Thesis submitted for the degree of
Doctor of Philosophy

EARLY PALAEOCENE
VEGETATION AND
CLIMATE OF NORTH AMERICA

by

Katherine Siân Davies

Department of Earth Sciences
and
St. Peter's College
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ABSTRACT

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Katherine Siân Davies
St Peter's College

Early Palaeocene floras from twenty seven sites within the Raton, southern Powder River and south-western Williston Basins of the western interior of North America were collected, and their leaf physiognomy, ecological character and depositional setting compared. Such a spread of samples enabled the study of spatial and temporal vegetational and climatic variations in the region, following the Cretaceous-Tertiary boundary event.

Climatic changes are observed across the Cretaceous-Tertiary boundary. Precipitation increased dramatically, and remained relatively high throughout the earliest Palaeocene. Temperatures were somewhat lower, compared to those of the Late Cretaceous, and seasonality in climate increased. Climatic and vegetation zones shifted southwards as latitudinal climatic equability decreased.

Palaeotemperature and palaeoprecipitation were determined using CLAMP and leaf margin analysis. Experiments carried out to assess the robustness of CLAMP to loss of foliar physiognomic data revealed that this data loss did not drastically effect palaeoclimatic determinations but that information about leaf size and margin type had the most effect on results.

Vegetation was of low diversity directly after the boundary event, but recovered to stable, but still relatively low levels, within a short time. Changes in diversity are difficult to interpret due to masking by taphonomic biases, which are important within the depositional environments analysed in this study. Climatic deterioration and the prevalence of disturbed environments ultimately facilitated expansion of the angiosperms, although their aspect was changed with a general increase in deciduous forms, in relation to increased seasonality and decreased equability.

These trends cannot be related merely to the impact of a bolide at the Cretaceous-Tertiary boundary, but reflect the more global and wide-ranging changes of the period, which were punctuated by this brief, deleterious event. Previous work has tended to concentrate on the North American continent but a more global perspective reveals that the Cretaceous-Tertiary boundary event was not a world-wide catastrophe within terrestrial environments.

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EXTENDED ABSTRACT

Early Palaeocene vegetation and climate of North America

Katherine Siân Davies
St Peter's College

This thesis presents a synthesis of vegetation, climate and depositional setting for the period following the Cretaceous-Tertiary boundary event in the Western Interior of North America. It aims to provide a general picture of the early Palaeocene environment in the region, using leaf megafloras and sedimentology to determine floral diversity and composition, depositional environment and palaeoclimate, whilst also allowing for biases introduced by taphonomic processes. This will increase the understanding of the terrestrial environment and state of vegetation following the Cretaceous-Tertiary boundary event in this region, as well as provide further insight on past climatic changes. In doing so it will complement existing palaeobotanical and palaeoclimatic work on the boundary period.

Much of the past literature pertaining to the Cretaceous-Tertiary boundary event, and the climatic and environmental conditions following it, has focused on North American data. In this study, in an attempt to address this problem, comparisons have been made with data from other parts of the world, where possible, to obtain a more global view of events at this time.

The Cretaceous-Tertiary boundary saw the extinction or disruption of many groups of organisms. Considerable research has been carried out in an attempt
to ascertain the cause of this ecological trauma. Current theories focus on the impact of an extra-terrestrial bolide upon the earth causing disturbances within ecosystems of both the marine and terrestrial realms, as well as perturbing climate. The study of terrestrial floras at this time allows assessment of the extent of damage to terrestrial ecosystems and, as leaf physiognomy is determined directly as a result of climatic conditions, climatic change.

Well-preserved leaf floras occur within Cretaceous-Tertiary boundary, and early Palaeocene sections in Laramide basins from the Western Interior of the United States. Early Palaeocene floras from twenty seven sites within the Raton, southern Powder River and south west-central Williston Basins (at palaeolatitudes 45°, 50° and 55°N respectively) were collected, and their leaf physiognomy, ecological character and depositional setting compared. Such a spread of samples enabled the study of spatial, as well as temporal, vegetational and climatic variations.

Sedimentological analysis of fossil-bearing sites in relation to previous work carried out in the regions, together with a comparison with taphonomic studies for floras preserved in similar environments, revealed taphonomic biases in fossil floras. It was found that the most diverse floras, those that best represented regional flood plain vegetation, came from lacustrine, overbank flood and crevasse splay deposits. Fossil floras collected from channel deposits were of low diversities and biased towards more robust leaf forms. Those from small-scale ponded environments were also of low diversity, and invariably dominated by aquatic plants. These taphonomic biases were found to mask diversity and morphological changes in some floras, which was an important consideration when determining climatic variables and floral
change through time. In the light of this, all analyses were assessed with due regard for depositional environment so that biases introduced, could be considered.

An assessment of the floras collected reveals that in the early Palaeocene, the Raton Basin was predominantly vegetated by a megathermal evergreen forest, although the fact that it was on the northerly edge of the megathermal climatic regime meant that, at times, it had a slightly more deciduous aspect. In the Williston Basin at this time, a mixed flora of conifers, angiosperms and water plants with a deciduous, mesothermal aspect is observed. The Powder River Basin supported a flora transitional between the two. Specific changes observed in angiosperm composition and morphology across the boundary period are primarily in response to the changing climate. In general, a relative increase in forms better adapted to a wetter and more seasonal climate is recorded with, for example, the occurrence of drip tips and dentate margins. This change is also observed in other areas of the northern hemisphere across the boundary period, but little change has been detected in floras from the southern hemisphere at this time. Climatic change identified in this study, together with the prevalence of disturbed flood plain depositional environments at this time, may have facilitated expansion of the angiosperms, because of their inherent morphological plasticity which facilitated adaptation to these changes.

Simple morphotype diversity curves, and calculation of similarity coefficients revealed ecological changes in fossil floras from the early Palaeocene. Vegetation was of relatively low diversity following the boundary event, with the number of morphotypes in a given flora at around a maximum of twenty. Low diversity levels were most pronounced in more southerly areas of the
North American continent, suggesting greater ecosystem disturbance in this area. However, diversity levels everywhere recovered relatively rapidly, but remained low, at less than thirty morphotypes for a given flora, throughout the early Palaeocene. Previous suggestions that floras underwent an ecological recovery on an evolutionary time scale following the Cretaceous-Tertiary boundary event, appear to have been exaggerated due to a disregard of the effects that taphonomy can have on the diversity and physiognomy of floral assemblages preserved. The calculation of similarity coefficients between floras reiterated the effects that taphonomic biases can have on fossil floras. Similarities in floral composition from sites of different stratigraphic level, but similar depositional setting were observed. Floras which appeared to best represent regional vegetation, in that they had high similarity indices with most other floras, came from overbank flood, crevasse splay and lacustrine deposits.

Univariate (leaf margin analysis or L.M.A.) and multivariate (CLAMP) statistical methods of interpreting leaf physiognomic characters were used to determine mean annual palaeotemperature and palaeoprecipitation. From the use of more than one method of determining palaeoclimates any bias that any one technique had was reduced. Reliance on these methods for absolute temperatures is not recommended because of the number of assumptions they make, and the possible associated errors. Experiments carried out to assess the robustness of CLAMP to loss of foliar physiognomic data revealed that this data loss did not drastically effect palaeoclimatic determinations, but that information about leaf size and margin type had the most effect on results. These results indicate that CLAMP is a useful method of determining palaeoclimatic variables when specimens from a flora are incomplete, but that loss of information about leaf size and margin type effect results most.
These methods of determining palaeoclimate from leaf physiognomy, together with sedimentological evidence, revealed that climatic changes were not uniform across the North American continent in the early Palaeocene. Mean annual precipitation was at considerably higher levels than it had been in the Late Cretaceous. This was observed throughout the continent, but was most pronounced at more southerly latitudes. Although the peak in precipitation observed directly after the boundary event drops off somewhat later in the early Palaeocene, precipitation levels remain relatively high throughout this period. Mean annual temperatures appear to be slightly lower than those of the latest Cretaceous, although there is no evidence for freezing associated with a post-impact winter. Disparate results are obtained from the two techniques used to determine palaeotemperatures. L.M.A. gives consistently higher M.A.T.s than CLAMP, for southerly floras, but consistently lower M.A.T.s than CLAMP, for more northerly floras. However, the general trends that they show are the same, and results from both suggest that palaeotemperatures still appear to have been slightly lower than in the Late Cretaceous. Varying evidence supports the idea of increased seasonality in climate in the early Palaeocene. Climate also became less equable at this time, with an equatorwards shift of vegetational zones. In other parts of the globe there is also evidence for cooling and humidization across the boundary.

The suggested increase in seasonality following the boundary event, would explain the higher proportion of dentate-margined leaves observed in floras from the early Palaeocene than the latest Cretaceous. This is in disagreement with previous theories which invoke a selection for dormancy features in angiosperms, such as dentate margined leaf forms, in response to the brief
deleterious effects of the boundary event. Supposedly, this results in an increased proportion of dentate margined leaves, which are 'out of step' with the climatic conditions experienced in the early Palaeocene. However, an increased seasonal aspect to climates produces the same type of leaf physiognomy. If this were the case, then the boundary impact may have had less direct evolutionary effect on early Palaeocene floras than previously thought. This raises the problem of short term ecological effects versus longer term evolutionary effects on boundary floras. Because angiosperms are generalists, it is more likely that the longer term climatic changes across the boundary period would have had an evolutionary effect on them, as opposed to the brief 'short sharp shock' of a post-impact winter, which would have had a relatively short term ecological effect.

There is much global evidence to suggest that the latest Cretaceous was a time of climatic and ecological change on land and in the oceans. Conversely, the evidence for a global catastrophe, within the terrestrial realm at the Cretaceous-Tertiary boundary, is primarily derived from the North American continent, and even here it is not conclusive. The trends observed at the Cretaceous-Tertiary boundary can not therefore merely be related to the impact of a bolide, and its associated phenomena. Instead, they reflect the more global and wide ranging changes of the period that were punctuated and exacerbated by this brief deleterious event.
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CHAPTER ONE

INTRODUCTION
CHAPTER ONE

INTRODUCTION

1.1 AIMS

Although there have been previous studies of vegetation and climate from the early Palaeocene of North America, these studies have tended to concentrate on one particular geographic area, or have not taken sedimentological, ecological and taphonomic affects into account, when interpreting floral and climatic data. This study aims to provide a broader picture of the terrestrial environment of the early Palaeocene in North America, through a combined study of palaeobotany, sedimentology and climatology, and then attempts to relate this to the Cretaceous-Tertiary boundary event in this region, and in other parts of the world.

The emphasis that has previously been placed on North American data has tended to bias views on the Cretaceous-Tertiary boundary event, and its effects on global climate and ecosystems. In an attempt to overcome this somewhat, evidence from other parts of the world has been assessed wherever possible in this study, and comparisons with North American data attempted.

The problems of using palaeobotanical data for climatic, ecological and evolutionary interpretations became apparent during the study, especially the bias that depositional environment can have on the composition of fossil floras and consequently the data that they yield. These problems are outlined, and suggestions for avoiding, or allowing for these, are made.
1.2 FIELD AREAS

Three basinal areas of the Western Interior of the United States were chosen to work on (Fig 3.1a). Their choice avoided conflict with other workers, and also enabled the study of a broad latitudinal spread of sites, encompassing several vegetational and climatic regions. The sites were located in the Raton, southern Powder River and south west-central Williston Basins (palaeolatitudes 45°, 50° and 55°N respectively). Twenty five separate sites from the early Palaeocene, plus two from the latest Cretaceous, were worked on, and floras were collected from twenty four of these. These floras yielded different degrees and quality of data due to their states of preservation and relative abundances of leaf morphotypes, which showed considerable inter-site variation.

Following regression of the Late Cretaceous Western Interior seaway, the areas studied evolved as basins, with uplift of the Rocky Mountains in the latest Cretaceous and early Tertiary facilitating accumulation of sediments from a variety of flood plain, deltaic and lacustrine environments. Leaf megafossils were collected from sediments representing a broad range of flood plain depositional environments from the early Palaeocene. Temporal constraints meant that very few floras could be collected from sediments of the Late Cretaceous. This meant that comparison with latest Cretaceous floras and climate could only be carried out in relation to previous work.

1.3 CONTENT OF THESIS

In chapter two, previously described Cretaceous-Tertiary boundary phenomena, and their subsequent possible effects on the earth, are reviewed. The evidence for a bolide impact is discussed, and other theories which have been put forward to explain the events observed across the boundary are
considered. The severity of the boundary event and its varying effects across the globe are also considered.

In chapter three, the basinal and depositional settings from which fossil floras were collected are assessed. Details of the sedimentology at each collecting site are described, and sedimentary logs presented. From these, and comparison with previous sedimentological studies, interpretations of depositional environments are made. Taphonomic problems associated with collecting leaf megafossils are identified and reviewed, and then specifically related to floras collected in this study. Finally, results are compared with those from previous taphonomic studies of flood plain floras.

In chapter four, the characteristics of latest Cretaceous and early Palaeocene floras collected in this study are described. These are compared with work previously carried out on contemporaneous floras, from both North America and other parts of the globe, in order to detect floral and vegetational changes across the boundary. Palynological changes across the boundary period are also reviewed.

In chapter five, the ecological aspects of early Palaeocene vegetation are described. The role of angiosperms within early Palaeocene ecosystems is assessed. Results of floral diversities and morphotype diversity curves, determined from floras collected in this study, are analysed to determine trends throughout the early Palaeocene. The similarity indices between floras are also calculated in order to identify the relationship between depositional environment, stratigraphic position and the composition of floras.

Chapter six analyses the climatic changes across the Cretaceous-Tertiary boundary. The rationale behind using fossil angiosperm floras to determine palaeoclimate is described, and the two methods used in this study are
introduced and discussed. Results from climatic analyses are presented and interpreted. These are combined with climatic inferences from non-angiosperm plants. The climate of the latest Cretaceous is reviewed and boundary climatic data from non-fossil leaf evidence also described. Comparisons are made with both climatic data from the latest Cretaceous, and with previous climatic estimations for the early Palaeocene from North America, and the rest of the world.

Chapter seven discusses the bearing this study has on previous interpretations of phenomena observed in terrestrial realms, following the boundary event. In an attempt to provide a general synthesis of the terrestrial environment of the early Palaeocene in North America, relationships between the sedimentology, palaeobotany, climate and ecology are presented. These are also placed within the perspective of the Cretaceous-Tertiary boundary event on a world-wide scale.
CHAPTER TWO

THE CRETACEOUS-
TERTIARY
BOUNDARY EVENT
CHAPTER TWO

THE CRETACEOUS-TERTIARY BOUNDARY EVENT

2.1 INTRODUCTION
Evidence for extinctions at the close of the Cretaceous has been observed and chronicled throughout the history of the subject of geology. The causes for these extinctions have been considered and debated for just as long (For example Newell 1962, Bramlette 1965, Van Valen and Sloan 1977). The publication of a paper by Alvarez et al in 1980 rekindled interest in the event or events that occurred at the Cretaceous-Tertiary boundary and their possible subsequent extinction-inducing effects on global environments and ecosystems. The hypothesis of Alvarez et al (1980), suggested that raised levels of iridium at boundary sites world wide were due to the impact of a large asteroid and prompted a massive research effort directed towards every conceivable aspect of the boundary event. This has yielded much evidence to support the hypothesis, as well as providing data for alternative theories to explain the observed phenomena.
### TABLE 2.1 PHENOMENA CITED AS EVIDENCE FOR METEORITE IMPACT AT THE CRETACEOUS-TERTIARY BOUNDARY

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(2) Álvarez et al 1988
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(8) Bohor et al 1987, Bohor 1988
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2.2 CANDIDATE IMPACT CRATERS

For a long time there was no evidence that would prove beyond reasonable doubt that a bolide did hit the Earth at the end of the Mesozoic. Only the identification of a crater structure of the appropriate size and age could really provide such evidence. At the time of writing, two impact structures of Cretaceous-Tertiary boundary age on or close to the North American continent have been identified.

The first of these was discovered in the U.S.A. at Manson, Iowa (Harting, Kunk and Anderson, 1988). The structure is 36km in diameter, contains shocked granitic rock, which has been dated at 66 million years (analogous to the date of boundary sites world-wide), and is in close proximity to those North American boundary sites that contain relatively abundant and large shock metamorphosed minerals (Izzet 1990, Figure 2.3). The structure itself comprises lower and mid Proterozoic granite and gneiss overlain by marine shales and limestones, which is consistent with the hypothesis that an asteroid impact must have been on continental crust overlain by marl sediments to produce the chemistry of tektite glasses found at boundary sites in Haiti (Sigurdsson et al 1991).

The second site, on the Campeche carbonate platform at Chicxulub, North Yucatan, in the Gulf of Mexico (Figure 2.3) has been discovered more recently. At 180km across it is the largest impact structure found on earth and has been radio metrically dated at 65 million years old, virtually indistinguishable from ages of tektite glasses in Haiti and Mexico (Swisher et al 1992). The structure contains shocked quartz grains up to 1mm across and its gravity and magnetic anomalies look remarkably similar to other crater structures on Earth (Smit 1991). The geological succession of the crater consists of andesitic igneous rocks, with compositions similar to those of tektites found at some
boundary sites, and glass interbedded with, and overlain by, breccias that contain evidence of shock metamorphism (Hildebrand et al. 1991).

Deposits near to the Chicxulub impact structure are suggestive of deposition by a tsunami. They occur at North American Cretaceous-Tertiary boundary sites at Brazos River in Texas, Arroyo el Mimbral in N.E. Mexico, Haiti, New Jersey, the Hatteras abyssal plain, Alabama and Haiti (Smit et al. 1992, Hildebrand and Boynton 1988, Figure 2.3). The first two of these have been studied in the greatest detail. The Brazos River section in Texas consists of a graded basal layer with large mud and calcite intraclasts overlain by a parallel laminated and wave rippled fine sand. This package is interpreted as being formed by a long period wave with a height of 50m (Borgeois and Wiberg 1988). The site at Arroyo el Mimbral reveals a deposit divisible into three main beds. The lower bed has shock features and a spherule layer with tektite glasses (Smit et al. 1992) with the upper two layers similar to those described in Texas. However, previously described 'tsunami deposits' from north-eastern Mexico and the Caribbean have been reinterpreted as gravity flow and channel deposits with no unequivocal evidence for them being impact-derived (Stinnesbeck et al. 1993, Keller et al. 1993).

The nature of these 'tsunami' deposits is, overall, complex which has led some workers to suggest that a second generation of giant waves affected the region, leading to mixing of sediments and confusion in the biostratigraphic record (Maurrasse and Sen 1991). This may explain conflicting evidence with respect to extinction horizons and positioning of iridium anomalies in the sequence. Triggering of the second tsunami event might be related to crustal rebound following an impact or to multiple impacts.

Craters have also been described from Russia, that have been related to the Cretaceous-Tertiary boundary event (Figure 2.3). These are the Kara and Ust-Kara craters at the edge of the Kara sea on the Arctic coast of Siberia (Koeberl
et al. 1988). Their age, from K-Ar dating, appears to be older than the Cretaceous-Tertiary boundary at 70Ma (Koeberl et al. 1990). Other crater structures identified, of an approximately similar age, have been discovered at Karsiky (Kolesinikov et al. 1988). More data on these craters must be collected and assimilated with other boundary information from Siberia before these can be viewed in the context of the event as a whole. They might support a multiple impact or comet shower theory (Hut et al. 1987).

2.3 THE BOUNDARY CLAY

The Cretaceous-Tertiary boundary is marked globally by a thin layer of clay (Plate 2.3A) but this claystone is neither the same from site to site nor is it homogeneous itself, variations in composition being more common than similarities (Tredoux et al. 1988). It is a complex package (Plate 2.3B) that consists of a 2-4mm. clay layer at all boundary sites overlain by a 15-25mm thick layer of distinct composition which appears to occur only at North American boundary sites (Hildebrand and Boynton 1988, Figure 2.3), although little research on detailed comparisons with clays from other parts of the globe has been carried out. The boundary claystone looks superficially similar to tonsteins but it exhibits unique mineralogic and petrologic characteristics that are distinct from other clay-rich beds (Pollastro and Pillmore 1986). These characteristics; shocked quartz with multiple sets of planar deformation, stishovite, magnesioferrite crystals, glassy spherules or tektites and altered lithic clasts Bohor (1990) has termed “impact signatures”.

The wide distribution of the clay suggests a fallout origin and the sharp contact between the two boundary claystone units in North American sections implies a genetic relationship and almost simultaneous deposition (Pillmore and Fleming 1990). This complex structure is apparently not compatible with a single oceanic impact (Sharpton et al. 1990) and would
suggest that more than one impact occurred at the boundary. Fastovsky et al (1989) have recognised at least one hiatus in sedimentation within the boundary clay in Montana, identifying significant weathering of the lower claystone layer prior to deposition of the upper layer, supporting multiple impact theories. Wolfe (1991) has attributed the lower horizon to fall out from a large distant bolide impact and the upper to a smaller impact affecting only the North American continent.

This claystone couplet or package is fine grained and amorphous with an imbricate fabric (Pillmore et al 1988) that may reflect original vitreous material (Pollastro and Pillmore 1986). Izzet (1990) has identified the differences between the two components of the couplet. The lower, thicker boundary claystone bed contains deformed vitrinite lamellae, root-like structures, carbonaceous material, slightly raised levels of Pt group elements and goyazite and kaolinite spherules. The thinner, upper impact layer contains planar laminae of vitrinite and kaolinite pellets, shocked quartz, rock particles, that are not derived from a local source, a major iridium anomaly and a microscopically 'wavy' framework composed of smectite and mixed layer clays, as opposed to the polygonal framework and planar lamellae of the lower kaolinite rich layer. The distinct differences between the two parts of the claystone package suggest a different depositional event for each.

Marine boundary clays do not show such complexity of features but most have a clay layer enriched in Pt group minerals, with shocked quartz grains and spherules (Alvarez et al 1988), which would suggest that they are derived from a similar source to terrestrial boundary clays. However, Rampino and Reynolds (1983) claim that the boundary clays at Denmark, Gubbio, Spain and El Kef are neither mineralogically exotic nor distinct from clays above and below, and Hallam (1987) considers that the widespread occurrence of a marine boundary clay can be attributed to the sudden loss of the carbonate
component of the bottom sediment as a consequence of mass extinction. In some marine boundary sites there is a lithological shift precisely at the boundary with lowermost Tertiary sediments deposited in substantially shallower water than those of the uppermost Maastrichtian (Schmitz 1988), so that the boundary itself is marked by a hiatus.

2.4 IMPACT SIGNATURES

Three of the most significant “impact signatures” within the boundary clay are shocked quartz, tektites and anomalous levels of iridium.

2.41 Shocked Quartz

Shocked quartz grains occur at boundary sites globally but are most abundant and largest, with respect to individual grain size, at the North American sites (Izzet 1986). The method of forming shock induced lamellae in these quartz grains has been strongly debated. Officer and Drake (1985) suggest the features to be characteristic of normal tectonic and shock metamorphism, but De Silva and Sharpton (1988) see no evidence of volcanically induced overpressures great enough to generate this. Sharpton and Grieve (1990) consider that the shock features that have been detected in volcanic rocks, such as the presence of single lamellae, bear little resemblance to those diagnostic features found at meteorite impact structures and within the K-T- boundary claystone. They go on to state that “the link between shock metamorphism and meteorite impact...is now established beyond reasonable doubt”. Owen and Anders (1988) consider that the shocked quartz was derived from a petrologically diverse source region without a volcanic source consistent with a crustal or supracrustal origin. Cathodoluminescence investigations of the shocked quartz support a non volcanic origin (Owen et al 1990). Bohor (1988) is more specific and attributes the essentially quartz and feldspar mineralogy of the grains to impact on continental quartzites, metaquarzites and granites. Even
advocates of non-meteoritic causative mechanisms for the boundary event find difficulties in explaining through an endogenous cause the production and distribution of shocked quartz at the boundary (McCartney et al 1990).

