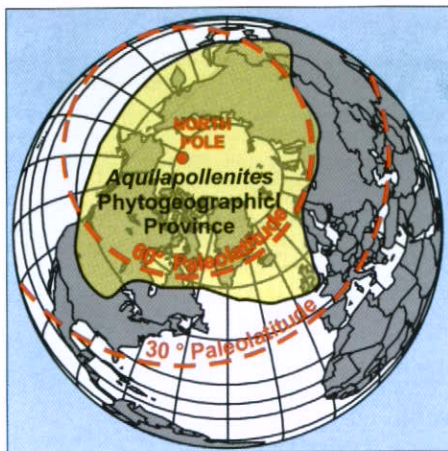


Figure 4 Polar projection showing the geographic extent of *Aquilapollenites* Phytogeographic Province (after Sweet and Braman, 2001, fig. 1). The orientation of the paleolatitudes shown approximate that of about 65 million years ago.

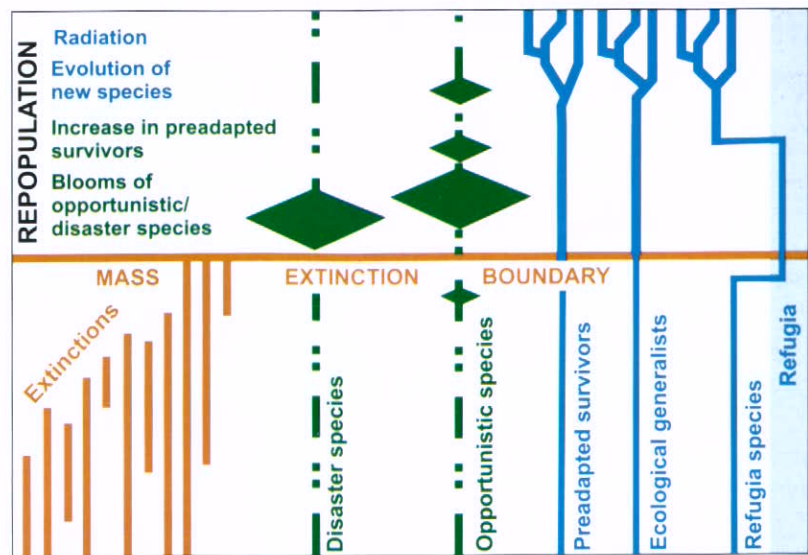


Figure 5 Aspects of biological responses across the K-T boundary (modified after Kauffman and Harries, 1996, Fig 2). See Kauffman and Harries (1996) for a complete discussion of the terminology used in the diagram.

restricted, being only sub-continental in scale. Although this killing event involved at least the partial destruction of plant communities and coincided with the last occurrences of some species, evidence is presented to suggest that its cause was not of sufficient areal extent to result in the extinction of cosmopolitan species within the *Aquilapollenites* Province.

Additionally, overlain on responses appearing to be directly related to the K-T boundary event, are variations in pollen and spore assemblages that may be better explained by changing paleoclimates, local depositional conditions, or differences attributable to paleolatitude.

Plant Extinctions Across the K-T Boundary Interval

There are complicating factors in estimating the number of plant extinctions. The fossil record of plants includes both vegetative organs such as leaves or wood, and reproductive organs such as seeds, pollen and spores. Estimates of plant extinction levels in the mid-continental United States have ranged from about 65% to 90% based on leaf assemblages, and from about 20% to 40% based on pollen and spores. The differences between these estimates have been variously attributed to: 1) the relative taxonomic sensitivity of leaves *versus* pollen and spores in defining "natural" plant species, and 2) the preservation of leaves of some plant groups, found to be affected by the boundary event, for which there is no parallel pollen record. For example, in mid-continental United States, leaves of the laurel family (Lauraceae) form a significant portion of latest Cretaceous leaf assemblages, and their disappearance at the K-T boundary contributes significantly to the estimated level of extinctions. As laurels are represented by few pollen taxa (Wolfe and Upchurch, 1987; Johnson, 1992), their disappearance at the K-T boundary has little effect on the estimated level of extinctions based on pollen and spores.

In addition to the effect of taxonomy and preservation on estimates of plant extinction levels, the problem of differentiating between local range tops and actual extinctions is not always resolved. Many pollen and leaf-based taxa endemic to the *Aquilapollenites* Province disappear near or at the end of the

Maastrichtian (Johnston, 1992; Sweet and Braman, 2001) and therefore these disappearances represent extinctions, but not necessarily impact-related. The North American range tops of such taxa may therefore represent extinctions. However, on a locality-by-locality basis, and without setting up local range tops against an independent datum throughout the geographic range of a taxon, it is impossible to know for certain whether local range terminations are indeed extinctions.

The importance of knowing the exact timing of range terminations in relation to the K-T boundary is illustrated by the multiple horizons with concentrations of range tops in the latest Cretaceous (Maastrichtian) of the Police Island Section, Northwest Territories (Fig. 6). Here, at most, only 30% of the total number of Maastrichtian range terminations occur in close proximity to the K-T boundary.

Hence, given the reported variations in the magnitude and timing of extinctions, and the problem in differentiating between range tops and extinctions, other aspects of the plant record need to be examined to gain further insights into K-T boundary environmental perturbations.

Factors in the Selectiveness of Plant Extinctions

Because most plants have reproductive

strategies that should insulate them against short-term catastrophic events inducing extinctions, even the minimum levels of extinctions inferred from the fossil record need to be further examined. These strategies include various kinds of vegetative reproduction and reproduction through seeds designed for long periods of dormancy (Traverse, 1988). Such mechanisms may explain the limited number of apparent extinctions among the gymnosperms, ferns, and fern allies. However, some groups of angiosperms were profoundly affected, and this needs further explanation.

The origin and radiation of flowering plants occurred during the Cretaceous. Their competitive advantage arose in part from structural modifications that further freed the sexual reproductive process from the vagaries of environmental conditions. These include flower structures adapted to attracting animals, including insects, and then using these animals to transfer the male gametophyte-containing pollen to female floral structures. This process is known as zoophily. In modern floras, such adaptations among the angiosperms have resulted in conspicuous flowers whose complexity and colouration are universally admired; contrast the showy *Hibiscus* flower with the inconspicuous flower-bearing catkins of the wind-pollinated (= anemophilous) birch. Although zoophily

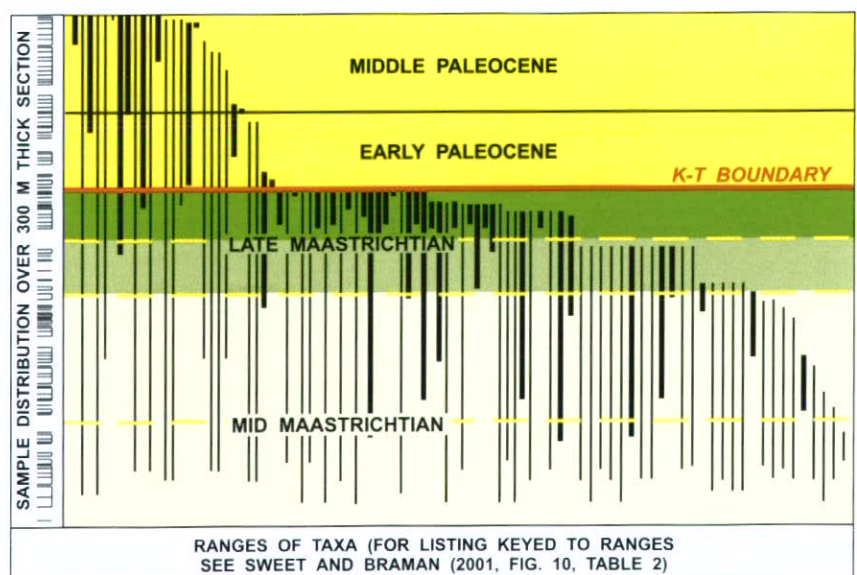


Figure 6 Diagram illustrating the multiple levels of concentrations of range tops in the Maastrichtian to middle Paleocene Police Island section, north bank of the Mackenzie River, NWT (modified after Sweet and Braman, 2001, fig. 10).

largely freed the process of cross-pollination from the vagaries of air currents, interspecific plant and animal dependencies were established by co-evolution.

Large (>40 µm) angiosperm pollen with conspicuous sculpture and thick and structurally complex walls, e.g., late Maastrichtian species of triprojectate pollen, are considered most likely to be from zoophilous plants, based on modern analogs. In contrast, medium-sized (between about 20 µm and 40 µm) pollen with an oblate to spheroidal shape, relatively simple wall and subdued sculpture are more likely to be anemophilous (Whitehead, 1969; Punt, 1986) (Fig. 7). The latter interpretation is supported by the finding of anemophilous-style flowers bearing pollen of the form-genus *Kurtzipites* (McIver *et al.*, 1991), an end-member in a Maastrichtian lineage that

became morphologically simple, within the otherwise morphologically complex (zoophilous) triprojectates. Many other pollen types do not definitively signal the primary mode of pollination, and this may reflect a mixed pollination strategy. Such pollen types are not used in the following examination of the role of pollination strategy in the extinction scenario.

During the Campanian and Maastrichtian ages of the Cretaceous Period, about a 20-million year interval, the prominence of relatively large and morphologically complex angiosperm pollen increased. These zoophilous pollen-types, at least in the mid and high latitudes of the northern hemisphere, were among the profoundly affected organisms across the K-T boundary interval. The many last appearances of

zoophilous pollen resulted in the lowered angiosperm pollen diversity in the early Paleocene. This lowered diversity is probably accentuated by most surviving early Tertiary pollen taxa being relatively small in size and having reduced sculpture and simple shapes (anemophilous, wind-pollinated types such as *Kurtzipites tripissatus*, *Syncolporites minimus*, *Triporepollenites plektosus* and *Ulmoideipites*). In modern anemophilous plants such as the birches, pollen from individual species is indistinguishable, and analogs to this can be expected among fossil anemophilous-type pollen.

Whitehead (1969) linked zoophily with high-diversity and dense tree stands, and anemophily to low-diversity tree stands, which are either broken by open areas or deciduousness, conditions that increase the effectiveness of wind pollination. Wolfe and Upchurch (1986, 1987) and Wolfe (1987) found deciduousness and its associated capacity for vegetative dormancy was advantageous, whereas the evergreen habit was disadvantageous, to plant survival at the K-T boundary in mid-continental North America. However, it may also be that the linkage between anemophily and deciduousness makes deciduousness appear to control survival among northern mid- and high-latitude angiosperms (Fig. 8). In any case, in mid-continental North America the advantage for survival passed to anemophilous angiosperms with their inconspicuous inflorescences and frequently associated deciduous habit. Within these post-impact surviving lineages, the progeny that prospered in a landscape depleted of more exotic angiosperms were the origins of the warm temperate, deciduous hardwood forests of the eastern seaboard and Appalachian region of North America. These lineages became pervasive in the Late Paleocene and Eocene, paralleling the Tertiary accession of the mammals.