2.42 Tektites

Tektites are glassy melt droplets formed by instantaneous fusion of terrestrial rocks during large-scale hypervelocity impact events (Izzet et al 1991). These are found at numerous boundary sites but with varying mineralogies, shapes and sizes. Those found at sites in Haiti have a composition that can be explained by the melting of heterogeneous carbonate and silicate rocks, not derived by volcanic processes (Blum and Chamberlain 1992). They indicate formation by fusion of anhydrite or gypsum-rich evaporite sediments in the presence of high silica melts, derived from the melting of continental crust, consistent with derivation from the Chicxulub crater in Yucatan (Sigurdsson et al 1992). In the Raton basin, the lower layer of the boundary clay package contains hollow spherules with teardrop and splash shapes which resemble microtektites; vesicles in this layer may also be altered impact glasses (Bohor 1988). At Dogie Creek, Wyoming, goyazite spherules occur, thought to be preformed, impact related bodies deposited through atmospheric fall out. These are somewhat replaced but more easy to identify than at other western interior boundary sites, where they have been altered to kaolinite (Bohor et al 1987). Tektites at Beloc and Arroyo el Mimbral have a $^{40}\text{Ar}/^{39}\text{Ar}$ age indistinguishable from the glassy melt rock that occurs beneath the impact breccia within the Chicxulub crater (Swisher et al 1992). These are coarse grained in the basal part of the sequence, but are amalgamated in to lenses in the upper part. It is suggested that the microtektites formed an initially pure layer at the base of the sequence, then this was reworked by a tsunami wave.

2.43 Iridium

It was the discovery that Cretaceous-Tertiary boundary sites in Denmark, Italy and New Zealand contained anomalously high levels of iridium (Figure 2.43)
that led Alvarez (1980) to postulate that the events associated with the boundary had an extra-terrestrial cause. Iridium is a platinum group metal which is depleted in the Earth's crust relative to its cosmic abundance, but relatively concentrated in chondritic type meteorites. The crustal iridium abundance is less than 0.1 ppb, which is generally thought to be too small to be the source for raised levels found world wide at the boundary (Crockett and Yuo 1979). These anomalous levels are at least ten times and generally one hundred times higher than any other iridium concentration peaks found in the Phanerozoic (Orth and Attrep 1988), even those associated with other extinction boundaries (Orth et al 1990).

Over fifty K/T boundary sites with raised iridium levels (figure 2.43) had been discovered by 1984 (Alvarez 1984) and by 1988 twenty such sites had been identified within terrestrial sites in the western interior of North America alone (Izzet 1988).

2.44 Other Signatures

It is not just iridium that occurs in exceptionally high amounts at the boundary. A number of workers have identified a range of metals at boundary sites that are present in amounts above those of normal background levels. Gilmour and Anders (1988) detected enrichments of nickel, gold, platinum, arsenic and antimony at seven widely distributed boundary sites. These all had an approximately constant proportion to iridium, implying that they were derived from the same source. Bohor (1988) found raised levels of nickel and iron in what he termed 'extra-terrestrial' amounts in magnesioferrite crystals at marine and non-marine boundary sites. He suggested that these were derived by condensation from a cloud of vaporised bolide and stated that such crystals had also been detected beneath other impact structures on earth (Bohor 1990). Working in the Raton basin, Gilmore et al (1984) found raised levels of scandium, titanium and
chromium as well as iridium in the boundary claystone. Within the Zumaya boundary sections in Spain, Margolis (1990) discovered the boundary marl to be enriched in iridium, platinum, nickel, chromium and arsenic concentrated in specific mineral phases and concluded that they were impact derived materials similar to those in a chondritic fireball or ablation debris. De Paolo et al. (1983) found isotopic evidence for foreign detritus in the marine boundary clay from Caravaca as well as low rare earth element concentrations and high nickel concentrations, which they viewed as evidence to support the hypothesis of a terminal Cretaceous impact, with the impact most probably occurring on oceanic crust.

Izzet (1990), working in North America found that the suite of elements in the boundary claystone was similar to that in tonsteins except for the anomalously high values of platinum group elements such as iridium. He was also able to detect differences between the impact layer and boundary claystone of the boundary package; iridium was found to be most abundant in the impact layer and much depleted in the claystone below suggesting that the lower layer may not be derived from altered impact material.

Other workers have found metal enrichments at the K/T boundary which they have perceived as being, at least in part, terrestrially derived. Hallam (1987) claimed that adsorption on to kerogen and low sedimentation rates had played a role in controlling enrichment levels at the boundary, but could not by themselves account for the global phenomenon observed.

Officer and Drake (1985), studying sites at Stevns Klint in Denmark, found that although iridium was present at raised levels at the boundary, it also occurred at levels above background for a considerable depth interval above and below this. They also saw this phenomenon at some oceanic sites and in the Texas sections, and it has been observed in the Bavarian Alp boundary
sections (Graup 1988). Officer and Drake (1985) concluded that ‘iridium and other associated elements were not deposited instantaneously at all sites at K/T time. Excess influx occurred on the order of 10,000 to 100,000 years.’ Amongst these associated elements were arsenic and antimony, occurring in excess of what would be expected for a meteoritic source and this led Officer and Drake (1985) to advocate a volcanic source. Zoller et al. (1983) found that airborne particles from the hot spot volcano Kilaueua were enriched in iridium by a factor of 10,000 to 20,000 times the concentration of normal Hawaiian basalts, and comparable to concentrations associated with meteorites supporting the volcanic source theory.

Gilmour et al. (1990) discovered that boundary clays showed enrichments of arsenic, antimony and zinc at 10-100 times that of the Cretaceous background. They concluded that the source was not meteoritic, as the ratios of these elements to iridium were considerably higher than those found in meteorites, and suggested that the target rock may have been enriched in arsenic, antimony and zinc or that there could have been some kind of sea water source. The trace element patterns they found could not be accounted for by volcanic sources. Kerr (1981) reports that strong ocean bottom currents stirred by climatic changes associated with extinctions might have winnowed away lighter particles leaving heavier particles, such as iridium, concentrated in a layer. Schmitz (1988) considers that some of the concentrations of noble metals observed at marine boundary sites may have accumulated thousands of years prior to the close of the Cretaceous and might have precipitated from marine waters. However, he does also state that a chondritic asteroid of approximately 10km. in diameter would contain 400 times more iridium than in the entire present day oceans, and that the Ir-rich marine clay could be related to metal absorbing algal matter that occurs in abundance in basal parts of the boundary clay.
Tredoux et al (1988) analysed the boundary clay from sites in Denmark, South Africa and New Zealand and found it to be heterogeneous with variations between sites being more common than similarities. Such differences are difficult to explain by secondary alteration of an originally chemically homogeneous deposit and they concluded that the source for the boundary clay was terrestrial, late Cretaceous volcanism. Keith (1982) questions the extra-terrestrial origin for iridium at boundary sites because of the variable oxidation states found at these sites and suggests that it is derived from stagnant ocean deposits formed under anaerobic conditions. He also notes that there are other iridium anomalies in the geological record related to anaerobic sediments such as pyrites and coals, and cites the Bonarelli bed of pyritic bitumen, which occurs 240m. below the Cretaceous-Tertiary boundary near Gubbio, which contains greater concentrations of iridium than the boundary clay itself. However this does not explain non-marine iridium anomalies. It is possible to calculate $^{187}\text{Os}:^{186}\text{Os}$ ratios to determine the source for iridium found at boundary sites (Turekian 1982). Using this method Luck and Turekian (1983) established that excess iridium was definitely not crustally derived but could come from a mantle or meteoritic source.

2.5 ATMOSPHERIC PERTURBATIONS

The presence of the boundary clay world-wide, and the other phenomena that it contains, yield evidence which can be used to ascertain the cause of events that occurred at the end of the Cretaceous. However, it is also important to look at the more long term effects of these event(s) and the ways in which they altered the atmosphere, oceanic and terrestrial environments on earth.

If a bolide did hit the earth at the end of the Cretaceous, it would have caused tremendous damage to the equilibrium of the earth’s atmospheric chemistry
and circulation as it plummeted towards its final resting place, in a time span of less than one second. Initial effects, occurring within hours of the impact, would be an increase in atmospheric pressure and a rise in air temperature of approximately 1°C (Emiliani et al. 1981). Passage of the impactor would cause shock heating of the atmosphere leading to formation of NO from the high temperature reaction between O₂ and N₂ (Prinn and Fegley 1988). This presumes that the impactor was less than a certain critical mass and size, so that speeds greater than the earth's escape velocity were not reached, otherwise shocked atmosphere would be able to escape from the earth's gravity field (Vickery and Melosh 1990). Interaction of the hot ejecta plume with the atmosphere, together with widely dispersed ejecta re-entering the atmosphere, would also facilitate NO production (Zahnle 1990). Theoretical and experimental techniques previously applied to the study of lightning and space craft re-entry, show that large amounts of NO released in to the atmosphere are soon converted to NO₂, N₂O₄, HNO₂ and HNO₃, with greatest concentrations at or near the site of impact (Prinn 1988).

The reaction producing NO₂ in the stratosphere also forms ozone. Ozone acts as a barrier to incoming ultra-violet radiation causing decreases in the amount of solar radiation reaching the earth's surface (Reid 1977). Consequently, cooling is experienced, as well as inhibition of photosynthesis as a result of diminished solar radiation.

Nitrogen compounds in the atmosphere would eventually form acid rain, atmospherically distributed on a global scale. Other toxic compounds would form through nitrate complexing with impactor derived heavy metals (Wdowiak 1988) including cyanides (Hsu 1986). These would have devastating effects on terrestrial and marine environments, although it is debatable whether such compounds would have been formed in amounts copious enough to produce lethal concentrations. Nitrogen with a
composition 10% heavier than that of normal background isotopes is found in the basal layer of boundary sites in New Zealand. This composition suggests that the nitrate it was derived from may have come from combustion of atmospheric nitrogen, and the fact that it is in the basal layer implies that acid rain was one of the first effects of the impact (Gilmour and Boyd 1988). Acid rain-out leads to foliar damage (Prinn and Fegley 1987), increased continental weathering (McDougall 1988) and acidification of the upper layer of the oceans (Hsu 1982). Nitrogen derived acid rain would be augmented by that which was CO₂ and SO₂ derived. A possible source for the CO₂ is vaporisation of the impact terrain, which could yield up to an estimated 10^{15} moles if such a terrain were composed of carbonate marl (Sigurdsson et al. 1991). As well as exacerbating the effects of the nitrogen derived acid rain, the carbon dioxide itself would also trigger global warming as it is the principal greenhouse gas (Baur 1988); this would be augmented in the short term by water vapour. Carbon dioxide may also have been released into the atmosphere at the close of the Cretaceous by the Deccan eruptions in southern India (Caldeira and Rampino 1990).

In complete contrast to these increases in CO₂, the widespread marine regressions at the close of the Cretaceous would have afforded an expansion of terrestrial ecosystems and consequent increased levels of photosynthesis, resulting in a decrease in CO₂ levels, an anti-Greenhouse effect. It is not just a simple increase in certain atmospheric gases that was experienced at the Cretaceous-Tertiary boundary, but a complex conflict of increases and decreases derived from a number of sources. The situation is further complicated by the seasonal timing of these events. This is important as it determines the changes and stresses occurring in the atmosphere in the different hemispheres. For example, an autumn impact in the northern hemisphere, when organisms are entering periods of hibernation and dormancy, would have had less effect on the terrestrial ecosystem than a
spring impact, a time when organisms are coming out of hibernation and dormancy. Airborne pollutants have least effect when plants are dormant in winter; with reduced atmospheric gas exchange most trees would have minimum susceptibility to non-corrosive air pollution (Tinus 1988).

An abundance of nitrogen compounds, particularly in acid rain, readily leads to the formation of nitrate compounds. These would have been able to complex with both the heavy metals derived from a chondritic meteorite (Wdowiak 1988) and with soil trace metals (Prinn and Fegley 1987). Such compounds are highly toxic.

An increase in certain chemical compounds in the earth's atmosphere would not be the only phenomenon to adversely effect the global environment. The impact would eject vast amounts of dust in to the atmosphere, forming Earth-enveloping clouds able to intercept sunlight and cause substantial global cooling, although probably not global freezing (Covey et al 1990). Large quantities of dust would only remain in the atmosphere for a maximum of up to six months, because of the particle density and coagulation sticking probability (Toon et al 1981). Increases in atmospheric moisture at the time, from an oceanic impact, may even mean that the existence of the earth enveloping dust cloud was less than six months. This so called 'nuclear winter' scenario could have been exacerbated by soot from widespread fires. Soot in the atmosphere would lengthen the period of darkness by its greater optical depth (Wolbach et al 1988), which enables it to absorb sunlight more effectively. Sulphate aerosols derived from the degassing of evaporite rich sediments may also have contributed to the decline in global surface temperatures, even prolonging them for several years because of the time dependant conversion of sulphur dioxide to sulphuric acid aerosol (Sigurdsson et al 1992). However, after rain out, remaining water vapour and clouds in the stratosphere could contribute to a rise in global
temperatures, exacerbating the greenhouse condition and persisting until photochemical and diffusion processes in the upper stratosphere had re-established equilibrium.

Ejecta from the bolide impact could well be spewed out beyond the earth's atmosphere and sent into orbit. This would be dependent on the trajectory dynamics of the bolide itself and subsequent trajectory of the dust cloud; high angle impacts would facilitate escape of ejecta from the atmosphere. If material entered into earth orbit it would have a longer residency time than that in the stratosphere, but the same sunlight inhibiting affects thus prolonging the climatic affects of the impact.

If oceanic temperatures decreased considerably before the boundary then this could result in restructuring of atmospheric motions (McGuirk 1979) or, in extreme conditions, the development of drought conditions over the continents; application of steady state models to a postulated drop in oceanic temperature yields quantitative estimates of up to 45% decrease in precipitation over continental areas.

2.6 OCEANIC PERTURBATIONS
Extinctions occurring in the oceanic realm at, and prior to, the Cretaceous-Tertiary boundary (Keller 1988) led to a decrease in biomass, with subsequent decrease in carbon dioxide available for global chemical circulation. Marine primary productivity seems to have been reduced for approximately 500,000 years after the boundary event (Rampino and Volk 1988) leading to the so-called 'Strangelove ocean' with its negative perturbation in carbon isotope values for the planktic fraction of sediments, and reduced fraction of dissolved carbonate ions in surface waters (Hsu 1988). Interpretation of stable carbon and oxygen isotopes at and after the boundary seems to give
conflicting results. Smit et al. (1988) have recorded a decrease in δ18O just above the ejecta layer. Such a decrease implies a warming with no evidence for a brief 'nuclear winter' cooling. Hsu (1982) has detected a 5°C cooling on the scale of a few hundred years from oxygen isotopes in the boundary layer. Following this period, he detects a 10°C warming for 30-50,000 years after the boundary. However, the period of cold and dark may have been too brief to be recorded in the marine geological record. D'Hondt and Linger (1988) have estimated a post boundary warming of 2 to 3°C from the recorded decreases in δ18O, and find no evidence for cooling at the boundary. However Wolfe (1991), studying the Tea Pot Dome terrestrial boundary site in Wyoming, found evidence for freezing at the boundary from the cuticle structure of fossil pond plants. Prior to the boundary δ18O trends indicate a late Maastrichtian cooling then warming (McLean 1978 and section 6.52).

Mechanisms cited for the extinctions in the oceanic realm revolve around chemical pollution and increased acidity. Acidification is mainly attributed to CO2 variously derived from lowering of the carbonate compensation depth and dissolution of calcium carbonate (Boston 1988), volcanism (Hanson 1990), and global wild fires (Gilmour et al. 1988). Other polluting agents suggested have been cyanide released by the falling impactor (Hsu 1980) and nitrous oxides. Tropical species would have been most affected by this pollution, because oceanic circulation patterns concentrate toxins here, although they would have been distributed globally by such patterns (Prinn and Fegley 1985).

The result of the elimination of most marine phytoplankton at the Cretaceous-Tertiary boundary could have caused a reduction in dimethyl sulphide production. This biogenic gas is a major precursor of cloud condensation nuclei over the oceans, so a reduction would result in a low reflectivity cloud canopy and warming of the earth's surface by up to 6°C, again exacerbating any greenhouse conditions (Rampino and Volk 1988).
2.7 TERRESTRIAL EFFECTS

Initial effects in the terrestrial realm, of an oceanic bolide impact near to the North American continent, would probably be a flooding of marginal lands (Fastovsky et al. 1989a). A hiatus at the base of Tertiary sequences in Montana and North Dakota would seem to support this theory (Favstovsky et al. 1989).

Longer term adverse effects would depend on acid rain, from various sources, which would initiate massive weathering of continental soils. For example, CO$_2$-rich rain with an enhanced water supply could result in an increase in primary production and root respiration rates of terrestrial plants, which elevates CO$_2$ concentration further. Together with the greater ground water flow and raised soil temperature, this combines to produce higher rates of chemical weathering in silicate and carbonate rocks (Prinn and Fegley 1987). Soils in such environments are characterised by higher ratios of insoluble to more soluble metals. Palaeosols at the boundary in Montana indicate deep weathering and a change to a more humid climate, the former of which has been attributed to acid rain (Retallack et al. 1987). Increased $^{87}$Sr: $^{86}$Sr ratios found in marine boundary sections (McDougall 1988) also indicates large amounts of continental weathering by acid rain.

Another possible effect of acid rain at the boundary is paludification of terrestrial environments (Klinger 1988), although there appears to be some circularity in the argument as paludal areas are themselves acidic and may simply be related to increased precipitation, not necessarily acidity. Extensive paludification explains the abundance of water plants at boundary sites in Montana and Wyoming (but these have also been discovered in sediments prior to the boundary, see 4.43), as well as the fern spore spike which is observed throughout Western Interior boundary locations. Such a
shift to wetter environments would have a negative effect on large terrestrial animals with extensive habitat requirements, due to the low trace element content of bog plants. Other more wide-ranging effects of paludification might be the lowering of atmospheric CO₂, because of the large amounts of carbon sequestered in bogs, and a decreased run off and nutrient flow to the oceans. However, vast areas of bogs would be required to have any such impact.

Not only would rain-out after a meteorite impact be highly acidic, but it would also include transition metals as soluble metal nitrates, which are considered to be the most toxic form. Nickel nitrates derived from meteorite ablation and subsequent water-ion complexing with nitric acid rain can cause chlorosis by inducing iron deficiency (Davenport et al 1990). This would severely inhibit floral recovery following the boundary event. The heavy metal contamination of top soil would exacerbate this (Wdowiak 1988) and could ultimately result in desertification and a change in the Earth’s albedo. It is also possible to mobilise soil trace metals through acidification, again resulting in toxicosis and increasing the degenerative effects of meteorite-impact derived heavy metal nitrates.

2.8 FIRE

A soot layer has been discovered at boundary sites in New Zealand, Europe and the U.S.A. (Wolbach et al 1988) with an estimated global total weight of 7x10^{16}g. (Gilmour et al 1988). It has been suggested that this soot was derived from combustion of terrestrial vegetation in wildfires triggered by a combination of radiation of the impact fire ball and the cloud of rock vapour ejected, as well as fall out of hot particles from the cloud (Wolbach et al 1985). This theory is supported by a chemical analysis of the soot (Gilmour and Guenther 1988). This reveals retene in large amounts which is characteristic of higher plants, especially temperate conifers and tropical angiosperms,
particularly when they are burned in oxygen poor conditions in large fires, which also increases soot yield. Coronene has also been detected, which is only typical of wood combustion at high temperatures again found in large fires. The soot also has a $\delta^{13}$C value close to the average for modern trees. Other theories as to the source of this carbon suggest that it may have been derived from the bolide itself or from fossil carbon from the impact crater (Wolbach et al. 1985), but evidence cited above does not support this. Another hypothesis sees combustion of oil-rich marine sediments, emergent with regression of late Cretaceous seas, as a source (Cisowski and Fuller 1986), but this may not account for the high percentages of retene and coronene observed.

Although it appears that the soot is derived from vegetation, the occurrence of a global scale wild fire is contentious (Argyle et al. 1986). The spread of such a fire would be terminated by the presence of seas, large lakes and topographic highs, which act as physical barriers, as well as changes in wind direction and increased precipitation, resulting from the large amount of impact derived particles and water in the atmosphere (Tinus and Roddy 1990). There is also a distinct lack of soot and fusain found at boundary sites in North America, where it tends to be the exception rather than the norm, indicating that wild fires at the boundary were not of a global scale.

Living vegetation has a low combustibility but dead trees killed by depressed temperatures and decreased levels of sunlight, as a result of the boundary event, would be highly flammable and could easily be ignited by a lightning strike. If trees were killed by such conditions following the impact, then the soot would not be synchronous with the iridium spike, as is seen in boundary sections (Wolbach et al. 1988). The boundary sections in New Zealand contain carbon in the lowermost 0.3cm. of the Cretaceous-Tertiary boundary clay implying that fires began before ejecta had settled (Wolbach et al. 1990).
If large stands of forest were destroyed by wild fires at the Cretaceous-Tertiary boundary, it does not necessarily follow that subsequent recovery of flora would be a slow process on an evolutionary time scale. Evidence from late Cretaceous sediments indicates that fires were common at this time and that Cretaceous vegetation was already adapted to a fire ecology enabling relatively rapid recovery after lethal conflagrations (Spicer pers. comm. 1992).

With the burning of vast amounts of organic material, extra toxic stresses would have been placed on the terrestrial environment by the formation of polynuclear aromatic hydrocarbons (PAH) which have been recognised at boundary sites in New Zealand, Italy and Denmark (Venkatesan and Dahl 1989). These can generate organic compounds capable of contaminating ash, surface waters and bottom material (Gilmour et al 1990). Environmental effects of these pollutants include O₂ depletion, toxicity to aquatic life and ground water contamination, due to the hydrophilic nature of PAH. Such pyrotoxins are mutagenic, affecting plants and animals for generations (Wolbach et al 1990).

The presence of large amounts of soot in the atmosphere, following the proposed fire, and its consequent events would have a devastating effect on the Earth. Soot particles are smaller, settle more slowly, are better light absorbers and are more resistant to rain-out than other ejecta lengthening any period of darkness (Wolbach et al 1988). Large scale fires would release nitrogen dioxide, carbon monoxide and organic pyrotoxins in to the atmosphere causing death of plants and animals and possibly explaining selectivity in extinctions. Effects could have persisted after the skies had cleared. Raised carbon dioxide levels would cause global warming and the continued presence of mutagenic pyrotoxins could lead to accelerated evolutionary damage.
2.9 TERRESTRIAL CAUSES

Most theories that do not advocate an extra-terrestrial cause for Cretaceous-Tertiary boundary events focus on more long term global phenomena. Courtillot et al. (1988) consider that extensive volcanism, sea floor spreading, polar wander and frequency of geomagnetic reversals must all be considered when looking at the shorter boundary time frame.

Arguments against an extra-terrestrial event at the close of the Cretaceous cite gradual and step wise extinctions prior to the boundary as proof that there was no single catastrophic event. Maurrasse (1988) has detected stepwise planktonic extinctions in sections in Haiti and Cuba. Keller and Barrera (1990) note that planktonic forams observed in marine boundary sections undergo extinctions 300,000 to 400,000 years before the boundary itself. Archibald and Bryant (1990) invoke a geologically rapid but non-catastrophic change such as habitat loss to explain the pattern of extinctions in non marine vertebrates across the boundary in Montana. These are just a few of many such examples (for example see Sloan 1988, Gallagher 1991, Kauffman 1982).

There was certainly extensive volcanism in the late Cretaceous. Such intense volcanism and emissions would have caused acid rain, a reduction in oceanic pH, global temperature change and ozone layer depletion; much the same effects as have been described for a bolide impact, but with a solely endogenous cause. Stothers and Rampino (1990) suggested that the intense volcanism was actually induced by comet impacts, which they believe disturbed mantle circulation. Hansen (1990) suggests one long volcanic event over 350,000 years, most likely that which formed the Deccan Traps, which caused volcanic dust veils, oceanic temperature fluctuations, emission of poisonous compounds and outgassing of CO2 with associated secondary effects.
McCartney et al (1990) have postulated a mechanism for such enormous basaltic outpourings. They describe a coupled core-mantle thermal release via periodically accelerated plume activity; this sends plumes of iridium-rich mantle material into the lithosphere. When it reaches the surface this material induces increased tectonism. Although it is believed that such a mechanism could account for the increased levels of iridium observed, the presence of shocked quartz can not be explained. Tredoux et al (1988) believe that the complex geochemical anomalies of the boundary clay can be easily explained by a volcanic source, and this has been reiterated by Courtillot et al (1990). However, although the Deccan traps poured out vast quantities of basaltic lava, emitting with this large amounts of CO₂, it appears that this would not have accounted for the global warming observed at this time. From the volume of basalt extruded, McLean (1985a,b) has estimated that a total of 5x10¹⁷ mols of CO₂ would have been released in to the atmosphere. This is likely to be an overestimate (Caldeira and Rampino 1988), but calculations by Caldeira and Rampino (1990) suggest that even this would have only been associated with a 'greenhouse warming' of less than 2°C, not enough to cause the mass extinctions observed. It isn't only on the Indian sub-continent that there were volcanic outpourings at the Cretaceous-Tertiary boundary, volcanic and altered ash occurs at the boundary in cores from the Weddell sea in the South Atlantic (Wise 1988).

Sea level changes at the close of the Cretaceous have also been used to explain the phenomena observed at the boundary. Hallam (1987) attributes these phenomena to a combination of volcanism and marine regression which caused a reduction of neritic habitats and seasonal extremes on land. Schmitz (1988) has recognised a lithological shift in marine sediments at the boundary itself with lowermost Tertiary deposits laid down in substantially shallower water than those of the latest Maastrichtian, supporting this hypothesis. Keith (1982) describes a 'stagnant ocean' in the late Cretaceous generated by climatic
warming and a subsequent decreased Earth albedo. This facilitates an increase in the sinking of warm evaporitic brines leading to a raising of the oxygen minimum zone and catastrophic mixing of surface waters with poisonous sulphide-rich deep waters. Trace elements occurring at raised levels in these stagnant waters would include those of the platinum group.

Gartner and Keany (1978) suggested what they termed the 'Arctic spillover hypothesis' to explain K-T boundary extinctions. In this hypothesis the Arctic ocean is supposed to have become isolated from the rest of the world oceans during the late Cretaceous and then became decreasingly saline. When rifting occurred in the North Atlantic 65 million years ago, this lighter Arctic water was able to spill out and cover oceans globally with a surface of low salinity water. This supposedly caused extinction of stenohaline plankton, then oxygen depletion lower in the water column and would have triggered rapid and intense climatic changes and associated ecological disasters (Gartner and McGuirk 1979). However, it seems improbable that the volume of water that would be contained in the Arctic ocean would be great enough to sufficiently cover all the World's oceans, triggering marine extinctions and subsequent climate change.

There are other theories used to explain the Cretaceous-Tertiary boundary events. Russell and Tucker (1971) determined that supernovae explosions with consequent fluxes of cosmic, gamma and X rays would cause significant perturbations in the earth's atmosphere and provoke the effects observed at the boundary. Simpson (1966) suggested that phases of extinction in earth history could be related to geomagnetic polarity reversals which ultimately modulate the cosmic ray influx impinging on the earth's surface and climate.

Of all the theories invoked to explain the Cretaceous-Tertiary boundary event, none seem to fit all the evidence collected better than the meteorite impact hypothesis. This does not mean to say that the other occurrences
described did not contribute to the phenomena observed. All theories must be viewed collectively and not in isolation. The sea level changes at the close of the Cretaceous and the basaltic outpourings of the Deccan traps certainly had their own adverse effects on the global environment and contributed to the changing terrestrial and marine conditions experienced throughout the latest Mesozoic. A meteorite impact was merely the 'coup de grace' in a succession of coincidental major earth events.
A PROBABLE K-T BOUNDARY IMPACT CRATERS

△ PROBABLY TSUNAMI DEPOSITS ASSOCIATED WITH IMPACT

K-T SECTIONS WITH COMPLEX BOUNDARY CLAY PACKAGE

FIGURE 2.3: LOCATION OF SOME OBSERVED K-T BOUNDARY PHENOMENA
PLATE 2.3A: THE K-T BOUNDARY CLAYSTONE
MADRID, RATON BASIN

PLATE 2.3B: CLOSE UP OF COMPLEX K-T BOUNDARY CLAY FROM TEA POT DOME (scale x2)
**FIGURE 2.43: GLOBAL K-T BOUNDARY IRIDIUM ANOMALY SITES**

CHAPTER THREE

SEDIMENTOLOGY AND TAPHONOMY
CHAPTER THREE

SEDIMENTOLOGY AND TAPHONOMY

3.1 BASIN DESCRIPTIONS AND HISTORY

3.11 Introduction

There are few outcrops of early Palaeocene rock to be found in Europe because here the Cretaceous-Tertiary boundary is often marked by a hiatus in deposition. The situation, however, is completely different in the United States where thousands of metres of sediments were deposited in the western interior at this time (Sloan 1987). The erosional remnants of this former continental sheet of sediments, which extended from the Rocky Mountains to the Gulf Coastal plains, are now all the evidence that is left. During the late Cretaceous, the whole area was occupied by a foreland basin but when Laramide deformation was initiated in the Maastrichtian, this foreland province was broken up into discrete local basins, sedimentologically isolated and separated by strongly emergent uplifts serving as localised sediment sources (Dickinson et al. 1988).

Synchronous with the emergence of the Rocky Mountains was the retreat of the Western Interior Late Cretaceous continental seaway. It left behind a landscape of low relief drained by streams meandering over swamp-like lowlands (Blackstone 1975) but as Laramide deformation progressed and intensified, discrete basinal depocentres developed (McGrew 1971).
The Williston, Powder River and Raton Basins (Figures 3.1a) were all “perimeter basins” during the Laramide orogeny, that is they were the easternmost of those along the west flank of the newly emerging Rocky Mountains. They comprised broad bowls with low structural relief along their flanks, merging with the stable continental craton (Dickinson et al 1988). Figure 3.1b illustrates the stratigraphic relationships between these basins.

3.12 Raton Basin
The Raton Basin is located in the east-central region of the New Mexico-Colorado border, on the western edge of the Great Plains (Figure 3.12A). It is a Laramide structural basin bounded in the west by the Sangre de Cristo uplift, in the north by the Wet Mountains uplift and the Apishapa Arch and on the east by the Sierra Grande Arch. It is asymmetric with its longer axis to the west and is separated structurally by the Cimarron, Arch which facilitated greater sedimentation in the north of the basin in late Cretaceous and early Tertiary times with maximum sediment thickness in this area of around twelve thousand feet (Baltz 1965). These sediments were essentially derived from uplifted Pre-Cambrian terrain to the west of the basin, the Brazos-Sangre de Cristo uplift (Smith et al 1985). This uplift was amagmatic in northern New Mexico. Sediments were brought down from the uplifted areas to the west by easterly and south-easterly flowing river systems that meandered across a fluvial dominated deltaic complex, prograding north east during the last regression of the continental seaway from the Western Interior (Close 1991).

The Raton Basin was initiated as a foreland basin in the latest Cretaceous and evolved into an intermontane basin during the earliest Tertiary (Flores 1987). Sediments deposited from the Campanian to the end of the Palaeocene have
been divided into three units on the basis of their environment of deposition (Lee and Knowlton 1917, Pillmore et al 1984):

(1) PIERRE SHALE: Campanian - Maastrichtian. Comprises prodeltaic and offshore environments of the Western Interior seaway.

(2) TRINIDAD SANDSTONE/VERMEJO FORMATION: Maastrichtian deltaic and barrier bar deposits, together with fluviodeltaic plains and back barriers formed following regression of the seaway, plus syntectonic fills from the Laramide orogeny.

(3) RATON FORMATION/POISON CANYON FORMATION: Intertonguing Maastrichtian and Palaeocene deposits of fluviual floodplains and swamps.

The Cretaceous-Tertiary boundary is very well defined (Newman 1987) and occurs in the lower part of the Raton Formation, which was further divided by Lee and Knowlton (1917) into a basal conglomerate, a lower coal zone, a cliff or barren series and an upper coal zone with the boundary itself occurring just beneath the cliff-forming barren series and the upper coal zone. Pillmore and Flores (1987) modified this subdivision so that it comprised only the Lower Coal Zone, the cliff-forming Barren Series and the Upper Coal Zone. These 'packages' comprise:

(1) LOWER COAL ZONE: A ledge-forming basal conglomerate and channel sandstone derived from braided streams and uplift in the west (Pillmore et al 1984) grading up into mudstone, siltstone, carbonaceous shale and coal interbedded with lenticular channel and tabular crevasse splay sandstone beds. The Cretaceous-Tertiary boundary occurs near the top of this zone.
(2) CLIFF FORMING BARREN SERIES: Thick stacked channel sandstones, devoid of coal, formed by meandering streams with high bedloads.

(3) UPPER COAL ZONE: Siltstone, carbonaceous shale and mudstone interbedded with channel and crevasse splay sandstone with coal beds up to four metres thick. Environments of deposition were similar to those of the lower coal zone, upper alluvial plain with discrete meander belt and floodplain environments.
(See figure 3.12B)

The Cretaceous-Tertiary boundary has been identified at over twenty sites within the basin (Pillmore and Fleming 1990) preserved only in ponds and coal swamps where the low energy environment prevented the likelihood of erosion prior to deposition of overlying sediments (Gilmore et al 1984).

Flores (1987) placed another interpretation on the Raton Formation, recognising three coarsening upwards intervals within the alluvial plain facies from fine, coal-rich facies to sand-dominated facies. He interpreted these as deposits of lower gradient and higher gradient; the lower gradient representing fluvial systems comprising meandering streams and the higher gradient, the product of braided streams with development related to syntectonic movements to the west. Sand-dominated facies can be equated to high bedload meandering streams formed during tectonic uplift in the source area and diminished basin subsidence, whereas the fine detritus is indicative of a stable source area and increasing basin subsidence.
3.13 Powder River Basin

The Powder River Basin forms a 22,000 square metre broadly rectangular area stretching from southern east-central Montana down through eastern Wyoming, with its southernmost limit in central Wyoming (Figure 3.13). In this state it is bordered by the Bighorn Mountains to the west; the Casper Arch, Laramie Mountains and Hartville Uplift to the south and the Black hills to the east. In Montana it is separated from the Williston Basin by the Cedar Creek Anticline to the north east and is bounded in the north by the Miles City Arch, Ashland Syncline and Bull Mountain Syncline. As a basin it attained its present structural configuration during the Laramide orogeny. Sediments of Cretaceous-Tertiary boundary transition age were transported by fluvial systems draining surrounding upland areas to the south and west in to the retreating Western Interior sea. Uplifts surrounding the basin were formed before the close of the Mesozoic, at the initiation of mountain building to the west, but were topographically subdued until later in the Palaeocene (Flores and Hanley 1984). The 6560 ft maximum thickness of these sediments was attained near the structural axis of the basin along its western flank (Flores and Ethridge 1985).

The area of study concentrated on the southern part of the basin near to and at the type locality of the Lance Formation (Stanton 1910), which is the name assigned to rocks of the latest Cretaceous and earliest Palaeocene in the region. They are equivalent to the Hell Creek Formation of the Williston Basin. Like the rocks of the Hell Creek Formation, they are characteristically of a sombre colour and comprise terrestrial alluvial flood plain sediments of massive sandstones interbedded with shales (Thorn and Dobb 1924, Dorf 1940)
The overlying Palaeocene sediments are described using the same nomenclature as their counterparts in the Williston Basin. These belong to the Fort Union Formation which is subdivided in to the Tullock, Lebo shale and Tongue River Members. In this study it is only the sediments of the early Palaeocene, those of the Tullock member, which are of interest. The environment of deposition during Tullock times in the southern part of the basin was that of an alluvial flood plain with rivers flowing in a north easterly direction (Figure 3.14B). Consequent facies variations show a common inter-relationship of channel levee facies bounded by floodplain and backswamp facies, analogous to the Mahakam River of Borneo today (Flores 1986). In this area, the Tullock member is 305m thick but it thins to the north (Kent 1986). The Lebo shale member records the development of lacustrine conditions which achieved their maximum extent during Torrejonian to early Tiffanian times. This was controlled by increased basin subsidence, together with a decrease in sediment supply. The onset of these conditions was rapid and is recorded by a sharp contact with the underlying Tullock Formation (Yuretich 1989).

The contact between the Lance and Fort Union Formation is traditionally taken as the lowest persistent lignite bed overlying the highest occurrence of dinosaur remains (Calvert 1912, Brown 1952), just as it is in the Williston Basin. Problems of positioning the Cretaceous-Tertiary boundary within this sequence are similar to those experienced in the Williston Basin (see 3.14). Leffingwell (1971) placed the boundary near to the formational one on the basis of palynology, and at Lance Creek the contact between the late Cretaceous 'A' palynological zone and the earliest Palaeocene 'B' zone is 10m below the formational boundary, implying that the upper 10m of the Lance Formation in eastern Wyoming is of Palaeocene age (Cherven and Jacob
More recent methods of locating the boundary precisely have focused on the characteristic impact signatures of the boundary clay such as the iridium anomaly and shocked quartz grains (Bohor et al. 1987, Izzet 1990). These have proved to be successful, although not applicable to field geology.

### 3.14 Williston Basin

The Williston Basin underlies most of North Dakota and parts of the adjoining states and Canadian provinces (Figure 3.14A). It is a broadly oblong shaped intercratonic basin on the Canadian shield. In the south-east the north easterly trending Transcontinental Arch forms the subsurface basin margin, but to the north the margin is buried beneath glacial drift. It is separated from the more southerly Powder River Basin by the Black Hills, Cedar Creek Anticline, Sheep Mountain syncline, Miles City Arch and Cat Creek Anticline. However, this was not necessarily so during the Palaeocene (Belt et al. 1984) thus allowing drainage systems of the Powder River Basin to flow freely in to the Williston Basin. Palaeocene strata occur at the surface over most of the basin and dip at low angles of 1-2° towards the basin centre where the sediments are thickest (Cherven and Jacob 1985). There are two sources for these sediments, a volcanic source terrain to the west of the basin and a sedimentary source terrain from the fluvial systems to the south west (Flores and Kaplan 1985).

The study of flora in the Williston Basin was confined to a number of sites in the McGuire Creek and Hell Creek areas of east-central Montana, to the south of Fort Peck reservoir in Garfield and McCone counties; that is towards the south west-central region of the basin. Although in general, river systems within the basin seem to have had a broad north east and easterly direction of flow (Belt et al. 1984) palaeocurrent data of various workers (Lofgren et al. 1985).
1990, Fastovsky and Dott 1987) indicates that sediments in this particular area were transported and deposited by south easterly flowing fluvial systems with their sources in the Powder River Basin, which was then confluent with the Williston Basin (Sloan 1987), as well as local uplifted areas.

The depositional environments of sediments of the latest Cretaceous and earliest Palaeocene in the western part of the basin are broadly governed by regressive and transgressive phases of the Western Interior seaway to the east. Recent stratigraphic and radiometric studies in the area imply that the first major regression started in the latest Cretaceous and continued into the earliest Palaeocene. The shoreline retreated approximately 400km. from its original position in western North Dakota but that there was also a subsequent minor transgression at the end of the early Palaeocene (Cherven and Jacob 1985). Given these conditions the sediments deposited in the western part of the basin were predominantly associated with meandering river, low grade channels and broad alluvial plain facies (Beaumont 1979, Archibald et al 1982, Favstovsky 1987) [figure 3.14B].

Rocks of the latest Cretaceous and earliest Palaeocene are assigned to the Hell Creek Formation (Brown 1952). They are characteristically of a sombre colour and informally named the 'sombre beds'. They comprise siltstones, lenticular lignites, carbonaceous shales and sandy palaeochannel deposits (Archibald et al 1982). Rocks of the Palaeocene are assigned to the Fort Union Formation and a distinct colour change is recognised across the formational boundary to much lighter beds. In the west of the Williston Basin the Fort Union Formation is subdivided into:

1. The Tullock Member (Mantuan-Puercan age)
2. The Lebo Member (Torrejonian age)
(3) The Tongue River Member (late Torrejonian-Tiffanian age)
(Correlation with mammal age zones after Sloan 1987)

It is only the Tullock Member and lowermost part of the Lebo member, together with the uppermost Hell Creek Formation, that are relevant to this study.

A well documented rise in the water table (Favstovsky and McSweeney 1987, Retallack et al. 1987) is observed at the transition between the uppermost Hell Creek Formation and the Tullock Member of the Fort Union Formation. This is reflected by the onset of peat swamp development and evidence for broad expanses of ponded water deposits. Sediments arising from such a suite of environments tend to be generally fine grained with better developed lignites than in the Hell Creek Formation (Norton and Hall 1969). These river dominated deltaic settings graded coastward (easterly) in to barriers and seawards on to the continental shelf (Flores and Kaplan 1985) (figure 3.14B), whereas the rocks of the Tullock Formation record a marshy low lying alluvial plain (see for example Norton and Hall 1969, Favstovsky 1990). The Lebo member indicates the presence of widespread lacustrine environments later in the Palaeocene (Yuretich 1989).

The stratigraphic positioning of the Cretaceous-Tertiary boundary in this part of the Williston Basin is problematic. It was originally placed at "the lowest persistent bed of lignite above the last in place dinosaur bone" (Calvert 1912, Brown 1952, Frye 1969). Norton and Hall (1969) and Olts (1969) perceived it as analogous with the formational boundary between the Hell Creek and Fort Union Formations and placed it at "the base of the stratigraphically lowest laterally continuous bed of lignite of the lignites characterising the Tullock
Member" and this lignite was termed the 'Z coal'. However, the continental beds of these formations are notoriously laterally discontinuous (Hotton 1990, Favstovsky and Dott 1987) and Archibald et al. (1982) consider that the 'Z coal' can not be treated as an isochronous unit, as it is transgressive. Archibald and Lofgren (1990) believe that in McConé county (figure 3.14) the uppermost and thickest 'Z coal' in a suite of Fort Union coals marks the formational boundary, but that the Cretaceous-Tertiary boundary is marked by a lower, but not necessarily the lowest, lignite in the 'Z complex'. In Garfield County they consider the formational and Cretaceous-Tertiary boundary to be coincident with the lowest of the 'Z complex' coals. Palynological study of the rocks stratigraphically above and below the formational contact imply that the uppermost sediments of the Hell Creek Formation in the McGuire Creek area are of the earliest Palaeocene palynologic zone (Hotton 1988, Lofgren pers. comm. 1991). There is some circularity in the argument for using a palynological boundary demarcation when studying leaf megafossils. However, palynological evolution is necessarily different to leaf megafloral evolution due to heterobathmy, and fossil pollen is affected differently to leaf megafossils by climatic and taphonomic variables. This overcomes the circularity somewhat. Palynological zones can also be matched with mammalian zones affording another stratigraphic reference. For this study the Cretaceous-Tertiary boundary in the Williston Basin was taken at the base of the 'z complex' of coals in the uppermost Hell Creek Formation.

3.2 FIELD WORK TECHNIQUES
At each of twenty seven sites from the early Palaeocene, within the three basins, an initial assay was carried out to determine which beds bore organic material and leaf megafossils. Megafossils were collected as described (4.12).
To place these floras within the context of their depositional environment and to gain an idea of taphonomic problems which may affect interpretation, the section encompassing a leaf bearing unit was logged. This also allowed comparison between sites.

3.21 Problems with determining stratigraphic location of sites

It is not viable to assume that height above a datum level in a stratigraphic sequence is a direct representative of the age of a bed yielding a fossil flora, even when the datum level is well constrained. The age of a bed is not proportional to height above that datum, but in fact it is dependant on the rate of deposition of the sediments laid down between the datum level and the bed that is being studied. Within a general depositional environment, in this study an alluvial flood plain, depositional rates may be similar only over brief periods of time under stable conditions, but this can not be assumed. In this study a number of correlations were employed to allow stratigraphic positioning of floral sites to be as accurate as possible.

In the Raton Basin, sites within the Lower Coal Series (up to 2m above the boundary, KSD 91 7.0, KSD 91 8.0, KSD 91 9.0, KSD 91 10.0, KSD 91 11.0, KSD 91 12.0) could not be correlated lithologically because of the lateral heterogeneity of beds and the distances between each site. However, as sediments from this small part of the Lower Coal Series are essentially all fine to medium grained and from similar depositional environments, it is assumed that depositional rates did not vary much from site to site. In these cases height above the boundary was taken to be proportional to the relative ages of the beds bearing floras. Sites within the Barren series (KSD 91 3.0, KSD 91 4.0 and KSD 91 5.0) were defined stratigraphically by the palynological zonation described by Fleming (pers. comm. R.F. Fleming, 1991) and also by lithologic correlation
along Potato Canyon Road, as all three sites were cuttings along this road. For sites within the Upper Coal Zone (KSD 91 1.0 & KSD 91 2.0) lithologic correlation was possible to determine their relative ages, but more precise stratigraphic positioning came from core information provided by York Canyon Mine (pers. comm. R. Pillmore, 1991).

In the Powder River Basin lithologic correlation was possible for sites at Lance Creek (KSD 91 17.0 &18.0) and at Tea Pot Dome (KSD 93 1.0 & 2.0) but was not possible between the two areas. Height above the boundary datum level could also be measured for all these sites.

In the Williston Basin, lithologic correlation was possible for sites at McGuire Creek (KSD 91 20.0, KSD 91 22.0A,B,C). There were problems with the stratigraphic positioning of site KSD 91 21.0, but its relationship to the 'z' coal suggests that it is Late Cretaceous in age. For sites in the Hell Creek area (KSD 91 19.0, KSD 91 24.0, KSD 91 25.0) stratigraphic position was determined relative to alphabetically named coals in the Tullock Formation (see section 3.633) and reference to U.S.G.S. field note books detailing localities and relative ages of field sites and floras.

3.3 OBSERVATIONS AND DESCRIPTIONS OF LOGGED SECTIONS

The following descriptions relate to locational details and sedimentary logs, which can be found in appendices A and B respectively. Their locations are displayed diagramatically in figures 3.12A, 3.13 and 3.14A.
3.3.1 Raton Basin

KSD 91 1.0 York Canyon Mine: Leaf megafossils occur in a bed of massive fine sandy siltstone with intermittent clay laminations, that is approximately 400m above the Cretaceous-Tertiary boundary. These laminations are carbonaceous and are the sites of deposition for the fossil leaves. The unit is part of a fining up sequence of 4.5 metres vertical extent. It is underlain by a massive sandstone containing disseminated organic material and fossil wood and bark, preserved as impressions. Overlying the bed is a thin friable shale containing fragmented leaf material. This fining up package of sandstone-siltstone-shale is bounded both above and below by packages of broadly similar composition and features. The underlying sequence, however, only contains fragmented carbonaceous material in its coarser parts and the shale is far more carbonaceous with discontinuous, thin coal bands. The overlying fining up sequence is interrupted by a laterally continuous coal bed which occurs between the sandstone and sandy siltstone units. It appears that the deposition of coarse sediments was initiated, halted during a period of coal formation, and then rapidly resumed with a channel down-cutting into the coal. The basal bed of this section coarsens up from a claystone to siltstone and contains fragmented carbonaceous material and leaf megafossils which occur as thin mats.