How then does this relate to the anomaly of a presumed sudden and short-term environmental perturbation resulting in a significant level of plant extinctions, notwithstanding the considerable capacity of plants for prolonged dormancy and vegetative regeneration? If one accepts that extinctions were concentrated among zoophilous angiosperms, it is logical to consider the vulnerability of

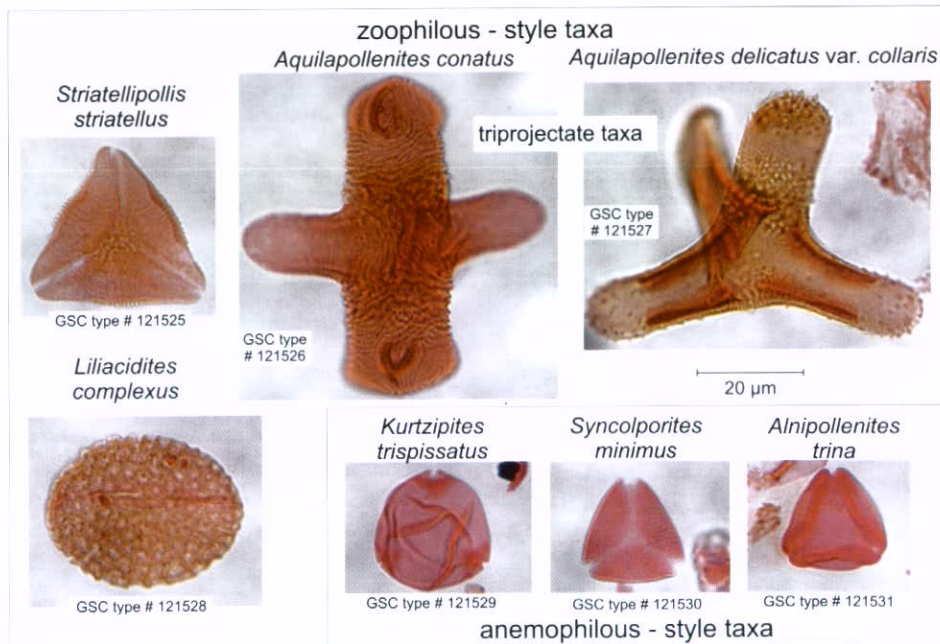


Figure 7 Illustrations of anemophilous (= wind-pollinated) and zoophilous (= animal-pollinated) pollen.

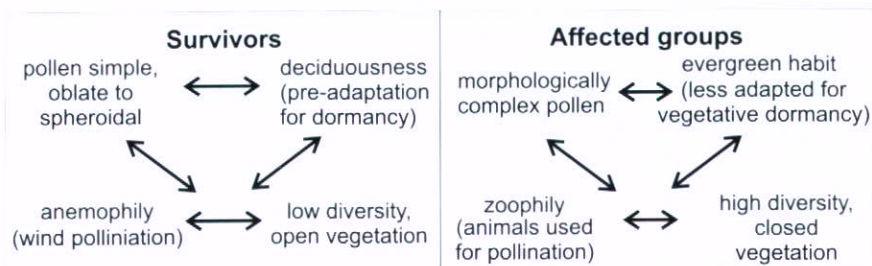


Figure 8 Linkages between pollination strategy, pollen morphology, and leaf and vegetation habit for groups that became extinct, and for survivors.

pollinators to extinctions. By virtue of their more constrained life cycles and possible lack of applicable dormancy mechanisms, insects and/or other pollinators were perhaps more vulnerable to short-term catastrophic events. Such a direct causal linkage between K-T boundary environmental perturbations and the extinction of pollinators would help explain plant extinctions, and would be consistent with evidence for the loss of insect taxa across the K-T boundary (Labandeira, 2000). A more general implication is that selectiveness according to pollination habit suggests that entire ecosystems were not overwhelmed by the boundary event.

A Story of Transition: Zoophilous-type Survivors

There are even further subtleties in the selection of the doomed and the survivors across the K-T boundary. Among zoophilous-type pollen taxa, *Aquilapollenites reticulatus* and *Wodehouseia spinata* were at first erroneously appraised to occur only in the Cretaceous, but are now known to persist into the Paleocene (Braman and Sweet, 1999). These taxa belong to the triprojectate and oculate pollen complexes, respectively, that together typify mid- to high-latitude latest Cretaceous pollen assemblages. The triprojectates, in particular, were profoundly affected by the K-T boundary event. A third associated taxon, *Tricolpites parvistriatus*, with mixed anemophilous and zoophilous characters, had origins in, and was also initially thought restricted to, the late Maastrichtian. All three taxa finally became extinct at or before the polarity chron 29r / 29n boundary in the early Paleocene (Fig. 9).

Aquilapollenites reticulatus, *W. spinata*, and *T. parvistriatus* occur in a wide range of lithotypes in the Cretaceous, but mostly in coal and coaly shales in the Paleocene. Therefore, it would appear that some feature of swamp and swamp-margin niches temporarily protected the parent plants of these pollen species from extinction caused by cometary impact, and promoted their continued survival in the earliest Paleocene. Their survival limits the pervasiveness of the most universal environmental consequences of the end-Cretaceous impact event, and raises questions regarding their

more or less coincident extinction some 200,000 years later, especially as they belonged to very distinct plant lineages.