KSD 91 2.0 York Canyon Mine: Leaf megafloras occur in two analogous beds in minor fining up cycles, three of which can be identified in this section. These are located approximately 380m above the boundary. These beds are of sandy siltstone with carbonaceous laminations concurrent with leaf fossils. They are overlain by carbonaceous shales containing fragmented organic material and thin coal layers. The uppermost cycle is topped by a laterally extensive coal and this is truncated at its upper surface by a fine sandstone of
variable thickness and with an erosional base, indicating the onset of higher energy erosive conditions, most probably connected with channel switching at this time and place on the flood plain.

**KSD 91 3.0 Potato Canyon Road:** An overall fining-up section preserves leaf megafossils near its base in a fine sandstone with thin clay intercalations of mudrock, at approximately 140m above the boundary. In overlying mudrocks there are also fragmented organics and twigs. Above these, coal lenses occur in a coarsening-up silty claystone which is capped by a coal bed. Organic-poor claystone dominates the upper part of the section.

**KSD 91 4.0 Potato Canyon Road:** Leaf megafossils occur in a cyclic sequence, approximately 200m above the boundary, where dominant laminated mudrocks alternate with massive sandstones. A sharp contact exists between the mudrocks and sandstones. Leaf fossils occur as individuals and there is little or no other carbonaceous material in the section. Overlying the cyclic sequence is a thick sandstone with a scoured base and trough cross stratification on a centimetre scale.

**KSD 91 5.0 Potato Canyon Road:** Leaf megafossils are preserved at the base of a fine sandstone that fines up to siltstone, at a stratigraphic position approximately 250m above the boundary. Intercalations of clay and fragmented carbonaceous material also occur within this unit. This is overlain by coals and non-organic mudrocks. At the upper limit of the section there is a reversion to predominantly coarse grained deposits.

**KSD 91 6.0 Old Raton Pass:** Only a few palms and some fragmented organic matter are preserved in coarse grained sediments above the boundary, although near the boundary sediments are fine grained. There is much
evidence for bioturbation with trace fossils visible on bedding planes (plate 3.31B). These are in full relief and appear to be a combination of crawling and resting traces, parallel to bedding. This, and the presence of a massive cross bedded sandstone just above the boundary, may account for the absence of leaf fossils.

**KSD 91 7.0 Berwind Canyon stream section:** Leaf megafossils occur throughout the section, mainly just above and 2m above the boundary, apart from a massive sandstone with scoured base which tops the sequence. The lower part of the section is fine grained comprising carbonaceous shales and coals, with the boundary clay package near the top. Although similar deposits occur above the boundary the characteristics of the sediments change considerably with the onset of Siltstone deposition. The siltstone fines up and yields a well preserved megaflora in its upper part, as well as twigs and fragmented leaves lower in the bed. An overlying sandstone with scoured base and trough cross-bedding preserves some singular, randomly distributed leaf megafossils. Few leaf fossils occur in the clayey mudrock above this, although it does contain streaks of coal and fragmented organic material.

**KSD 91 8.0 Berwind Canyon road section:** Leaf megafossils occur in a complex unit directly above the boundary coal. This unit coarsens up from a finely bedded claystone, to siltstone with muddy intercalations, to a ferruginous sandstone. Leaf fossils occur on distinct bedding planes in the basal clay and also within the sand at the top of the unit, although they are not so well preserved here. This sandstone also contains small scale trough cross-beds, fragmented organic material, sideritic concretions and fine laminations. Above this unit there is a broad fining up sequence from siltstone, to siltstone with shaley intercalations, to mudrock. It does not contain any carbonaceous...
material but is topped by a laterally continuous coal. At the uppermost part of this section there is a thick, massive, fine-grained sandstone.

**KSD 91 9.0, Starkville south:** At the base of the section, just less than 1m above the Cretaceous-Tertiary boundary, fine grained sediments contain mats of carbonaceous material which define discontinuous laminations. This is topped by a thin coal and above this is a massive silty claystone, which is the megafossil-bearing unit of the section. Above this, the sequence is dominated by typical alternations of clayey siltstones with sandstones containing little organic material.

**KSD 91 10.0 Clear Creek north** A thin coarsening up sequence is topped by a vertically extensive fine sandstone that is bedded only towards its upper limit and is overlain by a cyclic sequence of shales and siltstone-fine sandstone. The only organic material, at 15cm above the boundary, consists of twigs, *Equisitum* stems, palms, and a few isolated, dicotyledonous fossil leaves towards the top of the bed. There is also organic material in latest Cretaceous sediments.

**KSD 91 11.0 Clear Creek south:** Above the boundary claystone, which is towards the base of the sequence, there are two coarsening up cycles. The first is initiated with deposition of carbonaceous shale and thick coal. Fragmented carbonaceous material is present in the shales as are small lenses of coal. The coal seam itself is bounded by carbonaceous shale. Above these units there is a siltstone bed overlain by a silty sandstone with carbonaceous laminations and some isolated leaves with a very heterogeneous distribution. The upper coarsening-up sequence is initiated with deposition of a friable, organic poor mudrock which has a sharp base with the underlying silty sandstone. This
coarsens up into siltstone and small scale trough cross-bedded sandstone with small amounts of finely disseminated organic matter. This is overlain by a cyclic sandy-siltstone mudstone sequence that is observed at other sites in the Raton Basin (plate 3.31C).

**KSD 91 12.0 Gallinas Junction south:** In a predominantly coarse grained section leaf megafossils occur in a poorly bedded siltstone with sideritic nodules a couple of metres above the boundary. Towards the base of the bed there are thick intercalations of finer grained sediments, with individual leaf fossils occurring on specific bedding planes.

**KSD 91 13.0 Gallinas Junction north:** Leaf megafossils occur in the lower of two coarsening-up cycles, a couple of metres above the boundary. This cycle is initiated with deposition of a shale with coal streaks, rooted horizons and fragmented organic material at bedding planes. This is overlain by a fine sandstone with more silty intercalations. Leaf fossils occur at the base of the unit, but towards the top only finely disseminated organic material is preserved. This cycle is topped by a massive fine sandstone containing few dispersed leaf megafossils. In the second coarsening up cycle organic material is extremely rare.

**KSD 91 14.0 Madrid west:** Most of the section, above the boundary, is dominated by a massive, fine grained sandstone. Thin, fine-grained beds just below this bed contain minimal organic material. Leaf megafossils do occur at the base of a fining up sequence 70 cm below the boundary, in a fine grained sandstone with silty intercalations. This is overlain by a massive siltstone with some organic material and a carbonaceous shale containing coal streaks and mats of fragmentary organic material. Immediately below the fossil
bearing layer is a carbonaceous shale unit with similar characteristics to the one above.

**KSD 91 15.0 Madrid east:** Below the Cretaceous-Tertiary boundary, at the base of the section, lithologies are dominated by cyclic sedimentation, typical of the basin at this time, with alternations of sandy siltstone and silty claystone, but none of these yield organic material. This cycle, however, is topped by a relatively thick, laterally continuous coal and from above this, until the boundary, sedimentation is predominantly fine grained, although it contains little organic material. Above the boundary, deposits are thick, coarse grained and barren.

### 3.32 Powder River Basin

**KSD 91 16.0/18.0 Pointy Hill:** There are no well preserved leaf megafossils in the lower part of the section (Late Cretaceous in age) but it is not organic-poor. Monocotyledonous reed impressions and compressions are common in shaley claystones and also in intercalations of siltstone in fine sandstone units, up to 15m above the boundary. There is also woody material and fragmented carbonaceous material in fissile, claystone that is the dominant lithology of the section. A number of broad coarsening up cycles can be identified, but they are poorly defined.

The section is continued farther around the hill (represented by KSD 91 18.0), with the boundary claystone. The overlying sediments contain an abundance of organic material in claystones, as well as rooted horizons in coarser units. Abundant angiosperm leaf fossils are found in a unit of claystone, 2m above the boundary, grading up in to one with intercalations of sand and claystone; all poorly consolidated. The fossils are found at interfaces between the two lithologies, not necessarily horizontal to overall bedding, and are often
related to coarser grained lenses within the claystone. As with the lower part of the section fragmented organic material and reeds are common in fine grained, fissile horizons.

KSD 91 17.0, Dogie Creek sandstone ridge: A crystalline fine-grained sandstone from the Tullock Formation yields very few angiosperm leaf fossils and some monocotyledonous fossils. Fifteen metres below this a sandstone unit preserves symmetrical ripples on its upper bedding plane (Plate 3.32a). Underlying shales yield only fragmented debris and monocotyledonous reedy material.

KSD 93 1.0 Tea Pot Dome: The base of the section which encompasses the boundary, is predominantly fine grained. Just above the boundary a claystone preserves waterlily megafossils and rhizomes (J. Wolfe pers. comm., 1991), but the coals above this are barren. Megafossils in the section above this are rare but occur in coarser grained, poorly bedded deposits where they are randomly oriented or parallel to bedding, when associated with thin claystone beds. Leaves are larger lower in the section (1-2.5 m above the boundary) and form mats. Other organic material comprises woody mats, palms and monocots in the upper part of the section, where cross bedding is also observed.

KSD 93 2.0 Tea Pot Dome: The upper 1.5 metres of the section is predominantly coarse grained and homogeneous, lacking in organic material but strongly rooted. Below this, the style of deposition changes with thin alternate silty-claystones and silty-sandstone beds. Where thin sandstone layers cap thicker claystone beds, leaf megafossils are occasionally preserved at
levels of 3.5-4m above the boundary. These leaf bearing beds show considerable lateral heterogeneity in terms of abundance of fossils.

3.33 Williston Basin

KSD 91 19.0 Rick's Place: In a predominantly coarse grained, laterally heterogeneous section, leaf megafossils occur rarely and singularly in a massive, fine grained sandstone-siltstone of a fining-up unit, 4m above the boundary. They are most abundant at the top of the siltstone unit, where they occur clustered on bedding planes. This unit is topped by a dark carbonaceous shale trending to coal. The section is capped by a thick sandstone with cross-bedding on a metre scale, which marks the beginning of the next fining-up cycle.

KSD 91 20.0 McGuire Creek swamp: This section records three minor fining-up cycles with abundant organic material. Cycles are initiated with a fine sandstone or siltstone of varying characteristics, overlain by claystone and often coal-carbonaceous shales. Angiosperm megafossils only occur in massive claystones in the lower part of the 'Z' coal complex. Two such fossil horizons are identifiable in this section. Fine sandstones and siltstones preserve monocotyledonous material, centimetre scale lenses of coal, twigs at an angle to bedding, and rooted horizons (perturbing laminations). Coal beds thicken and coal lenses become more frequent further up in the section, but they are of low grade throughout. Beds of coal have stringers extending down in to beds immediately beneath them.

KSD 91 21.0 Toni's turtle, Nelson Creek: Angiosperm megafossils occur throughout this small section, just below the 'Z' coal, in siltstone, although they are concentrated at certain bedding planes. Also within the siltstone beds
are lenses of fine sand and fusain. The section is topped by a thin carbonaceous shale.

**KSD 91 22.0 McGuire Creek Barbed wire bluff:** The section comprises two coarsening up sequences topped by a predominantly fine grained sequence in the lower part of the 'Z' coal complex. Leaf megafossils occur at both the top and base of the cycles, as well as in the finer grained deposits. The stratigraphically lowest flora is found at the top of a coarsening up cycle in a cross stratified sandstone, with these cross-strata defined by clay drapes. The next flora is at the base of the overlying coarsening up cycle, and occurs in a claystone which becomes coarser at its upper contact. Other leaf megafossils occur in conjunction with monocots, macerated organic material, fusain and very thin beds of carbonaceous shale/coal, with stringers at their base.

**KSD 91 24.0 Cottonwood sheep canyon:** In two small coarsening-up sections leaf megafossils occur in claystone and iron indurated siltstone that is topped by sandstone. These sections occur between the X and Y coals of the Tullock Formation and in terms of age, the fossil floras are approximately analogous to the floras from York Canyon Mine.

**KSD 91 25.0 Last day bluff:** The lithology bearing leaf megafossils is an indurated fine grained sandstone which tops a bluff of massive claystone, weathered to a 'pop-corn texture'. This flora is approximately analogous to those from York Canyon Mine in terms of age.
3.4 PETROGRAPHY OF LITHOLOGIES YIELDING FOSSIL FLORAS

3.4.1 Mineralogy

All sites are petrographically similar. The petrography of lithologies yielding leaf megafossils is generally very homogeneous throughout the three basins, with green-grey clay minerals and quartz predominant, and only very minor amounts of biotite or muscovite present. When they are present, these are restricted to specific sites. The main differences observed, are in the amount and nature of quartz grains present. In general these are angular to subangular whether they are small and matrix-supported in fine grained rocks or whether they are larger, forming the major mineralogical component of more coarse grained rocks. This angularity of quartz grains would suggest only minor transport from source area to site of deposition. Deposition was on mature, low-lying alluvial flood plain, so either the quartz source was proximal to the area or it was derived and transported rapidly from its source, with little time for mechanical degradation to occur. Both explanations are plausible as all three basins have proximal source areas (Dickinson et al. 1988), in addition to receiving sediment from the more distal Rocky Mountains uplift to the west, which would provide abundant immature quartz grains. Rapid uplift ensures that erosion and transport to the site of deposition do not allow significant erosion of quartz. In general, lithologies bearing floras are relatively quartz-poor directly after the Cretaceous-Tertiary boundary event (although KSD 91 10.0 is an exception) but subsequently show proportional increases in quartz in all three areas studied. This could indicate more intense tectonic activity in the source areas or possible raised levels of precipitation, causing synchronous and increased erosion in the Western Interior at this time.
3.42 Organic material

Organic material observed in thin sections is of three types:

1) Finely disseminated throughout the rock
2) Discrete organic particles with well defined edges
3) Organic particles with poorly defined edges

More than one of these forms can occur within a rock in variable proportions. Often organic material will be concentrated especially linearly, defining bedding, as might be expected. However, it also occurs as swaley laminations in more fine grained, organic-rich rocks. This is particularly seen in rocks from the earliest Palaeocene in the Williston Basin. The amount of microscopic organic material in a rock yielding leaf megafossils seems to bear little relation to their abundance. A rock may contain relatively high amounts of organic matter, but few leaf fossils. For example, at KSD 91 17.0, leaf fossils were rare, but large particulate organics, at a maximum of 0.5mm diameter, are observed in thin section. Conversely, rocks with numerous leaf megafossils may only reveal finely disseminated organic material in thin section. The lack of well preserved leaf megafossils in rocks which contain much microscopic organic material may indicate that bioturbation or mechanical degradation has acted on and within these sediments prior to lithification, causing the break up of larger organics so that their original presence is now only recorded on a microscopic scale. This may be related to rates of deposition. Slower rates facilitate widescale bioturbation, causing break up of leaf fossils, whereas rapid influxes of sediment may preserve leaf megafossils at the substrate surface and discourage subsequent bioturbation by destroying conditions needed to support burrowing organisms, or they may bury sediments too deeply to be affected by burrowing organisms.
3.5 APPEARANCE OF LEAF MEGAFOSILS IN THE SEDIMENT

3.51 Relationship to bedding

Where leaf megafossils are preserved parallel to bedding they occur in fine grained sediments or in sections where a variety of lithologies occur, but where the predominant type is fine grained. Sedimentary structures here are fine laminations, often defined by organic material and good bedding. Leaf megafossils also appear bedding-parallel when found in stacked crevasse splay. Here they are not so abundant on one level as in fine grained deposits, where they often occur as mats.

Where leaf megafossils are not found parallel to bedding they often appear ripped and contorted, indicating rapid deposition after transport. The predominant lithologies which preserve this kind of leaf fossil are coarse grained and their sedimentary structures are poor or comprise swaley, discontinuous laminations defined by thin clay layers. Alternatively these coarser grained deposits have planar and trough cross bedding indicative of channel environments.

3.52 Degradation

Mechanical degradation of leaf fossils has been observed at a number of sites (KSD 93 1.0, KSD 91 18.0). Leaves appear torn and contorted (Plates 3.52A and B). Often torn leaves are found in coarser sediments with features suggestive of water transport. Biological degradation is rarely observed, but is less obvious than mechanical.
3.6 INTERPRETATIONS

3.61 Raton Basin

3.611 Overall environment

By the early Palaeocene, the Raton Basin was dominated by an established, low lying, well vegetated, fluvial flood plain (see 3.12, Figure 3.12B). This depositional setting is recognised from a number of diagnostic facies (Pillmore & Flores 1987) which were used as a basis for interpretation in this study. In finer grained sequences, backswamps, meander cut off lakes, coal-forming marshes and crevasse splay deposits have been identified. Coarser grained deposits are identified as channel, crevasse splay and interfluve.

3.612 Fine grained sediments

At and near the boundary, lithologies are predominantly fine grained and carbonaceous. Although finer grained deposits are common, the organic material they yield is generally either fragmented or it occurs as matted layers at bedding planes, where individual leaves are difficult to identify. The fragmentation is perhaps related to slow rates of deposition associated with these fine grained sediments, affording more time for mechanical and biological degradation prior to fossilisation. Three types of fine grained deposits can be identified:

1) Carbonaceous shales
2) Laminated mudrocks with occasional leaf material
3) Massive claystone (with coal streaks and fragmented organic material)

Carbonaceous shales often contain coaly laminations as well as fragmented organic material, and bound coal seams in some sections. They were probably formed in backswamp conditions which were not quite suitable for
sustainable coal deposition; as soon as a minor amount of coal was formed, influxes of fine grained material halted the process and so fine, discontinuous laminations of coal were formed within the shale.

Thin, laminated mudrocks near the top of fining-up sequences preserve organic material including twigs and in some cases (KSD 91 3.0 & 8.0), a leaf megaflora. The presence of laminations suggests that these deposits were not formed subaerially on the flood plain, because soil forming processes and bioturbation would have destroyed laminations. It is possible that they formed in meander cut-offs. These beds are overlain by coarser sediments implying that higher energy conditions ensued following deposition of finer grained sediments and silting up of the cut off lake. Preservation is largely of leaves derived from the flood plain, abscising directly into the cut off lake, with a higher energy aqueous transportational element essentially absent. One interesting anomalous depositional setting is that of laminated mudrocks yielding floras in a section of mudrock-sandstone cyclic sedimentation (KSD 91 4.0) but these could possibly be related to intermittently active meander cut-offs (Burnham 1989 and see 3.7).

Massive claystones contain little or no organic material indicating that their mode of deposition was not conducive to preserving carbonaceous material. This is probably due to unsuitable redox conditions causing breakdown of organic material or to thorough bioturbation of the sediment. One exception is the silty claystone at KSD 91 9.0 which preserves a good fossil flora. This bed has been interpreted as a lacustrine deposit following the discovery of fossil *Scenedesmus* algae (Fleming 1989), although it is not of great lateral extent in that it can not be correlated to other outcrops.
3.613 Coal deposits

Coal deposits are common in the few metres above and below the boundary claystone and further up in the early Palaeocene. The lower coal deposits observed occur as thin bands of up to 20cm. thick and are often associated with carbonaceous shales and organic-rich sediments, although they can be sharply truncated at their upper surface by massive sandstones with erosional bases. This abrupt change of lithology indicates rapid inundation by flood waters or channels loaded with coarse grained material. The rapid nature of such an event is evidenced by the erosive base of the coarser deposit and the absence of any coarsening up cycles between the coal and sandstone, which could have indicated that the change in conditions was a more gradual process. Some such flooding events must have been on a scale large enough to engulf substantial areas of raised mires in the case of thicker, more laterally persistent coal beds. The lateral heterogeneity of these coals is variable. Some extend a few hundred metres along an outcrop, whereas others are merely lenses on a centimetre scale. It has been suggested (Flores 1987) that the major coals formed in a situation analogous to that in the Baram River of Borneo today: a raised peat ombitrophic swamp setting that develops in interfluve and abandoned areas of the flood plain. The elevation of the peat surface above the level of the flood plain means that there is no mixing with suspended muds and the coals remain relatively pure. This mechanism, however, can not be invoked for the smaller scale coal deposits, let alone the small lenses that occur within carbonaceous shale beds. These are probably formed in minor depressions in boggy areas of the flood plain, and abandoned meanderbelts well away from the main channel. The associations with other fine grained and carbonaceous sediments would favour both mechanisms and deposition in settings distal to the main fluvial channel. Sometimes the coals are impure which suggests periodic, possibly seasonal,
Infusions of muds probably deposited from suspension during flooding events which were extensive enough to cover distal areas of the flood plain. The fact these infusions are of fine and not coarse grained material might merely suggest that there were periods when conditions on parts of the flood plain were not conducive to coal formation and that deposition of fine grained deposits under swampy conditions was favoured. This might be related to minor episodic changes in the level of the water table and the amount and nature of precipitation.

Initiation of coal deposition occurs again in the late early Palaeocene as witnessed by the relatively thick coal deposits of the York Canyon open cast mine. Coals here are thicker than in the earliest Palaeocene, reaching a maximum of 4m thickness for a single seam, indicating that conditions conducive to their formation at this time were more persistent than they were just above the boundary and also, perhaps, that basin subsidence was greater. In general, compaction from initial peat thicknesses to that observed for coal beds in the geological record is approximately one tenth (McCabe and Parrish 1992) which suggests that formation of peat mires was an enduring and extensive element of the flood plain of the Raton Basin in the late early Palaeocene. This could be climatically related or due to increased basin subsidence as a consequence of tectonic movements to the west (Flores 1987).

3.6.14 Medium to coarse grained deposits
The majority of florcas collected from within the Raton Basin are from siltstone and silty-sandstone deposits that generally occur near the base of broad fining-up cycles. These deposits are tabular and often have fine intercalations of mudrock and carbonaceous material. Such deposits do not necessarily contain leaf megafossils here but they invariably preserve some
organic material which is concentrated at bedding planes, often picking them out in sequences where bedding is poorly defined. Preservation of leaf megafossils is in the form of compression-impressions, but cuticular material is rare to absent and the preservation does not conserve delicate features. There is considerable lateral heterogeneity with respect to abundancies of megafossils within a bed (which may not be laterally continuous itself) which can be attributed to small differences in the original environment of deposition, allowing concentrations of leaves to build up, or a chance combination of taphonomic processes.

These deposits are interpreted as crevasse splays. The method of preservation and fossilisation of leaves within the crevasse splay sediments can be attributed to sedimentation after a bank-breaking flood when fluvial waters loaded with sediment spill over on to the alluvial flood plain. Leaves abscising directly onto the flood plain are preserved by this rapid influx of medium to coarse grained sediment. Often they can be found at the interface between the upper surface of a thin bed of claystone and the lower surface of a coarser grained deposit, indicating that leaves settled on the flood plain during a period of low energy deposition but were preserved by the rapid influx of coarser material during initial phases of overbank flooding. The fluvial system also transports leaves and other organic material from further upstream and this can be washed over on to the flood plain with sediment during a crevasse splay flood. This means that floras preserved in such deposits do not only represent lower flood plain vegetation but also elements from further upstream. However, only the more physically robust elements of a flora would be able to survive significant transport distances.
Gastaldo et al. (1987) studied organic deposits within crevasse splay deposits of a modern interdistributary estuary. Although this setting is not directly analogous to the alluvial flood plain of the Raton Basin, it is interesting to note that they found that crevasse splays were the sites most likely to accumulate plant bearing material with identifiable macrofloral assemblages, which is what is observed in the Raton Basin. They also discovered that the majority of leaves incorporated into the crevasse splay sediments did not originate from the surrounding vegetational communities but those further upstream. This suggests that crevasse splay settings from the Raton Basin may not necessarily preserve the local flora but are more likely to preserve a regional flora which is more useful when determining palaeoclimates and floral change (see section 3.72).

Whereas the predominantly coarser grained parts of a crevasse splay deposit are derived from the overbank flood, the fine laminations of mudrock are suggestive of calmer periods where swampy conditions were allowed to develop on the flood plain. The fact that coarser grained sediments are dominant suggests that these deposits are relatively proximal to the main channel. The stacked nature of crevasse splays in some sections indicates that breaking of major channel banks and flooding was a repeated occurrence.

Coarser beds within fine grained sections occur at the base of fining up sequences where they truncate finer grained sediments below. They have few carbonaceous laminations and preserve fossil palms, wood impressions and rare leaves. They contain few internal structures and are probably formed as crevasse splay channels proximal to main channels, as they are too thin to be major channels. Two exceptions are at KSD 10.0 and 14.0 where thick channel sandstones with scoured bases occur just above the Cretaceous-Tertiary
boundary. These precede the so called 'barren series' of the Raton Basin (Flores and Pillmore 1987).

Little organic material is found in the massively bedded, fine grained sandstones which dominate the Raton Formation 'barren series', just above the Cretaceous-Tertiary boundary. That which is, comprises mainly fossil palms, *Equisitum* stems and wood impressions (Plate 3.414); mainly the more robust vegetational elements able to withstand transportation and mechanical degradation. Isolated leaves can be found and these are occasionally quite numerous e.g. sites KSD 91 3.0 and 4.0. These deposits possess structures indicative of deposition in a channel setting; scoured bases and minor trough cross stratification. This and the coarse nature of sediment may indicate that higher energy fluvial systems were initiated in the early Palaeocene and then became dominant for a time in the Raton Basin.

There are a number of possible explanations for this switch. Renewed uplift in the source region to the west of the area is one possibility (Flores 1987). This would have provided an increased supply of sediments and also raised the energy of the system so that the sluggish, meandering river systems were rejuvenated and a braided river system dominated the flood plain (see 3.11). Climatic controls are also important. It has been suggested that precipitation increased in the early Palaeocene (Wolfe and Upchurch 1986 and section 6.64), partially as a consequence of the boundary event, and this could have increased the run off from the highland to the west of the basin and afforded higher rates of erosion and deposition in this region. Subsequent fluvial systems of the Raton Basin would have been loaded with larger amounts of coarse grained sediments in a predominantly braided river environment.
3.615 Conclusions

Most floras come from similar crevasse splay deposits and have therefore been subjected to the same taphonomic and depositional processes which should ensure that differences between floras are due to climatic variability and any ecological restructuring following the boundary event. The floras collected from other depositional environments dominated by low energy, fine grained sedimentation are not subjected to the transportational processes involved in the formation of crevasse splay deposits so their floras should reflect mainly flood plain vegetation which is only a subset of the regional vegetation.

3.62 Powder River Basin

Well preserved leaf megafossils are rare in the south of the basin, where field work was carried out. Fine grained, unconsolidated sediment preserves predominantly monocotyledonous material and coarser grained deposits contain only rare, isolated leaf fossils in the Lance Creek area. It is unusual to preserve large amounts of monocotyledonous material in the fossil record (Ferguson 1985) as their leafy parts are not abscised. Their preservation could thus be attributed to inundation and rapid burial whilst in life position, but is more likely to indicate the presence of large lakes with great expanses of reeds at their margins which merely died, fell to the lake bottom and were preserved in abundance in the fine grained sediments there.

These finer grained deposits are indicative of predominantly low-lying, swampy depositional environments that either did not support an abundant angiosperm flora, or allowed degradation of such organic material before it could be fossilised. Symmetrical ripples in a fine grained sandstone fifteen metres stratigraphically below site KSD 91 17.0 (plate 3.32a) were probably
formed by a bi-directional process attributed to the action of wind shear on the surface of extensive lakes. This indicates that extensive lacustrine conditions occurred in the area and that the presence of standing water on the flood plain was common at times during the early Palaeocene.

Leaf megafossils are, however, preserved at KSD 91 18.0 and KSD 93 1.0 & 2.0, where they are commonly found at the interface between lenses, or thin, discontinuous beds of sandstone, and claystones. It seems that the influx of coarser sediment is needed for preservation. Megafossils also occur within sandstone deposits where they are non-parallel to bedding, and often have contorted surfaces implying transportation and deposition under considerable flows. At KSD 93 2.0 leaf fossils occur preserved in sequences of clayey siltstones where they are capped by thin layers of fine sands, again influxes of sand are required for preservation. The repeated nature of these beds in the sequence might indicate seasonality, with regularly abscessed leaves preserved when abscession is coincident with rapid flooding by coarser sediment, which inhibits their degradation.

3.63 Williston Basin

3.631 Overall environment

During the Late Cretaceous the Western Interior seaway retreated from the Williston Basin area, leaving a low lying and swampy delta trending to a lower alluvial flood plain to the west (Cherven and Jacob 1985). The overall environment of the late Cretaceous and early Palaeocene in this area was predominantly swamp-like, with slightly raised more differently vegetated areas. Diagnostic facies of these environments that have been identified
(Cherven and Jacob 1985, Favstovsky 1987) are lacustrine, coal-forming swamp, fluvial channel and flood plain microenvironments.

### 3.632 Fine grained deposits

Floras were collected from predominantly fine grained deposits in the earliest Palaeocene which occur in mainly fine grained sequences of silty claystones, claystones and coals. The one exception is at KSD 91 22.0 where leaf megafossils are preserved in a claystone at the base of a coarsening up sequence. Claystones are massive and contain small lenses of coal, macerated carbonaceous material and rare fusain, in addition to leaf megafossils. The fact that they are massive suggests that bioturbation by either plants or animals has obliterated any laminations, which in turn suggests deposition under aerobic conditions. However, any bioturbation must have been intermittent otherwise all fossil leaves would have been destroyed along with depositional structures. Some floras from claystones predominantly comprise water plants such as *Paranymphaea* and *Nelumbo* (Plate 3.632A &B) and also contain *Azolla*, which are all suggestive of lacustrine conditions. However, the lakes need not have been deep or extensive. All claystone deposits contain at least fragmented organic material and the majority contain leaf megafossils, indicating that conditions on the low energy part of the flood plain were conducive to preservation of organic material, with possibly overall reducing, rather than oxidising, conditions. The two environments of deposition associated with fine grained sediments, and their dominance in the sections, indicate that the overall environment of deposition was very swampy with areas of standing water allowing water plants to develop, as well as areas which were better drained and partially bioturbated. Perhaps this was related to slight fluctuations in water table level. The presence of rare fusain in some sections suggests periodic forest fires although the scale of
these appears to have been relatively small, and it is unlikely that large areas of such a swampy environment would have sustained widespread fires. This is in contrast to the Everglades of S.E. U.S.A. today where extensive fires are quite common.

3.633 Coal
Stringers of coal in claystones, underlying beds of low grade coal, are common in sections from the earliest Palaeocene of the Hell Creek Formation. These stringers are fine vertical structures which extend downwards from coals into underlying beds for a couple of centimetres. The presence of stringers indicates autochthonous deposition, because they represent rooting structures penetrating the sediments below a coaly layer, which develop during deposition of the peat that is the precursor to coal formation. Coals are laterally discontinuous and thin but their very existence and abundance in the upper Hell Creek Formation raises problems with identification of the 'z' coal and the position of the Cretaceous-Tertiary boundary. As well as occurring as beds, lenses of coal are also common in both clay and sandstone and they were probably formed in small, water-logged hollows on the flood plain.

Thick beds of coal (given an alphabetical nomenclature, see Favstosky and Dott 1986) are present in the Tullock Formation where their formation has been attributed to deposition in both raised and low-lying coal swamps (Pocknall and Flores 1987)

3.634 Coarse grained deposits
Coarse grained deposits in general form a minor element of earliest Palaeocene uppermost Hell Creek sections. They preserve rooted horizons,
coal lenses, fragmented organic material and in some cases leaf megafossils (KSD 91 22.0). These coarse sediments are related to episodic overbank flooding transporting sediments on to the predominantly fine grained floodplain. Following deposition, plants were able to recolonise during quieter periods, as evidenced by root traces. Small waterlogged depressions accumulated very minor amounts of peat, resulting in low grade coal.

In the late early Palaeocene coarse grained deposits of the Tullock Formation are more common, as is also seen in the Raton and Williston Basins (see section 3.51) and channel deposits can easily be recognised (Flores 1981). Fossil floras occur in indurated silty sandstones underlain by claystones, which also contain some carbonaceous material. These deposits, at the top of coarsening-up sequences, could be formed by crevasse splays.

3.635 Conclusions
In the early Palaeocene, deposits that preserve leaf megafossils in the Williston Basin are generally formed under conditions of low energy sedimentation in a swampy environment, which indicates that floras are representative of the alluvial floodplain vegetation, where taphonomic processes involve small transportational distances. Floras from later in the early Palaeocene are from crevasse splay deposits, which involve a greater element of transportation prior to deposition, as well as preserving leaves falling directly onto the floodplain from plants growing in a riparian setting.
<table>
<thead>
<tr>
<th>SITE</th>
<th>LITHOLOGY PRESERVING FLORAL ASSEMBLAGE</th>
<th>DEPOSITIONAL ENVIRONMENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>KSD 91 1.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (F)</td>
</tr>
<tr>
<td>KSD 91 2.0</td>
<td>Siltstone + shale</td>
<td>Crevasse splay + intermittently active cut-off lake</td>
</tr>
<tr>
<td>KSD 91 3.0</td>
<td>Fine sandstone + mudrock + intercalations</td>
<td>Crevasse splay (F) + intermittently low energy periods</td>
</tr>
<tr>
<td>KSD 91 4.0</td>
<td>Mudrock-sandstone cyclic</td>
<td>Intermittently active cut-off</td>
</tr>
<tr>
<td>KSD 91 5.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (F)</td>
</tr>
<tr>
<td>KSD 91 7.0</td>
<td>Siltstone</td>
<td>Crevasse splay (F)</td>
</tr>
<tr>
<td>KSD 91 8.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (C)</td>
</tr>
<tr>
<td>KSD 91 9.0</td>
<td>Claystone (no angiosperms)</td>
<td>Lacustrine</td>
</tr>
<tr>
<td>KSD 91 10.0</td>
<td>Fine sandstone</td>
<td>Channel</td>
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<tr>
<td>KSD 91 11.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (C)</td>
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<tr>
<td>KSD 91 12.0</td>
<td>Siltstone</td>
<td>Crevasse splay</td>
</tr>
<tr>
<td>KSD 91 13.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (F)</td>
</tr>
<tr>
<td>KSD 91 14.0</td>
<td>Siltstone</td>
<td>Crevasse splay</td>
</tr>
<tr>
<td>KSD 91 15.0</td>
<td>Claystone (no angiosperms)</td>
<td>Floodplain</td>
</tr>
<tr>
<td>KSD 91 16.0</td>
<td>Siltstone</td>
<td>Overbank flood on swamp</td>
</tr>
<tr>
<td>KSD 91 17.0</td>
<td>Sandstone</td>
<td>Channel/crevasse splay</td>
</tr>
<tr>
<td>KSD 91 18.0</td>
<td>Sand-claystone intervals</td>
<td>Intermittently active cut-off lake (bayou)</td>
</tr>
<tr>
<td>KSD 91 19.0</td>
<td>Fine sand/siltstone</td>
<td>Cut-off lake</td>
</tr>
<tr>
<td>KSD 91 20.0</td>
<td>Claystone</td>
<td>Swamp/lacustrine</td>
</tr>
<tr>
<td>KSD 91 21.0</td>
<td>Claystone</td>
<td>Swamp/marsh</td>
</tr>
<tr>
<td>KSD 91 22.0</td>
<td>Sand/claystone</td>
<td>Swamp/marsh</td>
</tr>
<tr>
<td>KSD 91 24.0</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay (C)</td>
</tr>
<tr>
<td>KSD 91 25.0</td>
<td>Indurated sandstone</td>
<td>Channel</td>
</tr>
<tr>
<td>KSD 93 1.0</td>
<td>Fine sand</td>
<td>Crevasse splay/channel</td>
</tr>
<tr>
<td>KSD 93 2.0</td>
<td>Clayey siltstone with cap of fine sand</td>
<td>Flood plain</td>
</tr>
</tbody>
</table>

(C) denotes part of coarsening-up sequence  
(F) denotes part of fining-up sequence
3.7 TAPHONOMIC PROBLEMS

3.71 A definition of taphonomy
Taphonomy is the study of the transition of all or part of an organism and its traces from the biosphere to the lithosphere (Allaby & Allaby 1990). When applied to the study of fossil floras, it encompasses a wide range of terrestrial processes and pathways which ultimately affect the composition of the flora that is preserved, as well as its state of preservation in the rock record.

3.72 Concepts of plant taphonomy
When collecting fossil floras palaeobotanists have traditionally relied on a number of ad hoc suppositions (MacGinitie 1941, Chaney 1959, Hickey 1977a, Burnham 1987), to account for possible biases derived from taphonomic processes and over-representation of vegetation from certain environments. These suppositions are:
1) Streamside species are over represented in fossil floras because the majority of preserved floras come from sequences of alluvially deposited rocks.
2) Long distance transport of leaves acts to fragment them so that a true picture of the regional flora is not necessarily preserved, and flora proximal to sites of deposition is over-represented.
3) The most abundant taxa in fossil floras were derived from plants growing near the site of deposition.
4) The most abundant taxa in fossil floras were also dominant at the site of deposition.
5) Floristic and vegetational differences between fossil floras are due to climatic and age differences.
Examination of modern leaf assemblages and their transition from the biosphere into the lithosphere has allowed a more a priori analysis of taphonomic influences on foliar physiognomic character (Greenwood 1993). From studies of modern alluvial depositional systems preserving leaves, Burnham (1987) suggested that variances between fossil floras could not simply be attributed to different stratigraphic position, evolutionary or climatic change. She proposed (Burnham 1987) that the cause of this was local heterogeneity of flora within a broad depositional environment, together with the various taphonomic processes that act within subenvironments. Thus, if inferences about climate and ecology are to be made from a fossil flora, it is essential that the bed bearing that flora is put into its sedimentological context, so that the environment of deposition can be determined and taphonomic effects considered.

Floras from the same depositional subenvironments show distinct similarities, even when they are from different stratigraphic levels, (Burnham 1990). This raises problems in detecting evolutionary and climatic trends. Although sampling from such subenvironments, within a continuous sedimentary sequence, in order to detect small scale evolutionary or climatic changes ensures that each flora has been subjected to the same taphonomic process and was derived from plants within the same original environment, it may mean that such changes are obscured. This is because such plants have specific adaptations to their similar environment of growth and deposition, and these adaptations do not necessarily vary with time. This suggests that localised subenvironmental effects are dominant over broader regional effects, and have the ability to mask them. This is seen at site KSD 93 2.0, where a sequence of claystones capped by thin sandstones, suggestive of periodic influx of coarser sediment on a flood plain, preserves solely
stenophyllous leaves (plate 3.72), over a stratigraphic section of more than a metre. However, this also implies that it should be possible to build a picture of the regional flora at one particular time interval by sampling and combining floras from different depositional subenvironments at that interval. This may be the most desirable sampling strategy, but is not always possible in reality. For example, in the early Palaeocene of the Raton Basin most floras are derived from lithologies deposited in the same subenvironments; eight out of twelve floras are preserved in a crevasse splay deposit. In the Williston Basin the situation is similar, but here swamp environments are the dominant leaf preservers. However, changes are observed in the floras collected from the same depositional subenvironments at different stratigraphic levels, in both of these cases. Localised effects may dampen evolutionary or climatically induced adaptations in leaf morphology, but they do not mask them completely, and any broad, underlying changes affecting a region as a whole are seemingly preserved. Perhaps this is to be expected for these overbank, as opposed to channel, depositional settings because they are presumed to be better representative of the regional flora (Burnham 1989). Climatically induced floral adaptations are reflected in the variation in leaf morphology observed from floras derived from the same depositional environment but at different stratigraphic levels within the Raton Basin.

If floral assemblages from different subenvironments were available for comparison then there is no doubt that evolutionary and climatically induced changes in morphology would be clearer. However, this does not mean to say that inferences from floras collected from mainly one subenvironment are invalid, especially if that subenvironment is prone to preserving a fossil flora with a more regional as opposed to localised aspect.
Thin textured leaves can be transported up to a few kilometres by fluvial systems (Rich 1989), before widespread biological and mechanical degradation renders them unidentifiable. So, a depositional subenvironment which preserves leaves that have been transported from their site of growth to their site of final preservation, obviously reflects a regional flora better than a depositional subenvironment without that transportational element. The foliar physiognomic character of floras from quiet water overbank deposits such as ox-bow lakes more closely resembles forest-floor litter from the vicinity of the site of deposition, whereas those from environments incorporating a transportational as well as an overbank element, such as crevasse splays, have a more regional aspect to their floras. In the case of the Raton Basin, where floras are predominantly found in crevasse splay deposits, a more regional picture of vegetation could be preserved. In the Williston Basin, however, where the majority of floras are deposited in lower energy environments, a more localised flora may be preserved.

Greenwood (1993) looked at how taphonomic processes affected leaf size as preserved in the fossil record. He compared late Cretaceous and Tertiary plant bearing beds with modern forests in southern Australia and discovered that forest floor litter has smaller leaves than would be expected from its canopy vegetation source. Fluvially transported assemblages may exaggerate this bias, because larger leaves are more prone to mechanical degradation, so that separate sedimentary facies may require a more individual taphonomic correction. Therefore, although such facies may better represent a regional flora because they have a transported floral element to them, they also preserve size biases not so prominent in floras from non-transported assemblages. Possible affects of this size bias on climatic interpretations are discussed in 6.64.
3.73 Application to early Palaeocene floras

Throughout the early Palaeocene there are two broad depositional settings that preserve good fossil floras. The first of these is dominated by low energy deposition of fine grained sediments in back swamp or abandoned channel subenvironments. The second is formed under higher energy deposition of coarser grained sediment in crevasse splays. Both facies are typical of low lying alluvial flood plains dominated by a low energy meandering river system. Previous work (Potter and Dilcher 1980, Burnham 1989, Gastaldo et al 1989) has been carried out on the plant taphonomy of alluvial depositional settings analogous to those of early Palaeocene floras from the Raton, Powder River and Williston Basins. It is interesting to compare this with findings from this study.

Gastaldo et al (1989) studied the Holocene ox-bow lake system of the Alabama River in the south east Gulf coastal plain. Here they found that surface litter showed a predominant transport direction towards backswamp settings, but that transport following detachment from parent plants appeared to be minimal. Leaves found in such settings are well preserved and predominantly occur as bedded compressions and impressions with few signs of abrasion. Gastaldo (1989) states that backswamp abandoned channels are the sites most prone to preserving bedded leaf litter. In the Raton Basin, where leaves are preserved in such settings, they have similar non-abraided and bedding-parallel characteristics. However, few abandoned channel sites do actually preserve leaf megafossils and invariably such sites do not preserve any leaf megafossils at all. It is the coarser grained sediments, derived from higher energy crevasse splay deposits, that yield most floras. This suggests that in the Raton Basin, ox-bow lakes were only a minor element on the flood
plain in terms of leaf preservation, and that flooding and bank-breaking events were more important for preservation of fossil leaf assemblages

Evidence for the propensity of ox-bow lake deposits to preserve fossil floras also comes from Potter and Dilcher (1980) who studied the Eocene clay deposits of the Claiborne formation of Tennessee. They found that floras were restricted to clay lenses of two types. The first were relatively massive clay deposits with associated lignites (often above a coal). These did not yield any well preserved megafossils and are perceived as representing low lying areas of shallow water receiving fine grained sediments interspersed with some swamps. These can be related to fine grained sediments of the Raton Basin flood plain that do not preserve any leaf megafossils. Analogous deposits from the Williston Basin do, however, preserve leaf megafossils. The second deposits are small isolated clay lenses overlain by more carbonaceous clay, rich in plant fossils and lignites. They are underlain by cross beds and are seen to represent abandoned channels and ox-bow lakes. These deposits are analogous to a few beds yielding floras in the Raton and Williston Basins, for example KSD 91 19.0.

Perhaps the most detailed study relevant to early Palaeocene plant-yielding beds was that of Burnham (1989) who looked at the taphonomy of the Puget group in the north west of the United States. Within the alluvial flood plain setting of the group she recognised four facies that preserved leaf megafossils.

The first of these was the cut-off lake facies. These comprised fine grain sediments, situated below coals, deposited in quiet water settings, that preserved leaves in layers and mats. Analogous depositional environments occur in the Williston Basin, although swamp and marsh deposits are more
common, and evidence for persistent channels, with the ability to cut-off the fine grained sediment supply to these lakes, is lacking. Few of these units yield leaf megafossils in the Raton Basin.

The second of these facies was that of the intermittently active cut-off lake, analogous to present-day bayous. These comprised alternating laminations of clayey-silt and fine sand, with mats of fossils in the fine laminae, and isolated leaves in the coarser material were found in both fining and coarsening up sequences. These may be analogous to the sequences of alternating fine and coarse grained beds observed in the Raton Basin (e.g. KSD 91 4.0, Potato Canyon Road) and Powder River Basin (KSD 91 18.0) which preserve leaf megafossils.

The third of these facies was that of overbank flooding. These are identified by tabular clayey siltstones, with thin mats of fossils derived from overbank flooding, as well as abscission on to the flood plain and coals. These are probably analogous to earliest Palaeocene deposits from the Williston Basin.

The fourth facies was that of the distal crevasse splay. These were recognised by tabular clayey-silt and silty-sand beds, in coarsening up sequences overlying coals. Plants occur in beds above the coal seam singularly or in thin mats. This facies is analogous to Raton Basin crevasse splay deposits, which preserve the majority of floras.

Overall these four alluvial flood plain facies (Burnham 1989) are a good paradigm for sites of deposition of megafloral assemblages in the early Palaeocene. However, there are implicit differences between the three early Palaeocene Basins studied. In the Raton Basin, crevasse splays are the
predominant alluvial facies preserving leaf megafossils and in general the main fluvial channels appear to be well defined. In the Powder River Basin few angiosperms are preserved. The environment is generally swampy and where angiosperms are preserved, the environments are either riparian with a strong stenophyllous taphonomic bias, or relatively high energy small crevasse splay channels/floods where floras are more diverse but mechanically degraded. In the Williston Basin fine grained overbank floods and swamps are the predominant alluvial facies preserving leaf megafossils in the Lance and Hell Creek Formations. In general the main fluvial channel seems to be poorly defined, although this changes in the overlying, coarser grained Tullock Formation.

3.8 CONCLUSIONS

Results from this study show that the majority of well preserved floras from the early Palaeocene of the Raton Basin are derived from crevasse splay and extensive lacustrine deposits. In the Williston Basin at the same time, well preserved floras are predominantly found in overbank flood deposits. This indicates that environments subjected to relatively rapid influxes of sediment, due to flooding events, are the best for preserving floras within flood plain environments. Transportational processes inherent in the formation of deposits from these environments ensure that leaves are preserved from both the immediate vicinity and areas upstream. Floras collected from crevasse splay and overbank deposits thus reflect a regional, as opposed to local vegetation, and are less likely to preserve taphonomic biases associated with specific environments that only preserve leaves from their immediate vicinity.
FIGURE 3.1a: THE WESTERN INTERIOR OF THE UNITED STATES WITH BASINS STUDIED SHOWN
FIGURE 3.1b Stratigraphic and zonal relationships between the Raton, Powder River and Williston basins
FIGURE 3.12B: DEPOSITIONAL MODELS OF THE RATON BASIN DURING THE PALAEOCENE (After Flores 1985)
FIGURE 3.13 The Powder River basin (southern region)
FIGURE 3.14A The Williston basin
FIGURE 3.14B: GENERAL PALAEOGEOGRAPHY OF THE WILLISTON AND POWDER RIVER BASINS AT K-T BOUNDARY
(After Cherven and Jacob 1985)
PLATE 3.31B: BEDDING PLANE EXPOSING TRACE FOSSILS FROM KSD 91 6.0

PLATE 3.31C: CHARACTERISTIC RATON BASIN CYCLIC SEDIMENTATION
Figure 3.414: Fossil wood and bark from KSD 91 13.0 (Gallinas Junction North)
Figure 3.32a: Ripples in sandstone from below KSD 91 17.0 (Dogie Creek Ridge)
PLATE 3.52A & B: CONTORTED FOSSIL LEAVES FROM TEA POT DOME (KSD 93 1.0)

PLATE 3.72: STENOPHYLLOUS LEAVES FROM TEA POT DOME (KSD 93 2.0)
PLATE 3.632A: FOSSIL *Nelumbo* (KSD 91 20.0)

PLATE 3.632B: FOSSIL *Paranymphaea* (KSD 91 20.0)
CHAPTER FOUR

FLORA AND VEGETATIO
CHAPTER FOUR

FLORA AND VEGETATION

4.1 FLORAL COLLECTING AND LABORATORY TECHNIQUES

4.11 Field work
Twenty seven sites within the three study areas were assessed for floral remains, but only twenty four yielded floras suitable for collection. These were of variable preservation which meant that certain sites lend themselves more to floristic, palaeoclimatic and diversity analyses.