Pre-boundary, Catastrophy-driven and Recovery/Successional Paleofloras

Pre-K-T boundary floristic and environmental trends locally tended to either enhance or reduce the apparent magnitude of the physical effect of K-T boundary events. In most western Canadian localities, there are concentrated occurrences of pre-boundary pollen and spore range tops at intervals ranging from metres to centimetres below the boundary, which reduces the apparent singular importance of the K-T impact event as a causal factor in end-Cretaceous extinctions. In contrast, at Brownie Butte, Montana, there is no evidence for extinctions prior to the K-T boundary. Instead, there is a concentration of range tops coincident with the hackly claystone, which serves to enhance the apparent effect of the boundary event. These differences in the apparent survivability of taxa in the pre-boundary interval may reflect local favourable micro-environmental niches that allowed the continuance of typical Maastrichtian taxa (and their pollinators) up into the K-T boundary claystone. This interpretation is supported by the fact that there is a general correspondence between the

occurrence of coal and coaly shales (as opposed to mudstones) underlying the K-T boundary claystone in western Canada, and the maintenance of pollen diversity (Sweet, 1994). From a broader perspective, range tops of selected taxa occur earlier in more northerly latitudes, suggesting an underlying climatic influence on at least some range tops.

In addition to changes in pollen diversity, in western Canada the relative abundance of gymnosperm pollen, representing plants of the forest canopy (McIver, 1999), increases in the immediate pre-boundary interval (Sweet and Braman, 1992). In swamps, most angiosperms and ferns were probably part of the understory beneath the forest canopy. Thus the timing of this shift in floral composition often coincides with the onset of coaly shales and coal. The boundary event was superimposed upon these changing ecosystems.

Associated with the K-T boundary ejecta layer is a concentration of range truncations (some probably extinctions) and, in southern Saskatchewan and Alberta, an abrupt drop in the relative abundance of gymnosperm pollen that is interpreted to represent the destruction of more or less fully canopied swamps.

In the directly overlying satiny claystone and laminated shale, the pollen and spore assemblage is overwhelmingly dominated by *Cyathidites*, a trilete fern

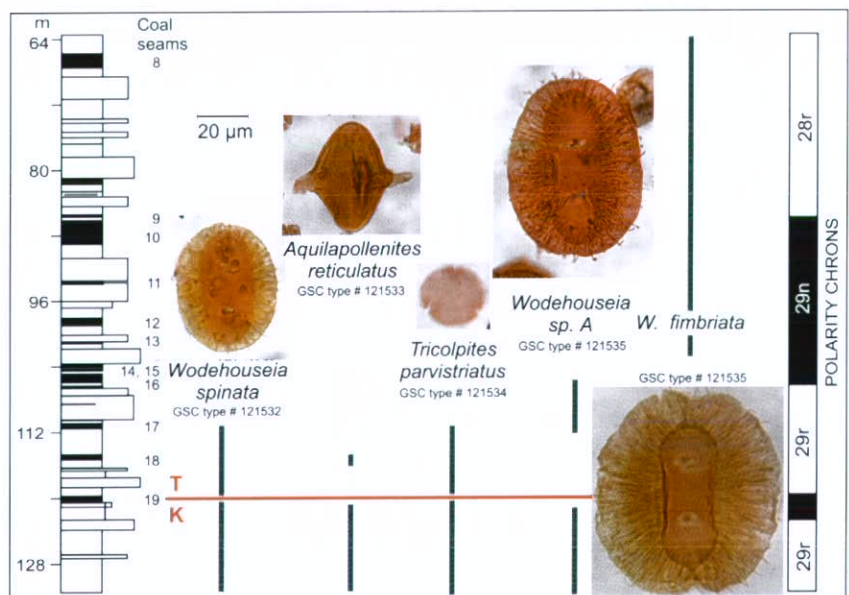


Figure 9 Diagram illustrating zoophilous survivors and their last appearances (extinctions) near the 29r/29n polarity boundary in the Wood Mountain K-T boundary corehole.

spore. *Ulmoideipites*, pollen of a probable anemophilous flowering plant, is the only angiosperm consistently present, albeit at low frequencies. The parent plants of these spores and pollen are taken to be

boundary event survivors that were left to dominate the post-event landscape during the deposition of the upper layers of the boundary claystone. This conclusion, as argued in Sweet *et al.* (1999), is based on

constraints imposed by the presumed short length of time separating the hackly and satiny claystones (Fig. 1) and the time required for ferns to reach reproductive maturity, if one were to assume that their fronds were destroyed by the impact event.

At the base of the overlying Paleocene-aged coal there is an abrupt shift to a dominance of a different type of fern community represented by monolet spores of the form genus *Laevigatosporites*, and a more diverse suite of angiosperm taxa. These are taken to be opportunistic species forming a successional recovery flora that usually continues, on average, through an interval of coal approximately 20 cm thick. As a final phase in the successional floras, the relative abundance of gymnosperm pollen progressively increases within the coal above the boundary claystone, and this is interpreted as signaling a return of the swamp forest.

The destruction of the swamp forest canopy in southern Saskatchewan and Alberta is likely to have been caused by the thermal pulse and fires predicted by the impact event scenario (Fig. 3). The probable survival of ferns raises questions as to the extent and effects of the thermal event and the predicted fires.