4.12 Considerations
When undertaking palaeobotanical field work of this nature it is desirable to consider a number of criteria:

1) A fossil flora should, as far as is possible, sufficiently represent the original diversity of the local community. This is necessary for accurate ecological and palaeoclimatic determinations.

2) The sedimentary sequence in which the flora occurs should be logged in detail so that the environment of deposition can be interpreted and assessed. This can then be used to help account for taphonomic biases.

3) A flora should be collected from a relatively small area of a bedding plane, in this study approximately a few metres square, and a similar sized area sampled at each site. If fossil leaves are collected over a laterally large area then the problems of facies changes and lateral heterogeneity, common in
terrestrial sediments, become important, because of the taphonomic biases that then start to influence composition of fossil floras.

These three major considerations were taken into account when collecting. To ensure that the true diversity of a fossil flora was represented by a sample morphotype diversity curves were drawn (see section 5.34). As far as was possible floras were collected from areas of only a few metres square, at a single stratigraphic level, which was accurately placed within a detailed sedimentary section. The only site where this proved to be difficult was at York Canyon Mine, where safety rules meant that it was not possible to work directly at the hard wall cut but from rubble piles at its base.

4.13 Laboratory techniques

Upon return to the laboratory each leaf sample was cleaned and any rock that obscured fossil material was mechanically removed. Following this, a black and white photograph was taken of each specimen. This was done to facilitate the process of placing specimens within morphotypic groups as the lack of laboratory space would not allow for direct comparison of samples. Specimens from each basin were assigned to morphotypes typical to that basin, and then the array of morphotypes across sites was analysed. The morphotypic system of analysis means that taxonomic relationships are not inferred. However, as comparison with other work on boundary floras was carried out, it was ultimately necessary to assign broad taxonomic affinities where possible. This was carried out by referral to, and correlation with, previous studies of Late Cretaceous and early Palaeocene floras (Lee and Knowlton (1917), Knowlton (1930), Brown (1962) and Hickey (1977)). Descriptions of each leaf morphotype and accompanying plates can be found in the appendices C and D. Floral lists of the morphotypes collected at each site are also located there, in appendix E.
4.14 Difficulties with assimilating previous work

When studying fossil floras it is useful to look at previous monographs and collections. This is of particular importance considering the broad geographic range and lengthy time span involved when required to assess changes at the Cretaceous-Tertiary boundary. However, it is often very difficult to integrate this information with recent work. When working with museum collections it becomes obvious that the flora collected is not representative of the flora as a whole. The best preserved or biggest specimens are retained at the expense of 'lesser' ones, even though both can yield an equal amount of physiognomic data. If palaeoclimatic determinations are to be carried out on museum collections, then one must be certain that the entire population of physiognomic attributes is represented, otherwise erroneous palaeoclimatic determinations are likely to be made. The precise stratigraphic and depositional settings of a fossil specimen are also sometimes missing from museum data sets, and without these the specimen immediately loses a substantial amount of its valuable information. The lack of information about depositional environments means that taphonomic processes, and their affects on a flora can not be considered. Monographs, again, are biased towards large, well preserved specimens although less so than museum collections. They also have a tendency to ally fossils with modern groups or assign them to nearest living relatives, and in doing so infer taxonomic affiliations which may well not exist.
4.2 THE USE OF CLASSICAL VERSUS MORPHOTYPIC APPROACHES IN PALAEOBOTANY

4.21 The classical approach
Conventional systematic taxonomy in palaeobotany is governed by the International Code of Botanical Nomenclature. The code has a long history (see Perry 1991), originating with the laws of De Candolle (1867) which were officially accepted by the International Botanical Congress in 1905 (Arnold, 1947). The rationale behind the code is to produce a system for naming plants which provides maximum explanatory power and ease of communication between scientists (Jefferey 1989). The system followed is Linnaean, conforming to the principle of binomial nomenclature as advocated by the Swedish botanist Carl von Linne (Bates and Jackson 1987), and was originally devised and developed for living organisms. Ultimately the code aims to stabilise the names of plant taxa and changes to it can only be made formally at successive botanical congresses, in order to reduce confusion and ease communication between researchers. The code has, however, caused problems when applied to palaeobotany. Fossil plant nomenclature has never been fully integrated with mainstream neobotanical nomenclature (Boulter et al. 1991) and concern has been expressed at recent changes to the ICBN with regard to the treatment of fossil plants as living plants (e.g. Hughes 1978). The treatment of fossil plants as living plants is problematic in that taxa of fossil species do not parallel those of living species (see section 6.12) and heterobathmy and convergence mean that there are difficulties with identifying true taxonomic links between groups of plants. Another problem in the application of conventional classification to plant fossils has been the nature of plant fossil preservation itself. It is extremely rare to preserve whole plants as fossils and invariably only certain organs are preserved. This has led to the situation where two different organs from the same plant are given
different names and to help alleviate this problem Bateman (1992) has suggested that palaeobotanists should utilise a more open nomenclature.

4.22 Modern approaches to palaeobotanical nomenclature
The drawbacks described above have led to the development of new approaches in naming fossil plants. New approaches have tended to disregard the traditional ICBN in favour of more morphological methods. This has meant that palaeobotany has been left with two extremes, neither of which necessarily allow easy application (Boulter et al 1991), either by non-palaeobotanists or with regard to other palaeontological techniques. De Smet (1991) proposed an alternative nomenclature designed to serve the non-taxonomist scientific community, but perhaps the most forceful proponent of the use of non-classical nomenclature in palaeobotany has been Hughes. Hughes (1989) argues that the Linnaean system was devised and developed for living organisms with verifiable genetic limits which cannot be tested for in fossil plant. He also considers (Hughes and Moody-Stuart 1967) that the classical approach to palaeobotanical nomenclature is cumbersome and considers its application to be too time consuming at the expense of palaeobotanical field observation and research. Hughes' aims in recommending a new classificatory scheme were to pay more attention to the creation of fuller, reusable records of each individual occurrence of fossils than to the aggregation of records by lumping them into taxa (Hughes 1989), thus fossil plant taxa are rendered more universally useful by making it possible to reach back behind their nomenclature for retrieval of basic data. In effect, record making is taken back to the observation stage and becomes free from the legalities of nomenclature (Hughes 1989). By developing such a scheme, Hughes has left behind the ICBN and devised a method of recording palaeobotanical data through a single code which he named the Palaeontologic Data Handling Code, or P.D.H.C. (Hughes 1986). This advocates no absolute identification of a fossil by an author, but requires the placement
of all plant fossil records in stated grades of comparison with information on
the author's name, date of analysis, specimens for comparison, variation
within a group of specimens and morphological characters. Such a record is
termed a biorecord (Hughes and Moody-Stuart 1969), and a biorecord defines a
conceptual taxon or palaeotaxon. Hughes admits that his scheme may not
necessarily be the only possible alternative to the ICBN (Hughes 1991) stating
that 'it is possible that further alternative schemes may be constructed but it
seems clear that fossils should be taken out of the troublesome Botanical and
Zoological Codes for the benefit of the whole field of study.'

Hughes' scheme has come up against much criticism (e.g. Schopf 1978,
Chaloner, comment to Hughes, 1991) and has not been readily accepted by
palaeobotanists even though it was presented in its initial form in the
literature over twenty years ago. Schopf (1978) considered that current
nomenclature was not meant to deal with the problems of systematic study
but provide an agreed upon language base from which such problems could
be discussed, and therefore criticised the fact that data on methods of study
and occurrence of material were included in the biorecord scheme. In a
critique of the PDHC Schopf (1978) concluded that acceptance of Hughes'
method would produce more chaos than it would cure and suggested that
many independent methods of special classification could be used for
determining specifics such as age and correlation.

4.23 Relevance to this study
This study uses leaf fossils primarily for determining palaeoclimate using the
CLAMP method (Wolfe in press). This method requires the identification of
certain leaf morphological characters that are sensitive to climatic variables.
Because of this, leaves analysed were described and grouped solely in terms of
the features needed to apply CLAMP. This is a utilitarian approach with the
application of CLAMP the only criterion for establishing morphotypes. Such a
simplified approach allowed the presentation of data in a way suited to elucidating the workings of CLAMP. This is important because CLAMP is a new technique which should be readily accessible to non-palaeobotanists so that it can be used in a range of climate-related research. Although use of the palaeotaxon scheme advocated by Hughes was considered, it was not deemed appropriate for the work of this thesis. If reference had to be made to palaeotaxon codes as well as CLAMP morphological information and score sheets, the presentation of data in the study would have been more complex and the main aim of CLAMP, that it is a simple technique which can be readily applied by non-palaeobotanists, would have been obscured. In one of the first studies to use a new technique it is important that data is presented in the simplest way possible in order to enable clear understanding of the technique. It was felt that the application of the palaeotaxon scheme would have detracted from the presentation of CLAMP data and methodology. However, it would be possible to apply the specimens used in this study to the P.D.H.C. in the future. This is facilitated by descriptions of each morphotype (appendix D) and the designation of identities to all specimens (appendix D) which are available for viewing in the University Museum, Oxford.

Some morphotypes, as distinguished by their CLAMP features, are allied to classical groupings of fossil plants in section 4.4. This was carried out to allow comparison with previous work on early Palaeocene floras, which have been described using a traditional approach. A review and comparison of early Palaeocene floras from North America and other regions of the World was a fundamental aim of the thesis and although direct assignment of extant genera to fossil leaves is not desirable, without the designation of affinities such a review could not have been attempted.
4.3 LATE CRETACEOUS VEGETATION

4.31 Introduction
The study of angiosperms across the Cretaceous-Tertiary boundary is of particular interest because at that time they were in the midst of an evolutionary expansion, only appearing to attain any kind of dominance in floras during the Late Cretaceous. This is opposed to many groups of organisms that were in a period of decline at the close of the Mesozoic, so that adverse conditions at the boundary merely accelerated or exacerbated their demise.

4.32 Late Cretaceous vegetation - a global perspective
From their emergence in the Early to Mid Cretaceous the angiosperms gradually spread throughout the globe. From palynological evidence it seems that they originally rose to dominance within the regional floras of the low to mid latitudes (Saward 1992), at the expense of other floral elements. However, by the Turonian in the northern, and the Maastrichtian in the southern hemispheres (Hickey 1981) they had reached relatively high abundances in mid to high latitude floras (Spicer 1989). This earlier angiosperm prevalence in lower, as opposed to higher latitude floras, supports the theory for poleward migration of angiosperms from the Tropics (Spicer et al 1987). This is further supported by the greater diversity of angiosperms in Tropical belts at this time, where they dominated shrubland vegetation (Saward 1992), compared to higher latitudes, where they played a more minor role.

There are distinct differences between the high latitude floras of the northern and southern hemispheres in the Late Cretaceous. In northern high latitudes angiosperms were mainly deciduous with a herbaceous 'taiga' aspect (Spicer and Chapman 1990). In southern high latitudes, however, evergreen angiosperm taxa were predominant with a cool temperate rain forest
character (Spicer and Chapman 1990). It appears that in the north, major clades were derived from lower latitudes (Spicer et al. 1987) but in the south, the higher latitudes themselves were the cradle for angiosperm innovation and radiation (Askin and Spicer, in press).

Angiosperms displayed a certain broad provinciality in the Late Cretaceous (Hickey 1984) and showed considerable diversification (Retallack and Dilcher 1974). This diversification was probably facilitated by their inherent high degree of morphological plasticity (Spicer 1986). Their adaptability meant that they became common on lowlands (Retallack and Dilcher 1974), where disturbed habitats were predominant. These environments also showed a particular propensity for deciduous forms of angiosperms which were rare elsewhere (Wolfe 1987). Wing et al. (1993) have suggested that, although common, angiosperms were not necessarily the dominant component of these disturbed Late Cretaceous floras, although they were a common element. In general, however, by the end of the Cretaceous the rudiments of modern floristic provinces and higher taxonomic groups of angiosperms had already appeared and they were a common element of most lowland vegetation (Retallack and Dilcher 1974).

4.3.3 Late Cretaceous vegetation - a northern hemisphere perspective

It has already been established that northern hemisphere floras differed from their southern counterparts in that they migrated poleward from a low latitude equatorial origin in the Early to Mid Cretaceous (section 4.2.2). The majority of floral evidence from the latest Cretaceous comes from the North American continent, but some workers have integrated megafloral and palynological evidence to build a picture of vegetation throughout the northern hemisphere in the Late Cretaceous. From evidence in Central Asia, Europe and America, Krassilov (1981) suggested warm temperate zones occupied by Laurophyllous/Sequoia forests, with lower latitudes consisting of
sclerophyllous scrubland. From palynological studies, Hickey (1984) showed that there appeared to be two distinct floral provinces at mid northern latitudes at this time. The first of these, the normapolles palynoprovince, covered eastern North America and Europe, while the second, the aquilapollenites palynoprovince, encompassed western North America and Siberia. This second province appears to have been decimated at high to mid latitudes at the end of the Cretaceous. More specific data from north-eastern Siberia (Golovneva, in press), shows the mid Maastrichtian floras to be dominated by angiosperms, but with a different species composition to contemporaneous floras from Canada, possibly because of the provinciality described by Hickey (1984). The situation changes towards the end of the Maastrichtian, when those provincial differences decrease. This floral change, however, takes place before the end of the Cretaceous when a decrease in evergreen conifers, cycads and coriaceous entire margined angiosperms is seen, together with an increase in conifers, ferns, platanoids and large sized angiosperms (Golovneva, in press).

4.34 Late Cretaceous vegetation - a North American perspective

From the mid Cenomanian to Maastrichtian in North America, leaf physiognomy was able to stabilise in relation to environmental parameters (Spicer 1987) so that angiosperms became an important element of floras, although even as late as the mid Maastrichtian they may not have been dominant element in all environments (Wing et al 1993).

From an analysis of floras in the Western Interior of the North American continent, Wolfe and Upchurch (1987a) recognised three major biogeographical zones in the latest Cretaceous. From 40-50°N megathermal, open canopy, broad leaved evergreen vegetation dominated; from 50-65°N vegetation was primarily open broad leaved evergreen and conifer, and at palaeolatitudes above 65°N deciduous species were predominant. In general
the broad leaved plants were of low diversity (Wolfe 1987) and most
deciduous types were low grade rosids, platanoids, hamamelids and
trochodendroids. These were rare, predominantly found in disturbed habitats
at mid to low latitudes, but were taking over the polar broad leaved
deciduous forests by the Maastrichtian.

Alaskan floras of the late Cretaceous are dominated by conifers with a ground
cover of ferns and *Equisetites*, although by the Maastrichtian, vegetation
became more open with development of small stature trees and herbaceous
angiosperms, indicative of temperate, seasonal environments (Spicer 1990).

Johnson and Hickey (1990) see major megafloral changes prior to the
boundary in the northern Great Plains, with step wise extinctions, and Hickey
has suggested (1977) that the record of angiosperms across the boundary is in
fact a continuum in which modern families and genera gradually appear, and
archaic types are lost. Upchurch (1989) has also recognised that clades of
vascular plants with archaic morphotypes showed considerable decline in
diversity during the Maastrichtian.

At the close of the Cretaceous in North America, the spatial and temporal
vegetation distribution appears to have been a complex mosaic with
established floral zones being infiltrated by diversified forms of angiosperms
able to occupy disturbed environments, at the expense of archaic forms. Late
Cretaceous flora in North America was already undergoing change prior to
the events at the Cretaceous-Tertiary boundary.
4.4 AN ASSESSMENT OF EARLY PALAEOCENE FLORAS COLLECTED

4.4.1 Raton Basin

Two latest Cretaceous floras (KSD 91 14.0 & 15.0), collected from just below a well defined boundary, are of low diversity with a predominantly riparian aspect. The most common morphotypes are stenophyllous and are allied to *Rhamnus, Salix, Dryophyllum, Prunus* and *Quercus greenlandica* although there are also rarer palmately veined forms and Laurales. The distinctly stream side and disturbed aspect of these floras can be attributed to their environment of deposition. It is interesting to note that the "most disturbed" looking floras come from below the boundary. This could therefore shed doubts on the validity of classing early Palaeocene floras as 'disturbed' and early successional, on the basis of the Cretaceous-Tertiary boundary event and its effects alone. It also stresses the importance of taking depositional environments into account when studying fossil floras.

At sites less than 1m above the boundary (KSD 91 7.0 and 11.0) diversities are low, at between five and fifteen morphotypes. The majority of leaves are stenophyllous, allied to *Salix* and *Prunus* and indicate a riparian or disturbed habitat of growth, or they are palmate and related to *Acer, Amelopsis, Platanus* and *Cissus*.

As soon as stratigraphic levels approach 1m above the Cretaceous-Tertiary boundary, diversities are already greater, especially at site 9.0 (Starkville south KSD 91 9.0). Entire margin morphotypes related to *aff. Averrhoites (sensu Wolfe) Carya, Sapindus, Magnolia* and *Laurus* appear, although their presence varies from site to site, perhaps indicating that they were not yet widespread on the flood plain. Some stenophyllous morphotypes survive, allied to *Salix*, but these are now dominated by other morphotypes, suggesting that their disturbed habitat was becoming stabilised, or that other
morphotypes were now able to colonise disturbed riparian environments. Palmate deciduous morphotypes are abundant, but vary in diversity and type between sites, the most important allied to *Cercidiphyllum, Platanus, Pterospermites, Cissus, Amelopsis* and *Acer*. Morphotypes with micro teeth such as those allied to *Euonymus* occur rarely. Other than angiosperms, palms are also represented as well as reeds and *Equisitum*, which is abundant at site KSD 10.0. Floras are exhibiting greater floral diversity and mixing than those nearer the boundary, but there are still big differences between sites which are related to environment of deposition. KSD 9.0 (Starkville south) shows the most variety and diversity of plants which may be due to its lacustrine depositional environment (Fleming 1989). This stresses the bias of floras form riparian settings and the importance of considering a combination of floras from a number of depositional environment to assess the regional flora.

From 10-20 metres above the boundary, entire margin species are abundant and dominate floras. Forms with affinities to *Laurus, Carya antiquorum, Magnolia, Ficus, Pterocarya, Pterospermites, Nyssa* and *Averrhoites* all occur. However, a wide selection of dentate-margined morphotypes are still preserved, such as those allied to *Quercus, Cissus marginata, Corylus* and the palmately veined forms with affinities to *Acer, Cercidiphyllum* and *Platanus*. Palms are present but the reedy plants occurring at sites stratigraphically nearer the boundary are absent. Microdentate and stenophyllous forms are also absent, indicative of a less disturbed environment of growth, or stabilisation of ecosystems following the Cretaceous-Tertiary boundary event.

Site KSD 91 5.0 (Potato Canyon Rd.) is important because it bridges the gap between the lower portion of the barren series and the upper coal series. Its flora is very diverse with a wide variety of dentate-margined morphotypes comprising forms with affinities to *Quercus, Betula, Juglans, Ulmus,*
Carpinus, Hicoria, Corylus, Pterospermites, Viburnum, Porthenocissus and Sapindus. Palmate forms related to Amelopsis, Acer and Cercidiphyllum also occur. Entire margin forms allied to Credneria, Laurus, Pterocarya and Asimina are present, but the diversity of such forms is reduced from the levels observed at the base of the barren series. This may reflect cooling and a less stable environment of growth, but it is difficult to make interpretations from this single site.

Floras collected from York Canyon mine, in the upper coal series, are dominated by entire-margined morphotypes of paratropical aspect with abundant laurales, magnoliids and Ficus (also possibly forms with affinities to Averrhoites and Persea). Palmate and dentate forms are not as diverse as those within the barren series and comprise morphotypes allied to Cissus, Platanus, Quercus, Sapindus, Carya, Ulmus and Viburnum. Stenophyllous forms are now virtually absent from floras and palmate and dentate forms have decreased in diversity such that entire margin leaves are most abundant.

4.42 Powder River Basin

Floral localities in the southern part of the basin are limited. There is an abundance of monocotyledonous reedy material immediately above the boundary at Lance Creek, and poorly preserved leaves occur that are predominantly small and variously entire margined, microdentate and palmately veined. Here, the predominance of water plants observed in the earliest Palaeocene of McGuire Creek (Williston Basin) and Tea Pot Dome (KSD 93 1.0 &2.0) are not observed.

Directly above the boundary, at Tea Pot Dome (KSD 93 1.0) there is an abundance of water lilies allied to the modern Nelumbo and Paranymphaea (Plates 3.632A &B). They only occur at one level and are not observed further up the section. Just above this fossil water lily bed, in coarser grained
sediments, large predominantly entire margined leaves forming mats are found. Some two metres above the boundary there is a more diverse, but poorly preserved, assemblage with entire-margined morphotypes (allied to Aff. Averrhoites); small, palmately veined forms and larger pinnate forms with dentate and microdentate margins. At KSD 93 2.0 diversities are very low with entire margined stenophyllous forms allied to Averrhoites (J. Wolfe pers. comm., 1993) (plate 3.72) and some compound forms, the only leaf fossils found throughout the section.

4.43 Williston Basin

Floras just above the boundary are, in general, relatively more diverse than their southern counterparts from the Raton Basin (KSD 91 22A & B, KSD 91 20.0). However, at some localities (KSD 91 22C), floral assemblages are of low diversity and are dominated by water plants such as Paranymphaea and Nelumbo (Plates 3.632A & B). There are rare palms, as well as a diverse assemblage of angiosperms. Entire-margined angiosperms are not allied to the Laurales and Magnoliids, they tend to be stenophyllous and have affinities with Carya, Asimina, Sapindus, Prunus and Myrtophyllum. A diverse variety of palmately veined and dentate-margined angiosperms includes forms with affinities to Amelopsis, Vitis, Platanus, Cercidiphyllum, Platanophyllum, Eucommia, Quercus, Hamamelites, Cissus, Betula, Juglans, Fraxinus, Rhamnus, Sapindus, Nyssa and Cornus. Conifers allied to Metasequoia, Glyptostrobus and Taxodium are common at some sites close to the boundary.

At Rick's Place (KSD 91 19.0), a flora from 2.5 metres above the boundary consists of more entire-margined forms than those directly above the boundary. However, there is still a high diversity of non entire-margined forms, with morphotypes similar to those found just above the boundary.
allied to *Eucommia, Quercus, Betula, Rhamnus, Dillenites, Lindera, Amelopsis, Platanus* and *Platanophyllum*. Large leaves are also common.

Floras collected from the late early Palaeocene (KSD 91 24.0 & 25.0), approximately stratigraphically analogous to those from York Canyon Mine in the Raton Basin, are dominated by non entire-margined and palmately veined forms. The flora from site KSD 91 24.0 (Cottonwood Sheep Canyon) is particularly diverse, comprising morphotypes allied to *Cissus, Platanus, Cercidiphyllum, Vitis, Amelopsis, Platanophyllum, Eucommia, Quercus, Hamamelites, Cissus, Betula, Juglans* and *Fraxinus*. It also has entire-margined forms with affinities to *Myrtophyllum, Prunus* and *Carya antiquorum*, as well as an abundance of the fern *Onoclea*. At KSD 91 25.0, the flora is preserved within a channel deposit. Diversity is low, and morphotypes are riparian in aspect with relations to *Quercus, Acer* and *Dryophyllum*.

The flora analysed from Nelson Creek (Toni's Turtle, KSD 91 21.0) is problematic as boundary control here is poor. From a study of the flora, it could be dated as latest Cretaceous, due to the large number of entire-margined forms characteristic of the Late Cretaceous climate, but it also contains a variety of dentate types allied to *Acer, Quercus, Hamamelites, Juglans, Betula, Viburnum, Platanus, Cercidiphyllum, Vitis* and *Platanophyllum*, the majority of which also occur at early Palaeocene sites. This would suggest that either the site is from the earliest Palaeocene, but by virtue of its depositional setting and environment it preserved a flora with a more dominant element of entire margined forms, or that a large proportion of leaf morphotypes survived the boundary event in the Williston Basin.
4.5 DISCUSSION OF EARLY PALAEOCENE FLORAS AND COMPARISON WITH PREVIOUS WORK

4.51 Raton Basin

It is suggested (Wolfe and Upchurch 1986) that the latest Cretaceous of the Raton Basin is dominated by a diverse broad leaved evergreen assemblage of high spatial heterogeneity, with specific adaptations to dry habitats such as small leaves, paucity of drip tips and thick, hairy cuticles. Although two floras collected in this survey exhibit physiognomic features different to these, this was attributed to their riparian depositional environment, which biased the flora towards leaves with a stenophyllous form. In comparison to general Late Cretaceous floras, those collected from the Palaeocene display leaf physiognomies with adaptations for a wetter climate. They are larger, have a higher proportion of drip tips and non-entire margins and lack the thick hairy cuticles of Late Cretaceous forms. When a similarity analysis of floras was carried out (see section 5.431), the two floras from the late Cretaceous showed far less similarity with those from the early Palaeocene than any analyses between early Palaeocene floras did. This suggests that there were few similarities between floras from the latest Cretaceous and early Palaeocene of the Raton Basin, although taphonomic biases associated with the floras from the late Cretaceous may exacerbate this.

Four post boundary floral stages analogous to a 'quasi succession' have been described by Wolfe and Upchurch (1987b):

1) The fern spore spike, angiosperms are not present.
2) The very earliest Palaeocene, prior to the barren series. This is a recovery phase dominated by low diversity floras with Cissites, celastraceans and protolauraceans.
3) Just below the barren series to 200 metres above the boundary. This is a late successional flora indicative of megathermal rain forest dominated by *Cissus*, *Cissites*, *Ficus*, Lauraceae and Celastraceae.

4) 270-420 metres above the boundary, represented by low diversity flora indicative of megathermal rain forest comprising palms, evergreen dicots (Protolauraceans, Laurales, Euphorbiaceae and Tiliaceae) and few deciduous dicots (e.g. *Carya antiquorum* and *Eucommia serrata*).

This succession of floral change is not entirely in agreement with observations made from floras collected in this study. Floras directly above the fern spore spike, within tens of centimetres of the boundary, are of low diversity and are dominated by palmate and stenophyllous forms indicative of disturbed vegetation and initial angiosperm recovery. However, less than a metre above the boundary, at KSD 91 9.0, an assemblage occurs in a lacustrine deposit with a diversity of over 20 morphotypes. Many of the leaf forms have entire margins, not necessarily associated with early successional deciduous vegetation. This indicates that recovery may be somewhat more rapid than previously suggested, and that the nature of the depositional environment in which a post-boundary flora is preserved is also important in determining its composition and appearance. Consequently, the time scale of ecological recovery of floras following the Cretaceous-Tertiary boundary event (Wolfe and Upchurch 1987b) may have been overstated because depositional environments, and the taphonomic bias that they introduce have not been fully accounted for. A flora deposited in a riparian environment may have a 'disturbed' or early successional appearance and therefore this appearance can not simply be related to ecological recovery following the boundary event.

Within the barren series, there is a wide variety of both entire-margined and dentate morphotypes, as well as palms. Dentate forms could be relicts from a deciduous selection in response to the deleterious affects of the boundary
event, or may reflect a geographic position that is only bordering on the paratropical megathermal climatic zone. Further up in the barren series the flora is predominantly non entire-margined, which is in contrast to the predominantly megathermal rain forest physiognomy of leaves described by Wolfe and Upchurch (1987b). It is suggestive of cooler, seasonal climates and could, again, mean that in the early Palaeocene the Raton Basin only bordered on the megathermal paratropical rain forest region, and was subject to climatic and ecologic fluctuations. These fluctuations may be due to the increased basin subsidence and tectonic activity, associated with deposition of the barren series (Flores 1987), causing instabilities and disturbance in depositional environment. By the time the upper coal series is reached, however, the flora is dominated by evergreen dicots with a paratropical aspect, in accordance with the fourth post boundary phase (Wolfe and Upchurch 1987b) and the diversity of deciduous, dentate-margined forms has decreased (see table 5.3). The fluctuations of the barren series had now become stabilised, giving a clearer climatic and vegetational signal.

4.52 Powder River Basin

Dorf (1942) recognised the Lance (Late Cretaceous) flora in the southern Powder River Basin as having a transitional warm temperate-subtropical to subtropical-tropical aspect with 67% of species having entire margins. Limited evidence from Lance Creek (KSD 91 18.0) and the lower section at Tea Pot Dome (KSD 93 1.0 & 2.0) suggests that by the earliest Palaeocene the flora was more mixed, with an increased proportion of non-entire margined leaves indicating cooling and humidization. Woody, dicotyledonous angiosperms are not preserved in abundance, and in some areas reeds and water plants dominate the vegetation. This phenomenon has also been recognised by Nichols et al (1989) who interpreted reedy monocots and water plants as representing early successional plants. Wolfe and Izzet (1987) have also observed early successional aquatic plants overlain by sediments containing
aff. *Averrhoites*, a deciduous early successional plant, at Salt Creek and Lance Creek. Similarities can be drawn with fossil floras from Tea Pot Dome (KSD 93 1.0 and 2.0). Here water plants are present directly above the boundary and aff. *Averrhoites* leaf fossils occur in abundance higher in the section, in fine grained sediments, but between them, in coarser sediments, is a more diverse assemblage of large and small leaves with both entire and dentate margins, indicating that the situation is not simple, and that the predominance of aff. *Averrhoites* may owe as much to a riparian setting as to early post boundary ecological successation. This situation can be compared to that of the early Palaeocene in the Raton Basin (section 4.41).

Stratigraphically higher, within the lower Tullock Formation, low diversity deciduous plants such as 'Cissus marginata' and 'Carya' *antiquorum* are common (Nichols et al 1990), which are also observed at sites in the Williston Basin (section 4.43). By uppermost Tullock time it is thought that diversity had increased and the proportion of entire margined species decreased so that the prevailing vegetation represented a low biomass, broad leaved and coniferous deciduous forest (Nichols *et al* 1989).

It appears that a low diversity flora comprising aquatic and monocotyledonous plants, as well as woody dicots, existed in the southern Powder River Basin in the earliest Palaeocene. Depositional environments were such that floral remains are not abundant but it seems that the early Palaeocene flora eventually emerged as having a cooler and more humid aspect than that of the latest Cretaceous, with features also possibly related to increased seasonality.

### 4.53 Williston Basin

Johnson (1989) has recognised a total diversity of 80 taxa in the Cretaceous of the upper Hell Creek Formation with floras dominated by *Dryophyllum* (not
observed in early Palaeocene floras from this study) and *Platanophyllum* (observed in early Palaeocene floras from this study, plate W39 in appendix C), this was then followed by a drop in diversity to 63 taxa, just prior to the boundary, with gradual floral turnover leaving *Dombeyopsis trivialis* and *Cissus marginata* as dominant taxa. Floras from the earliest Palaeocene of the Marmath area have a total diversity of 72 taxa, and are dominated by *Cercidiphyllum, Platanus, Populus, Paranymphaea, Dictyophyllum* and *Taxodium* (Johnson 1989), all of which have been recorded in Williston Basin floras of this study (appendix D). However, only 21% of these taxa survive from the latest Cretaceous (Johnson and Hickey 1990). Major floral turnover is implied at the boundary, preceded by gradual floral turnover in the latest Cretaceous. Floras collected from the Hell Creek and McGuire Creek areas of this study gave a total morphotypic diversity (as compared to species diversity which, may be different) of around 50 morphotypes in the earliest Palaeocene, which is in agreement with Johnson's hypothesis (1989) of relatively diverse floras in the northern Great Plains at this time. Floras in the Williston Basin certainly appear more diverse after the Cretaceous-Tertiary boundary event than those from the Raton Basin.

Hickey (1984) has described a broad radiation of the palmately lobed leaves of platanoid/platanophyll form during the latest Cretaceous, based on his work throughout the northern Great Plains. Although the radiation dropped off somewhat in the early Palaeocene, possibly affected by the boundary event, the platanoid form accounting for the widespread occurrence and abundance of morphotypes allied to *Platanus, Credneria* and *Cissus*” at this time, was widespread throughout the whole of the Western Interior and plays a dominant role in the floras collected from this area in this study.

The abundance of aquatic plants, allied to the modern Nymphaeales and Nelumbonales, which occur just after the boundary in the southern Powder
River Basin, is also observed in the McGuire Creek (section 4.33) and Marmath areas (Johnson 1989) of the Williston Basin. Where they are preserved, they occur in very low diversity assemblages (for example KSD 91 22.0C), but these are in close proximity to stratigraphically equivalent floras of more than twenty morphotypes (KSD 91 22.0B) (table 5.3). This, again, illustrates how important small scale differences in depositional environments are in determining the composition of fossil floras. Hickey (1984) recognises the presence of fossil water lilies in the latest Cretaceous of the area. Whether this is merely due to the problem of placement of the Cretaceous-Tertiary boundary in the northern Great Plains, so that plant megafossils that are early Palaeocene in age appear to be from the latest Cretaceous, or to the appearance of the suggested "early successional" aquatic plants before the boundary event, is problematic. If such plants were common in the latest Cretaceous, then it implies that precipitation and standing water, facilitating their proliferation, were increasing prior to the boundary event in the northern Great Plains.

Results from this study are in accordance with previous work (Hickey 1984, Johnson 1989, Johnson and Hickey 1990), in that the flora of the earliest Palaeocene from the Williston Basin is of mixed composition with conifers, angiosperms and water plants all represented. Features of angiosperm physiognomy, such as predominantly dentate margins and relatively small leaf size, are indicative of dominantly deciduous mesothermal forests.

4.54 Other areas
Other areas in the northern part of the Western Interior with boundary floral assemblages include the early Palaeocene of the Clark's Fork Basin which records low diversity broad leaved deciduous forests succeeded by broad leaved evergreen forests (Hickey 1980) and the Golden Valley flora of western North Dakota, of the later Palaeocene, which records a strong community
shift towards a broad leaved evergreen forest (Hickey 1977), both indicating a
shift away from deciduous leaf forms common in the earliest Palaeocene in
the region.

4.6 DECIDUOUSNESS, DORMANCY MECHANISMS AND EXTINCTIONS

4.6.1 Deciduousness

Deciduousness in angiosperms is associated with disturbed habitats and
seasonal climates. Although some new deciduous taxa were evident in the
polar broad leaved forests and disturbed habitats of the late Maastrichtian,
Wolfe and Upchurch (1986) suggest that it was the adverse conditions caused
by the terminal Cretaceous event that prompted the switch from domination
by broad leaved evergreen mesothermal forests to that of broad leaved
deciduous ones at mid to high latitude areas of North America until the end
of the Palaeocene. This increase in deciduous leaf forms has been linked with
a selection for dormancy features at the boundary (Wolfe 1987), affording
vegetation better resistance to environmental stresses. Aside from the
deciduous habit in leaves, sharp growth rings in wood and resting spores of
algae found at this time indicate that adaptations enabling plants to survive
periods of adverse climatic and environmental conditions were
advantageous (Upchurch 1989). An increase in the proportion of deciduous
forms, however, could also be explained by climatic cooling and enhanced
seasonality, for which there is other evidence (see section 7.1). Evidence from
this study suggests that leaves of a deciduous aspect in the early Palaeocene
may have developed in response to increased seasonality. At Tea Pot Dome,
(KSD 93 2.0) repeated deposition of fine sand units only a few mm thick has
preserved stenophyllous leaves at seven different levels, in less than one
metre of fine grained sediment. All leaves are of a similar size, indicating
death at a similar stage in growth, and it is possible that their repeated
occurrence, and this size similarity, is due to periodic abscission associated with seasonality and deciduousness. When seasonal abscission occurs in conjunction with an incursion of coarser grained sediment, such as that associated with an overbank flood event, these leaves are then preserved. If seasonal abscission does not occur during a flood event, the leaves are more susceptible to degradation because the cap of coarser grained material, which facilitates preservation, is absent. This means that not every seasonal leaf fall would have been represented in the fossil record, but enough were to detect the repeated occurrence of the event.

Vegetation from higher latitudes would be more likely to have adaptations for seasonality and a more inclement climate because it has to survive periods of winter darkness. This might explain why more northerly floras from the Williston Basin do not appear to undergo the same changes as those of the Raton Basin.

4.62 Extinctions
Wolfe and Upchurch (1986) stated that extinctions were higher in the southern part of the North American continent than they were in the north, affecting evergreen taxa more than deciduous. Upchurch (1989) put the level of floral extinctions at up to 75% in the megathermal southern Rocky Mountain region but down to 25% in the polar broad leaved deciduous forests in the region of Central Alberta. This is in accordance with work from this study, where Raton Basin floras appear to be more disturbed, following the boundary event, than their counterparts in the more northerly Williston Basin. Hickey (1982) quotes a more generalised figure for megafloral extinction across the Western Interior with levels similar to that of palynofloras of 40-60%.
Some workers have observed changes in floras before the boundary. Hickey and Johnson (1988), working in the Marmath area of the Williston Basin in North Dakota, have detected what they term a 'considerable megafloral turnover' in the latest Cretaceous. If rapid floral turnover did start to occur prior to the boundary, then it would imply that environmental and climatic perturbations characterised the whole period and were not merely prompted by the boundary event. Hickey (1984) has noticed that some leaf forms from certain lithotypes show an unbroken continuity across the boundary. This he interpreted as indicating the absence of severe disturbance of plant communities at this time. This is similar to evidence from Siberia (see 4.62), where floral disturbance occurs prior to the Cretaceous-Tertiary boundary (Golovneva, in press). It would seem that other, more wide ranging and global forces, were the driving mechanisms behind restructuring of vegetation across the boundary period in mid to high latitudes. In this study it is the southerly areas that seem to have the more disturbed earliest Palaeocene floras, with their low diversities and changed character. The more northerly floras appear to have been affected less by the deleterious affects of the boundary event in terms of diversity and composition, perhaps because they were already undergoing turnover in the Late Cretaceous (Johnson and Hickey 1989) or because they were able to adapt more easily to the climatic perturbations of the time. The Raton Basin is also nearer the proposed main impact site in the Gulf of Mexico, which may mean that affects, such as fallout of ejecta and acid rain, were initially more catastrophic in this region.

4.7 BOUNDARY FLORAS IN OTHER PARTS OF THE WORLD

4.71 Introduction

Most of the work that has been carried out on Cretaceous-Tertiary boundary floras has focused on North America. However, the pattern of global
vegetation at this time cannot be fully assessed by evidence from just this continent, and it is not valid to make inferences across continents. It is therefore essential to look further afield. At present the literature only allows a discussion of boundary floras from Greenland, Russia, East Asia, Australia and New Zealand.

4.72 Russia

Work done by Golovneva (in press), in the Koryak upland of north-eastern Russia, suggests that non-catastrophic extinctions throughout the Late Cretaceous and early Palaeocene may be attributed to natural evolution and ongoing climate change. The period spanning the boundary is split into the Gonorechinian (mid Maastrichtian) and the Rarytkinian (late Maastrichtian and Danian). Floras from the Gonorechinian stage exhibit angiosperm dominance over rare ferns, cycads and conifers with common forms allied to *Cissites*, *Platanus*, *Quereuxia* and *Trochodendroides*. Conifers include *Sequoia* and *Metasequoia*. The major floral change is at the transition to the Rarytkinian stage (figure 4.62), and is marked by an increase in leaf size, together with an increase in the abundance of conifers, ferns and *Platanus*, a decrease in numbers of coriaceous and entire margined angiosperms and the disappearance of evergreen cycads and conifers. These changes have been attributed to a trend towards a cooler, more humid climate and are similar to those observed in the northern Great Plains of North America. Extinctions of approximately 60% at the Gonorechinian-Rarytkinian boundary are no greater than those observed earlier in the Cretaceous in the region, and are comparable in intensity to extinctions observed in other Late Cretaceous floras of north-east Asia. The Cretaceous-Tertiary boundary is placed within the Rarytkinian stage which means that floral change appears to occur prior to the boundary. This may be analogous to the floral turnover observed by Johnson and Hickey (1990) in the northern Great Plains, but seems to be unlike extinctions in the Raton Basin. This suggests that extinctions prior to
the boundary event, at palaeolatitudes of approximately 50°N, were not only confined to North America. The Tsagajan flora of eastern Asia is the only other one that has been described in the region. It has been correlated with the Fort Union flora with a generally temperate aspect dominated by deciduous trees and 30% entire margins (Krassilov 1975).

4.73 Australia and New Zealand

The latest Cretaceous floras of the southern hemisphere had a distinctly different aspect to their northern hemisphere counterparts during the latest Cretaceous (see 4.22). Megafossil floras from the early Tertiary of southern Australia consist of taxonomically diverse rain forests of evergreen conifers and angiosperms (Axelrod 1984). Modern species allied to these Tertiary forms are currently found restricted to tropical and subtropical rain forests of similar regions (Christophel and Greenwood 1989).

Terrestrial boundary sections from the South Island of New Zealand preserve an angiosperm megaflora that appears superficially similar to modern northern hemisphere deciduous Hamamelididae, Fagaceae and Aceraceae (Johnson 1992), and it has been suggested that it represents a now extinct southern hemisphere deciduous vegetation growing under a polar light regime. Changes occurring in this fossil flora across the boundary are substantially less than that observed in the northern hemisphere, although greater than those of the microfossil record in the region. Like North American high latitude floras, floras from high latitudes of the southern hemisphere appear to have undergone relatively small changes across the Cretaceous-Tertiary boundary. It is not possible to relate these Australian and New Zealand floras with low latitude southern hemisphere boundary floras because these do not exist, or have not been recorded, which leaves an unfortunate gap in the data.
4.74 Arctic and Antarctic regions

During the early Palaeocene, mixed conifer and deciduous hardwood forests rich in herbs, resembling sparsely forested taiga (Spicer and Chapman 1990), blanketed the Arctic region, but in the Antarctic at this time Axelrod (1984) suggests that the flora was dominated by forms that have nearest living relatives in the broad leaved evergreen angiosperms and conifers of cool temperate rain forest; the deciduous habit appears to have been far better developed in the northern hemisphere than in the southern.

4.75 Greenland

Koch (1963) worked on the flora of the early Tertiary of Greenland. He determined it as angiosperm dominated, with an older Cretaceous element containing associates of *Credneria*, *Dryophyllum* and few gymnosperms. This he interpreted as indicative of a temperate climate with an East Asiatic element, although it also bears similarities with North American floras. Wolfe (1980) has equated the Palaeocene Agatdelan flora of the Nugssuaq peninsular with that of Alaska and northern Siberia, all characterised by broad leaved evergreens with few deciduous species and some conifers.

4.8 PALYNOLOGY THROUGHOUT THE BOUNDARY PERIOD

4.81 Introduction

The importance of palynology in unravelling the events that occurred across the Cretaceous-Tertiary boundary can not be overstated. The palynological record has helped to define the composition and extent of floral and biogeographical provinces at that time, as well as elucidating the change in floras across the boundary transition.
4.82 Late Cretaceous provincialism

At the close of the Cretaceous, a distinct provincialism of palynofloras existed (Tschudy 1984). Two main palynomorph suites can be recognised, *Aquilapollenites* dominant in western North America, Siberia and the Pacific and *Normapolles* dominant in western Russia, Europe and eastern North America. Mixing of these floras appears to have been non-existent, even across the North American continent, where the Western Interior seaway acted as a barrier (Tschudy 1971). The *Aquilapollenites* province, however, lost its identity at the Cretaceous-Tertiary boundary (Hickey 1977) and this is often used as an identification tool where the boundary is poorly defined lithologically. This breakdown in provinciality may be attributed to the withdrawal of the Western Interior seaway as a barrier to migration.

4.83 The fern spore spike

The most remarkable phenomena observed in the palynological record across the boundary transition is the fern-spore abundance anomaly, occurring in the earliest Palaeocene from sites throughout the Western Interior from Saskatchewan to New Mexico (Fleming and Nichols 1990). The anomaly was first recorded by Tschudy *et al* (1984) in the Raton Basin and Hell Creek areas, where fern spore abundance was seen to rise dramatically from late Cretaceous levels of approximately 25% to between 65-100% in the earliest Palaeocene, at levels of 0-15cm above the boundary. Not only does relative abundance of fern spores increase but dominance of just a few species is seen to occur within the fern assemblage (Fleming and Nichols 1988), although different ferns dominate at different localities. At this fern spore spike level, the palynological record is almost completely devoid of angiosperm pollen. Hall and Norton (1967), working in eastern Montana, recognised a decline in the number of fern species across the boundary from ten in the Cretaceous, which then became extinct, as opposed to four new species in the early
Palaeocene, but relative abundancies were not discussed, so the fern spore spike could still be present.

The anomaly occurs regardless of lithology and is isochronous, even though it is observed over a wide geographic range. The fern-spore 'spike' has been interpreted as representing the recolonisation of an apparently near barren landscape by opportunistic plant species (Nichols and Fleming 1988) and an analogy has been drawn with the vegetational response similar to that observed following the eruption of Krakatoa (Fleming and Nichols 1988). Although the fern-spore spike indicates widespread and synchronous devastation of flora, with subsequent ecological recovery by pioneer species, the palynofloral succession observed at some boundary sites indicates a somewhat more complex situation. Nichols et al. (1986) observed a second fern-spore abundance above the boundary at a site in south-central Saskatchewan, and in western Canada Leberkmo et al. (1987) recognised a diverse assemblage of angiosperm pollen above the boundary iridium anomaly, at the same stratigraphic position as the fern spore spike. This may suggest that the ecological trauma experienced in North America was less intense at more northerly latitudes. The fern spore spike is not observed in boundary sections from other parts of the globe, which supports the theory that the adverse effects of the boundary event were most strongly felt in the North American continent.

4.84 Patterns of extinction and diversity

Provinciality of floras becomes less defined at the boundary, and extinctions at specific and generic levels appear to be a combination of a gradual transition of floristic composition following evolutionary trends (Tschudy 1984), as is observed in some more northerly leaf megafloras, (see section 4.52 and 4.63) as well as more abrupt extinctions. Tschudy and Tschudy (1986) identified four patterns of extinction and survival in the palynofloral record
during the Cretaceous-Tertiary transition following extensive work in North America:

1) Species extinction.

2) Rare Cretaceous species unable to compete in the Late Cretaceous but finding new, unoccupied econiches in the early Palaeocene and consequently prospering.

2) Cretaceous survivors and less common species finding new avenues for diversification in the early Palaeocene.