Northward Attenuation of Swamp Forest Destruction

Based on fossil leaf cuticle, swamps existing immediately before the boundary event were forested by the gymnosperms *Glyptostrobus* (Chinese swamp cypress) and *Metasequoia* (dawn redwood) (McIver, 1999). Immediately below the boundary claystone, the average relative abundance of gymnosperm pollen is about 30% of the total assemblage (Fig. 10), but at some localities in southern Saskatchewan and central Alberta their relative abundance ranges as high as 60 to 90% (Sweet and Braman, 1992). Over this same area, in the boundary claystone and immediately overlying coal, the relative abundance of gymnosperm pollen sometimes drops to zero, and on average to near zero (Fig. 10). This provides evidence for swamp forest destruction over an even larger area than that represented by the sampled localities, given that the gymnosperms present below the boundary were anemophilous and very

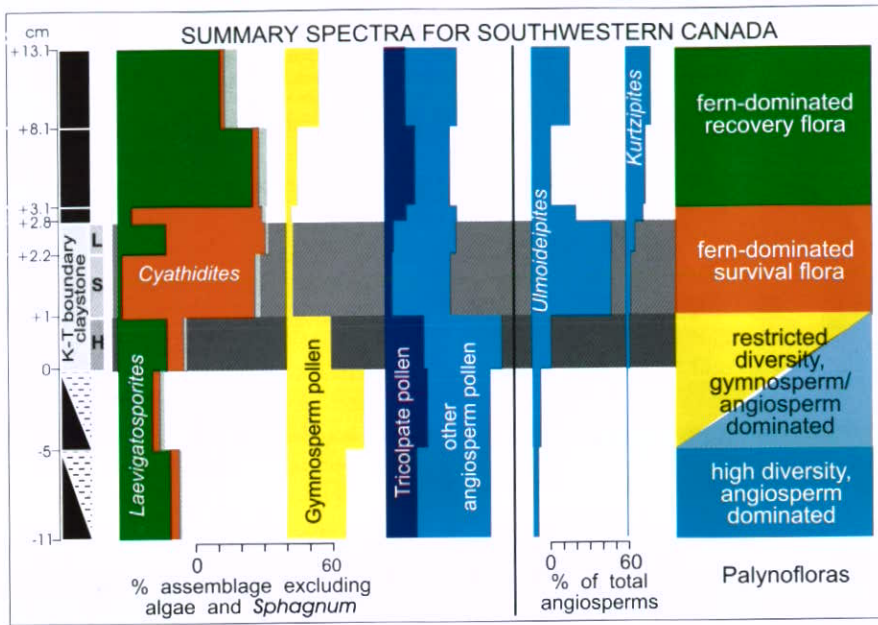


Figure 10 Relative abundance spore and pollen profiles across the K-T boundary, based on weighted averages of data from localities in Alberta and Saskatchewan. These spectra illustrate the collapse in the abundance of gymnosperm pollen, and spikes in the abundance of fern spores and angiosperm pollen, presumably produced by plants of the canopy and understory respectively (modified after Sweet *et al.*, 1999, fig. 16). See Sweet *et al.* (1999) for a complete discussion of data used to construct the diagram.

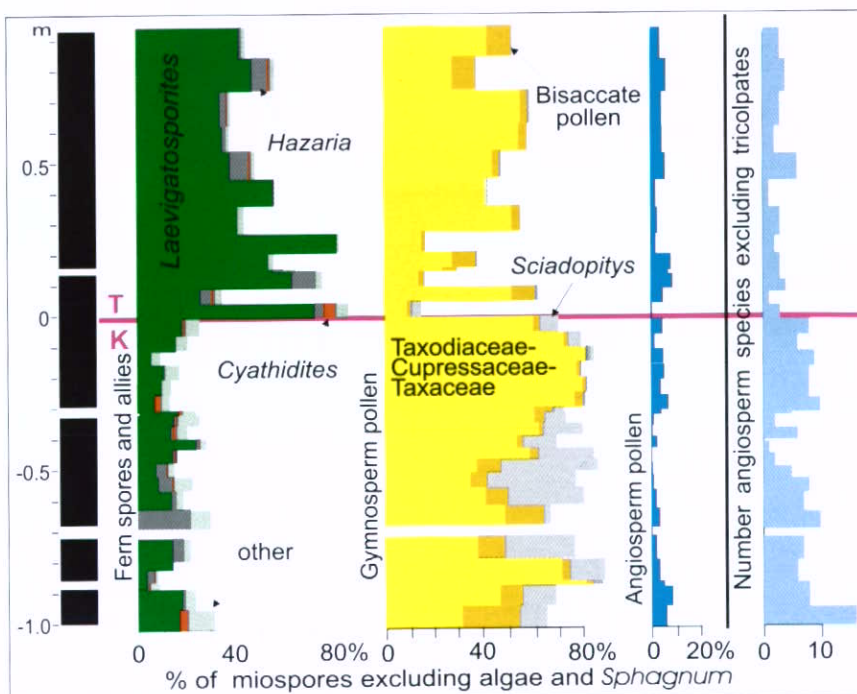


Figure 11 Relative abundance spore and pollen (miospores) profiles across the K-T boundary interval, Police Island Section, NWT (modified after Sweet and Braman, 2001, fig. 11).

prolific pollen producers.

Farther north, in the Police Island section, Northwest Territories (Fig. 2), the abundance of gymnosperm pollen does not drop below 10%, although their relative abundance is sporadically low over a 28 cm-interval immediately above the K-T boundary (Fig. 11). This latter observation is taken as evidence for a northward attenuation in the near disappearance of gymnosperm pollen in the immediately post-boundary event interval, and therefore a more limited destruction of the swamp forests at higher latitudes. This interpretation places a probable sub-continental limit on the destructive power of the impact-generated energy pulse.

Anemophilous-type Angiosperm Survivors: A Story Involving Both Continuity and Discontinuity in Stratigraphic and Geographic Trends

Wind-pollinated angiosperms are prolific pollen producers. Their high numbers in fossil assemblages allow for their relative abundance to be reliably quantified by counts of 200 pollen grains and spores per sample. Such counts provide examples of both continuities and discontinuities in geographic and stratigraphic trends of pollen-based species across the K-T boundary.

A climatically controlled north-to-south latitudinal gradient within mid-continental North America at the time of the K-T boundary event is indicated by variations in plant communities (Nichols *et al.*, 1990), and regional differences in the timing of range-truncations over a paleolatitudinal distance of 4300 kms. In western Canada, the earliest Tertiary successional floras reveal a paleolatitudinal difference in the most prominent anemophilous angiosperm pollen. *Syncolporites* is most prominent at Judy Creek and Coal Valley, *Kurtzipites* in the Red Deer and Frenchman valleys, and *Ulmoideipites* in the Wood Mountain area and Brownie Butte, Montana (Figs. 12, 13). These north-to-south differences occur over about 700 kms in paleolatitude (Fig. 12).

Stratigraphic continuities, and discontinuities in the pattern of relative abundance trends of these taxa, can also be seen across the K-T boundary (Fig.

13). Examples of continuity in profile trends include the pollen spectrum of *Kurtzipites* at Coal Valley, Knudsen's Farm and Brownie Butte. Examples of discontinuities include the abrupt truncation in the occurrence of *Kurtzipites trispissatus* at Judy Creek and of *Syncolporites minimus* at Brownie Butte. In the more southern Frenchman Valley, Wood Mountain area, and Brownie Butte localities the relative abundance of *Ulmoideipites* spp. is enhanced in the upper layers of the boundary claystone (satiny claystone and laminated shale), whereas its relative abundance generally drops off in post-boundary samples from more northern sections. These observations are taken to infer that local conditions affected the sensitivities of these taxa to the boundary event. Thus the immediate ecological effects of the boundary event, although profound, were apparently mitigated regionally, as reflected by geographic variations in the response of anemophilous angiosperms. This implies that the physical effects imposed by the K-T boundary event were of lesser magnitude than other ongoing changes controlling the distribution of anemophilous angiosperm taxa in western Canada. Examples of the continuation of geographic and stratigraphic trends in relative abundances across the K-T boundary, with only transitory interruptions, provide additional evidence for only a brief perturbation in pre-existing environmental conditions.

DISCUSSION

Three events were directly associated with the boundary impact: the deposition of the hackly claystone; the extensive destruction of the forest canopy; and range truncations and/or extinctions among primarily zoophilous angiosperms. Of the proposed physical consequences of the impact event, the timing and geographic extent of a thermal pulse, driven by the release of energy from the ejecta blanket (Hildebrand *et al.*, 1998) seems to correspond most closely to the abrupt drop in the relative abundance of gymnosperm pollen and the inferred regional removal of the swamp forest canopy. Other, more universal physical consequences of the boundary event, such as dust-related cooling, ozone depletion and/or acid rain (Fig 3), must have caused

the extinction of affected zoophilous plants throughout the *Aquilapollenites* Province. It is this more universal component that appears to have triggered the collapse of an interactive plant/animal ecosystem.

Although there is no question that the K-T boundary impact event contributed to extinctions within the angiosperms, it does not appear to be the only cause of Maastrichtian extinctions. Recognition of factors underlying pre-boundary environmental changes detrimental to either Maastrichtian zoophilous plants or their pollinators may lie in a more integrated explanation, such as the Pele hypothesis of Landis *et al.* (1996). This hypothesis embraces cause and effect relationships between processes that could have acted to stress Maastrichtian ecosystems before the boundary event, including the release of carbon dioxide during mantle degassing, and eustatic changes in sea level.

Given its association with the satiny claystone and laminated shale, the *Cyathidites/Ulmoideipites* assemblage (Fig. 10) likely represents the selective survival and propagation of plant taxa adapted to conditions of low light, lowered temperatures, and high acidity. As the *Cyathidites* spore-spike starts in the lower part of the satiny claystone, it seems probable that the parent ferns were survivors from the Cretaceous, which continued to be reproductively successful. This is the most likely explanation if the layers of boundary claystone are viewed as an internally

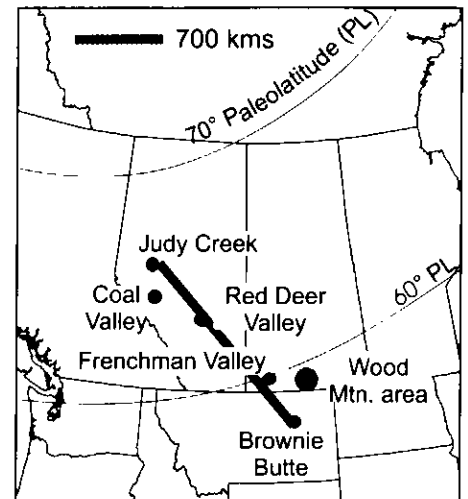


Figure 12 Map showing paleolatitudes and locations referred to in Figure 13.

conformable, graded air-fall deposit, although this is counter to the postulation of a denuded landscape later recolonized by ferns (Tschudy *et al.*, 1984). Also implicit in the above survival interpretation is that the finer boundary claystone sediment, while still resident in the atmosphere, may have contributed to reduced light and cooling, but did not force environmental conditions below thresholds required for some species to continue sporulation. This precludes an initial period of several years of near

blackout and freezing (Pope *et al.*, 1994), especially because, following the return to conditions amenable for plant growth, additional time would be required for the parent plants to reach reproductive maturity. The restriction of this survival assemblage to the satiny and laminated layers is consistent with the postulation of Pope *et al.* (1994) that it took 8-13 years to clear the atmosphere of sulphur aerosols and dust.

If the *Cyathidites/Ulmoideipites* fern-dominated assemblage is presumed

to have had the competitive edge during a period of reduced light and temperature following cometary impact, the abrupt shift to a *Laevigatosporites/Kurtzipites* assemblage, coincident with conditions amenable to the accumulation of peat, should correspond to the final clearing of the atmosphere of light-reducing particles and aerosols. The positive effects of increased light may have been further enhanced by elevated amounts of carbon dioxide and a resultant greenhouse effect, as discussed by Pope *et al.* (1994).

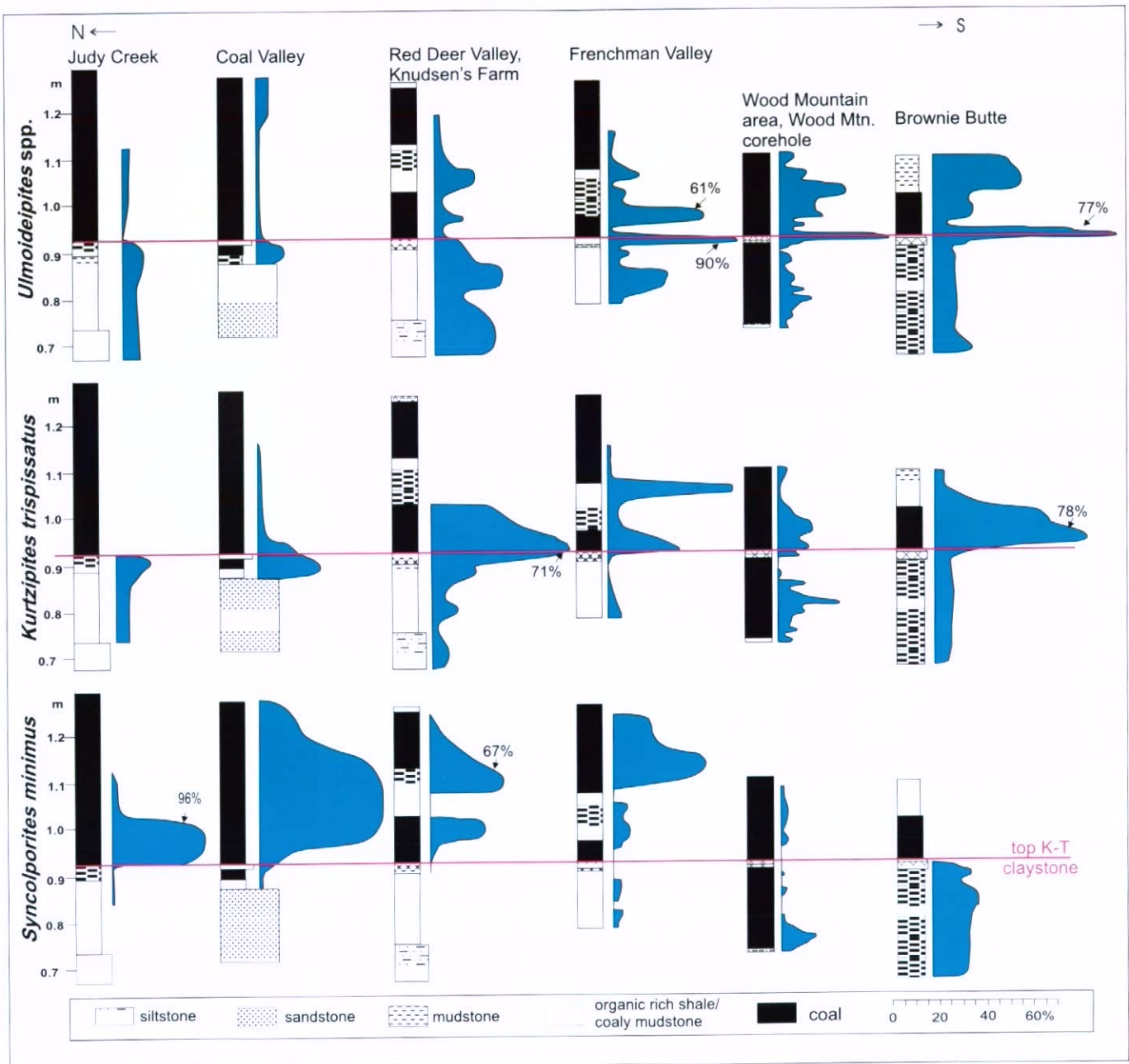


Figure 13 Southward and upward changes in the prominence of selected angiosperm pollen, and continuity and discontinuities in the spectra of anemphilous pollen (modified after Sweet and Braman, 2001, figs. 13, 14).

In western Canada, a shift back to gymnosperm-dominated assemblages occurs some 10-40 cm above the base of the coal, and is taken as a return to canopied forested-swamp conditions and "normal" environmental conditions.

In contrast to catastrophic aspects of the plant story, anemophilous angiosperms and restricted numbers of probably zoophilous plants, occupying swamp and swamp margin habitats, were only temporarily affected by the boundary event. Also, the southward shift in peak abundances of anemophilous taxa through time, with only a temporary interruption at the boundary, argues that the effect of the boundary event was neither of the magnitude nor prolonged enough to override ongoing climatic change trends.

The palynofloral observations presented herein suggest a gentler and more regionally restricted K-T boundary perturbation than the "living hell, a dark, burning, sulphurous world where all rules governing survival of the fittest changed in minutes" of Hildebrand (1993, p. 112). Is it possible to reconcile the plant record and the postulated impact-driven environmental perturbations? The optical effects of atmospheric impact-derived dust and aerosols and the amount of energy transferred across the surface of the earth appear to be overestimated. Can it be that the proportion of impact energy lost into space and the residency time of impact-induced dust and aerosols in space and/or sub-space has not been estimated correctly?

The K-T boundary plant record has further significance. A component of the impact event was a sudden shock release of CO₂ from the carbonate-rich terrain of the Yucatan Peninsula (O'Keefe and Ahrens, 1989; Pope *et al.*, 1994). Hence, floral shifts in the earliest Paleocene can provide an excellent case study for examining the consequences of a rapid (even in human terms) infusion of CO₂ into the atmosphere, and a revealing perspective from which to view the present "greenhouse" warming debate.

SCENARIO INVOLVING PLANTS (FIGURE 14)

A rain of superheated glass beads generated a thermal pulse that ignited a forest canopy fire that raced across the latest

Maastrichtian swamps. This was not an all-consuming, world-denuding wildfire, however. Even in North America it was selective, as it left behind the understory ferns and angiosperms that aggressively responded to their release from the covering forest canopy by cycles of sporulation following the impact event.

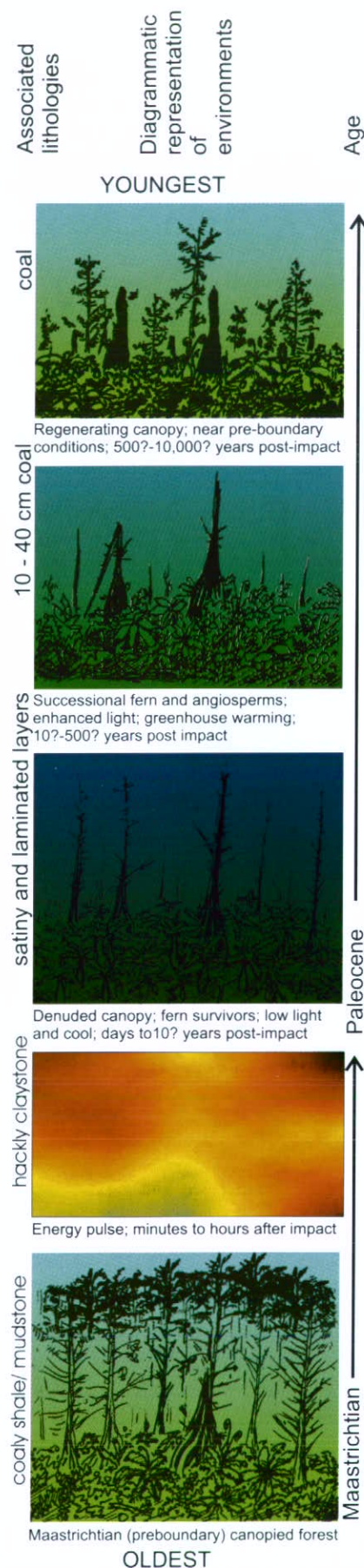
The fine impact debris and aerosols that darkened and cooled the days were deposited continuously on this well-saturated landscape. A fern-dominated vista reached over much of mid-continental North America and was interrupted only by the charred spars of the dead canopy vegetation. With the clearing of light-blocking impact debris from the atmosphere over time, the boundary event survivors were replaced by other, successional ferns and angiosperms better adapted to the increasing light and warmth of the now greenhouse conditions. Some hundreds if not thousands of years after the last of the charred spars had fallen, gymnospermous trees returned to regenerate swamp conditions similar to those of the Cretaceous, except for the missing exotic angiosperms.

If *Triceratops* and *Tyrannosaurus* had survived into the Tertiary, they would have found these conditions alien and in strong contrast to the well-drained landscapes of the late Maastrichtian in western Canada. However, the very absence of large herbivores may have contributed to the pervasiveness of marsh/swamp conditions. These prodigious Mesozoic Era consumers and, by their movements, degraders of organic material, were removed from the ecosystem. No large trampling animals were left to break tributaries free of dams formed by the grasp of plants and their debris, thus decreasing the capacity of the landscape to shed itself of Paleocene rain (Sweet *et al.*, 2000). Until the land was uplifted some 2 million years later, swamps and sluggish drainage systems dominated the early Tertiary landscape.

CONCLUSIONS

1. Two separate but overlapping processes affected plant communities at the K-T

Figure 14 Diagrammatic representation of the floral changes across and contiguous to the K-T boundary interval. Art work by Patrick R. Sweet.



boundary in western Canada: a selective killing event, which resulted in the loss of the swamp forest and shifts in the quantitative composition of plant communities; and a selective extinction event, which eliminated most zoophilous angiosperms from the early Tertiary floras.

2. Swamp and swamp margin environments appear to have provided a refuge for selected zoophilous angiosperms following the cometary impact event.
3. The presence of abundant *Cyathidites*-type fern spores and *Ulmoideipites* in the satiny claystone and laminated shale is taken as evidence that understory plants survived the impact event and were able to maintain their reproductive capacity during the immediate post-K-T boundary event interval.
4. There is evidence, from gymnosperm pollen relative abundances, of a northward attenuation in the completeness of the killing of the forest, even within North America.
5. Geographic and stratigraphic patterns in the relative abundances of anemophilous angiosperm pollen indicate that the environmental effects of the boundary impact event were not of sufficient magnitude to completely suppress the effects of other ongoing environmental trends.
6. Observations based on spore and pollen assemblages from western Canada argue for a less profound environmental effect from the K-T boundary impact event than that suggested by some of the proposed scenarios, an effect that did not completely override other factors in environmental change.

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