4) Some species surviving in to the Palaeocene but then becoming extinct, unable to compete with the expanding Palaeocene flora or adapt to an altered climate.

Work that Sweet (1988) has carried out on Canadian palynofloras also indicates that there is a varying response to the terminal Cretaceous event with some sections recording extinctions at up to 10m. below the boundary. It appears that palynofloras showed complex extinction patterns across the boundary, which were dependent on adaptations to a changing environment.

At a number of boundary sites it has been observed that palynofloral diversity as a whole is reduced in the early Palaeocene (for example Hall and Norton 1967, Tschudy 1970, Nichols et al 1990) but it seems that the composition of the angiosperm assemblage is most disturbed. Frederiksen et al (1989), working on the North Slope of Alaska, noticed that both Late Cretaceous and early Palaeocene palynofloras comprised a variety of conifers, abundant ferns, mosses and club mosses, but angiosperms differed between pre-boundary entomophilous understorey plants to post-boundary broad leaved deciduous types. From these low diversity floras, pollen and spore groups rise in number throughout the Palaeocene (Penny 1969) such that a permanently reorganised flora developed with new plant groups eventually appearing (Nichols and Fleming 1988).
4.85 Non North American palynological record

Although the majority of evidence concerning boundary palynofloras comes from North America, limited work has been carried out elsewhere. Saito et al (1986), working in Japan, recognise the *Aquilapollenites* 'palynoprovince' as dominant in the late Cretaceous but it appears to continue as such into the earliest Palaeocene, unlike the breakdown observed in North America. Askin (1986) studied the palynoflora across the boundary on Seymour Island, Antarctica. Here, a gradual change in the palynoflora occurs over a 12cm. interval at the Cretaceous-Tertiary boundary, eventually resulting in a lower diversity Palaeocene assemblage. The boundary is not detected palynologically in India although this was the site of Deccan Trap extrusion.

4.86 Considerations

Sweet (1988) has pointed out that changes in pollen and spore assemblages only indicate changes in ecological conditions, and that sampling intervals and continuity of the rock record, within individual sections, can affect perceived floral changes and their rates. Although palynology is of the utmost importance in defining the boundary, through identification of certain indicator palynomorphs, especially in regions where other 'impact signatures' are weak, and it gives a reasonable picture of climatic and ecological conditions at this time, where often there is no other palaeontological evidence, it must be studied in association with plant megafloras to give a more accurate impression of these conditions.

4.9 CONCLUSIONS

From the analysis of floras collected in this study, it seems that the deleterious effects of the boundary event were most severely felt in the more southerly Raton Basin than in more northerly areas of the North American continent. Floral diversities are lower in the Raton Basin in the earliest Palaeocene than
they are in the Williston Basin and floral compositions are more different to their latest Cretaceous counterparts here than in northerly sites. In the early Palaeocene of the Raton Basin, floral physiognomy shows adaptations to a wet and warm climate with the occurrence of drip tips and entire margins, but the proportion of dentate margins in floras collected also indicates seasonality. In the Williston and Powder River Basin floras there is a predominance of leaf forms adapted to wet, seasonal climates with temperatures lower than those of the Raton Basin.

The evidence for ecological succession on an evolutionary time scale as suggested by previous authors is deemed to be ambiguous due to the taphonomic biases placed on floras by virtue of their environment of deposition. Previous theories about selection for deciduous leaf forms at the boundary are also questioned, with evidence from this study suggesting that the selection can be explained by climatic change alone.

Comparing results of this study with those of workers from other parts of the world, it is suggested that floral change across the Cretaceous-Tertiary boundary transition was greatest in the North American continent. This floral change has been attributed to a combination of ongoing environmental and climatic change prior to the boundary event as well as the short, sharp shock to the terrestrial environment induced by the boundary event. Work from this study concludes that previous theories of global ecological trauma within terrestrial environments at the Cretaceous-Tertiary boundary have been overstated and that instead it was concentrated on the north American continent.
FLORISTIC CHANGE IN N.E. RUSSIA NEAR K-T BOUNDARY

Pekul'nei Rarytkin Amaam Ugol'naya

Lake Ridge Lagoon Bay

<table>
<thead>
<tr>
<th>Era</th>
<th>Location</th>
<th>Deposits</th>
<th>Floristic Type</th>
</tr>
</thead>
<tbody>
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<td>Upper</td>
<td>Volcanogenic and terrigenous</td>
<td>Gornorechenskian Floristic Type</td>
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<td></td>
<td></td>
<td>deposits &quot;Kakanaut&quot; Fm.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Middle</td>
<td>Continental deposits</td>
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</tr>
<tr>
<td></td>
<td>Lower</td>
<td>Marine terrigenous deposits</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maastrichtian</td>
<td>Upper</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Campanian</td>
<td>Lower</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

FIGURE 4.62 (After Nessov and Golovneva, 1990; Herman, 1993 (pers. comm.))
CHAPTER FIVE

ANGIOSPERM ECOLOGY
CHAPTER FIVE

ANGIOSPERM ECOLOGY

5.1 INTRODUCTION

Determining the ecological characteristics of angiosperms within a flora is important in considering the way in which they reacted to environmental changes across the boundary period. The ability of angiosperms to adapt to environmental perturbations, and how this may have affected their recovery following the boundary event, must therefore be assessed. Floral diversities in the Raton and Williston Basins were tracked throughout the early Palaeocene to discover the nature of recovery following the boundary. Statistical comparisons have also been made to determine similarities between floras and have then been related to stratigraphic position, environment of deposition and geographical position to see how these factors have any bearing on the composition of a flora.

5.2 ANGIOSPERM ADAPTATION AND ECOLOGICAL SUCCESSION

5.2.1 Angiosperm adaptation to unstable ecosystems

According to Krassilov (1981) tectonism and cooling in the Late Cretaceous caused instability in many terrestrial ecosystems, inducing shifts in K/r selection pressures, so that diversity declined at the expense of K-strategists. This, together with the retreat of the Western Interior seaway, could have facilitated changes in flora observed in the latest Cretaceous in the Western Interior of North America. R-strategist angiosperms, with their morphological plasticity, allowing rapid adaptation to environmental change,
would have been better equipped than other plants to survive the long term ecological changes experienced throughout the boundary period. In addition to this, Wing et al (1993) has recognised the prevalence of angiosperms in disturbed environments from the Late Cretaceous. This preference for disturbed habitats, which is related to their R-strategy, could have facilitated angiosperm survival across the Cretaceous-Tertiary boundary and consequently ensured their continuing radiation throughout the Tertiary.

5.22 Ecological succession following the boundary event

If a boundary impact is perceived as covering at least the Western Interior of the North American continent with a thin layer of ejecta, then the subsequent plant colonisation would have been one of primary succession (Tsuyazaki 1989), where pedogenesis and accumulation of nitrogen in the immature soil must initially occur. This total coverage may have occurred at certain sites, but was probably not uniform across the North American continent, and factors other than this would also have affected the destruction of vegetation and its subsequent recovery (see 2.7). Evidence for the absence of angiosperm fossils and the relative abundance of fern spores in sediment directly above the boundary layer is well documented (Tschudy et al 1984, Tschudy and Tschudy 1986). This has been attributed to primary succession similar to that following a volcanic eruption such as Krakatoa (Fleming and Nichols 1988). Initial colonisation of opportunistic ferns able to withstand harsh post-boundary conditions would have allowed modification of the physical environment and enabled recolonisation by the higher plants.

There is not only evidence for abundant ferns just above the boundary. In central and northerly areas of the Western Interior, aquatic plants are often observed in copious amounts at or just above the boundary (Wolfe and Izzet 1987 & see section 4.43). Such plants are also known as early successional colonisers. Their aquatic environment of growth also means that they would
have been more buffered to environmental changes at the boundary than terrestrial plants, which may have enabled their survival. However, angiosperms are noted in sediments the boundary, indicating that it was not long before they recolonised the land, essentially within disturbed habitats. An analogous example of this is the more recently observed recolonisation following the Mount St. Helen's eruption, where dicots showed considerably greater morphological response to tephra deposition than other plants (Antos and Zobel 1985), due to their adaptational abilities and morphological plasticity. Angiosperms were able to maintain stability and a plateau of diversification throughout the latest Cretaceous and early Palaeocene (Tiffney 1981) because of this ability, with long term affects of the boundary event seemingly minimal to their expansion (Knoll 1984). Their ability to adapt and colonise disturbed environments (Wing 1993) may ultimately have secured their dominance within northern hemisphere floras in the Tertiary.

5.3 FLORAL DIVERSITY IN THE EARLY PALAEOCENE

5.3.1 Floral diversity and its relation to ecological recovery
As an ecosystem develops its components are able to stabilise and diversify (Odum 1961) so that a survey of floral diversities throughout the Cretaceous-tertiary transition period might indicate the time scale and nature of ecological recovery following the boundary event. This was carried out by drawing morphotype diversity curves in the field as well as analysing floral composition back in the laboratory.
<table>
<thead>
<tr>
<th>SITE</th>
<th>No. MORPHOTYPES</th>
<th>LITHOLOGY</th>
<th>DEPOSITIONAL ENV.</th>
</tr>
</thead>
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<td>KSD 91 1.0</td>
<td>23 (16)</td>
<td>Fine sand/siltstone</td>
<td>Crevasse splay</td>
</tr>
<tr>
<td>KSD 91 2.0</td>
<td>25</td>
<td>Sandstone &amp; shale</td>
<td>Crevasse splay &amp; cut off lake (bayou)</td>
</tr>
<tr>
<td>KSD 91 3.0</td>
<td>9</td>
<td>Sandstone</td>
<td>Crevasse splay</td>
</tr>
<tr>
<td>KSD 91 4.0</td>
<td>20</td>
<td>Laminated mudrock</td>
<td>Cut off (bayou)</td>
</tr>
<tr>
<td>KSD 91 5.0</td>
<td>27</td>
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<td>Crevasse splay</td>
</tr>
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<td>KSD 91 7.0</td>
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<td>Siltstone</td>
<td>Crevasse splay</td>
</tr>
<tr>
<td>KSD 91 8.0</td>
<td>13</td>
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<td>Lacustrine</td>
</tr>
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<td>Channel</td>
</tr>
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<td>Fine sand/siltstone</td>
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</tr>
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<td>Crevasse splay</td>
</tr>
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<td>Floodplain</td>
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</tr>
<tr>
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<td>21</td>
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<td>Cut off lake</td>
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<td>Sand &amp; claystone</td>
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<td>KSD 93 2.0</td>
<td>7</td>
<td>Silty-claystones capped by fine sandstones</td>
<td>Periodic overbank flood onto flood plain</td>
</tr>
</tbody>
</table>
5.32 Morphotype diversity curves

Fossil leaf morphotypes were distinguished and defined by variations in their physiognomic characters (Appendix C), with particular attention paid to the characters described by Wolfe (in press, see figures 6.232A &B) for palaeoclimatic analysis. Morphotype diversity curves were then drawn at certain fossil flora localities whilst in the field. This was carried out for two reasons:

1) These curves provide an approximate measure of the point at which the majority of a flora has been sampled. The curves are constructed by systematically recording and identifying fossils collected, synchronously plotting them on a graph of number of morphotypes against number of fossils collected. At the point where most morphotypes have been observed the graph is seen to reach a plateau because a decreasing number of 'new' morphotypes are being collected. There are a number of ways in which this can be carried out. The method employed in this study involved collecting fossils in batches of five, the number of 'new' morphotypes within that batch being recorded on the graph. In general, this means that the initial part of the graph is steep and then flattens off towards the 'plateau level'. It is a useful method of estimating when sufficient morphotypes from a flora have been collected to fully represent its character, and is particularly important when time available in the field is at a premium. Even when diversity curves were not drawn, counts of specimens collected were carried out and morphotypes noted.

2) Comparison of such graphs allow diversities of floras to be qualitatively contrasted. Of particular interest in this study are those from different stratigraphic levels within the Palaeocene. It has been suggested (Burnham 1987) that around 400 fossils need to be sampled to reach the plateau level of a diversity curve. Sometimes a 'false plateau' can be reached in a diversity
graph, so it is important to extend the number of specimens collected beyond the first plateau level that is reached. The number of fossils sampled from these Palaeocene sites before a plateau level was reached, was generally only around 200. This is due to the overall low diversity of Palaeocene floras. In his study of boundary floras in the northern Great Plains, Johnson (1989) collected an average of 132 specimens at each site and considered this sufficient to identify the floral dominants, so it is likely that the collections made in this study allow the same degree of identification.

5.33 Drawbacks and considerations

It is noted that in an ideal situation as many specimens as possible should be collected from a site to gain the fullest insight into a flora. Diversity curves merely help in deciding when a sufficient representation of a flora has been collected, when other constraints do not allow collection ad infinitum.

When analysing such diversity curves it is important to determine the depositional environment from which the flora was collected, as taphonomic affects can considerably alter the diversity that is observed in the fossil record (see section 3.7 and 5.35). It is not sufficient to consider only the stratigraphic level with respect to diversity changes, particularly in the laterally heterogeneous terrestrial beds common to the early Palaeocene of North America.

Analysis of floral diversities do not necessarily yield information about relative abundances of morphotypes within a flora. Wing et al (1993) has suggested, from work on Late Cretaceous floras, that although angiosperms are the most diverse element in a flora, their distribution is limited to disturbed habitats and conifers, pteridophytes and cycads may be far more abundant, although their diversities low. Whether this situation continues in to the Palaeocene is uncertain. Collections made in this study suggest that
angiosperms were dominant by then, because very few other plant fossils have been observed. However, all floras were collected from flood plain environments, which are themselves disturbed, so this bias may still operate.

5.34 Results

5.341 Raton Basin

Two detailed diversity curves were drawn at sites in the Raton Basin, although more ad hoc methods of determining diversities were carried out at all sites. The first of these (fig. 5.341A) was drawn at site KSD 91 9.0 (Starkville south), for a flora occurring less than a metre above the Cretaceous-Tertiary boundary. A plateau level on the graph was reached after only one hundred or so specimens had been collected and total diversity of the flora (not just angiosperms) was counted at fourteen morphotypes. In comparison the second curve was drawn at KSD 2.0 (York Canyon Mine), a site from the late early Palaeocene at approximately 300m above the boundary. Here the curve plateaued after about two hundred specimens (fig. 5.341B) had been sampled, with a total diversity of twenty three specimens. On the most simplistic level it would appear that an increase in diversity occurs from the earliest Palaeocene to the late early Palaeocene. However, it is interesting to note that when additional collections were made from the same beds, but at different locations along them, at both sites KSD 91 2.0 and 9.0, the diversity varied from that of the initial curves drawn. This indicates that when only a small area of a bedding plane is sampled, the true diversity of a flora is not necessarily revealed, and that lateral heterogeneity of floral composition along a bedding plane is large. This may be overcome, to some extent, by multiple collections along one stratigraphic level, regardless of lateral facies heterogeneity at a locality.
5.342 Powder River Basin

Diversity curves were not drawn in the field due to poor preservation and lack of fossils, but an assessment was made (table 5.3). Diversity seemed to be highly dependant on depositional environment with coarser deposits yielding more diverse floras (KSD 91 18.0 & KSD 93 1.0) than those finer grained ones (KSD 93 2.0), irrespective of stratigraphic position.

5.343 Williston Basin

Two diversity curves at each of two sites were drawn in the Williston Basin, although, again, an assessment of diversity was made at all sites. These diversity curves were drawn for sites KSD 91 20.0 and 22.0, both just above the boundary. The two curves at each site related to the same stratigraphic level, but were for floras collected some twenty metres apart. By doing this it is possible to check how local lateral variation in floral taphonomy and preservation can affect diversities observed in the fossil record. Site 20.0 (Figs 5.343A and 5.343B) was of particularly low diversity with plateau levels reached after sampling of 100 specimens at 20.0A (diversity only six morphotypes, predominantly water plants) and 110 specimens at 20.0B (diversity eleven morphotypes). This low diversity in deposits dominated by water plants indicates that the small lakes that supported them had little transport of identifiable organic material into them, and were possibly closed systems. The picture is vastly different at site 22.0 (Figs 5.343C and 5.343D) where plateaus are reached after collection of 140 specimens (19 morphotypes) at KSD 91 22.0A and 250 specimens (21 morphotypes) at 22.0B. Again there is distinct lateral heterogeneity in diversities, and in this case it may be due to the dominance of a ponded environment at KSD 91 20.0, where diversity is lower than at the non-ponded depositional environment of site KSD 91 22.0.

Diversity differences observed at sites where curves were drawn may be a relict of initial spatial variations in environment of deposition and
preservation, in that environment. Where curves were not drawn diversity differences may indicate insufficient sampling at a site.

5.35 Megafloral diversity changes of the early Palaeocene

Graphs of diversity changes throughout the early Palaeocene for the Raton and Williston Basins were drawn (figs 5.35A & 5.35B). These do not reveal any obvious diversity trends throughout the early Palaeocene in either basin, although an approximate increase in floral diversity is discernible in the Raton Basin. Diversity levels are similar in both basins with minima of less than 10 morphotypes within a flora. In general these low diversity floras occur within 20 metres of the boundary. Maximum diversities peak at around 30 morphotypes at well over 100 metres above the boundary.

Variability in floral diversity of the early Palaeocene can partly be attributed to the influence of depositional settings. Channel deposits from all three basins consistently yield the lowest diversity floras reflecting their high energy environment of deposition and low potential for floral preservation. Crevasse splay and swamp/marsh deposits generally preserve relatively high diversity floras, although this is not always the case. The one flora from a lacustrine setting of any areal expanse (KSD 91 9.0), yielded a relatively high diversity flora despite its stratigraphic location close to the Cretaceous-Tertiary boundary. Floras from more ephemeral, smaller lakes in the Williston Basin (for example, KSD 91 20.0A) preserve low diversity floras composed of predominantly water plants. Within the few sites studied in the Powder River Basin the affect of depositional environment on floral diversity becomes clear, with stratigraphically lower floras from coarser grained deposits yielding higher diversities than stratigraphically higher floras from fine grained deposits (see table 5.3 and section 3.72).
Although some relationship can be detected between floral diversities and environment of deposition, in general diversities are at their lowest directly after the boundary event and at their highest more than a million years after this. Whether this supports the idea of ecological succession on an evolutionary time scale is debatable because of climatic and microenvironmental differences which obscure evolutionary signals. With diversity differences observed for floras collected from the same stratigraphic level (see 5.343) it seems unwise to directly compare the diversity of floras from different stratigraphic levels, except where the environment of deposition is kept constant or combinations of multiple samples from different environments are used. However, if the environment of deposition is kept constant when sampling, this immediately introduces taphonomic biases and may mean that only a subset of the regional flora is actually sampled.

One anomaly of note occurs in the Williston Basin (KSD 91 21.0), where a flora of 30 morphotypes (circled on fig. 5.35B) appears to exist within 0.1 metres of the boundary. The flora also comprises leaf forms allied to those common in the Late Cretaceous (section 4.33), which suggests that the relatively high floral diversity observed could be due to erroneous placement of the boundary, such that the flora may actually be from the latest Cretaceous.

The fact that general diversity levels and trends are not greatly disparate between the Williston and Raton Basins may suggest that there is some overall forcing mechanism governing floral diversities in the North American continent in the early Palaeocene that is independent of the climatic, environmental and depositional variances between the two basins.
5.4 FLORAL SIMILARITIES BETWEEN SITES

5.41 Use of community coefficients

It is possible to compare the composition of floras between two sites quantitatively, in an attempt to assess their similarity. This can then be related to stratigraphic position and environment of deposition, in an attempt to determine what affects these have on floras. The method employed is described by Whittaker (1975) and has been used by Burnham (1987) in taphonomic studies. This Sorensen's community coefficient, as it is known, is determined by:

\[
\text{community coefficient} = \frac{2 \times S_{ab}}{S_a + S_b}
\]

Where \( S_{ab} \) = the number of shared morphotypes between floras \( S_a \) and \( S_b \)
\( S_a \) = the number of morphotypes in flora \( S_a \)
\( S_b \) = the number of morphotypes in flora \( S_b \)

This coefficient was calculated between all floras from the Raton Basin and between all from the Williston Basin (Tables 5.41C and 5.41D), but not the three floras collected from the Powder River Basin because of their poor preservation.

**TABLE 5.41A: SHARED NUMBERS OF MORPHOTYPES BETWEEN FLORAS**

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### TABLE 5.41C: SORENSON'S COMMUNITY COEFFICIENT - RATON BASIN

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5.42 Discussion of floral assemblage comparisons

Pairs of floras with 'high' Sorenson's coefficients (greater than or equal to 0.5) were noted and compared with respect to their environment of deposition and stratigraphic position to see if their similarities could be explained.

5.421 Raton Basin

Raton Basin floras with high coefficients tended to come from crevasse splay, lacustrine and intermittently active cut-off lake (bayou) environments with the highest for a pair of crevasse splay derived floras. Together with the relatively high diversity of floras from such environments, this suggests that floras from these environments best represent regional floodplain floras as a whole (section 3.72). However, the situation is not simple. Some floras that appear similar, seem to be so by virtue of their stratigraphic position rather than their environment of deposition. For instance floras from KSD 91 9.0/7.0 & KSD 91 9.0/13.0 (each pair from a similar stratigraphic level above the boundary) are similar and both pairs comprise floras from a lacustrine and a crevasse splay environment. The flora from the lacustrine environment (KSD 91 9.0) is most diverse and it is proposed that this best represents the regional floodplain flora.

The lowest community coefficients in the Raton Basin (zero, where no morphotypes are shared between floras) generally belong to pairs of floras, where one pair is from one of two floras sampled from the latest Cretaceous. This indicates that earliest Palaeocene floras share few similar morphotypes with those of this time. However the fact that the Late Cretaceous floras are of low diversity may skew the results as the calculation of the coefficient seems biased towards more diverse floras.
5.422 Powder River Basin

Flora KSD 91 17.0, from the earliest Palaeocene of the Powder River Basin was compared to those of the Williston and Raton Basins and in general was found to be dissimilar, suggesting that there was considerable spatial variation in floral composition between basins. Leaf forms found from the same depositional environments at site KSD 91 18.0 and KSD 93 1.0 were similar, but those found at site KSD 93 2.0 were not. This was interpreted as a taphonomic bias and dominance by stenophyllous leaf forms at site KSD 93 2.0, related to depositional setting (see section 3.72).

5.423 Williston Basin

In the Williston Basin, the most similar pairs of floras are not only of the same depositional environment, but also from the same stratigraphic level at just above the boundary, reflecting the homogeneity of the environment in the Northern Great Plains during the earliest Palaeocene. Where similarity exists between two floras that are not from the same stratigraphic level and depositional environment, one flora is from site KSD 91 24.0 which is a crevasse splay deposit from later in the early Palaeocene. This suggests that this more diverse flora retained elements of the earliest Palaeocene flora, as well as confirming the hypothesis that crevasse splay deposits best represent regional floras.

Within the Williston Basin, the most dissimilar floras (zero coefficients) are observed when one flora is from a low diversity channel environment (KSD 91 25.0), suggesting that channel deposits preserve floras dissimilar to those from other facies. However, the bias against low diversity floras must also be considered, as channel deposits are of particularly low diversity.
5.4 Comparison between basins

If the average community coefficient is calculated for the Williston and Raton basins it is observed that for the former it is slightly higher, at 0.33, than for the latter, at 0.28. This could be a reflection of the more heterogeneous environments that are observed in the Raton Basin, or the fact that results for the Raton Basin include two late Cretaceous floras which are distinctly dissimilar to any in the early Palaeocene.

5.5 CONCLUSIONS

This study shows that floral diversities are low following the Cretaceous-Tertiary boundary event in the Western Interior of North America, especially in more southerly areas. They recover rapidly but remain at relatively low levels throughout the early Palaeocene, with no more than thirty morphotypes in any one flora. Results reveal that diversity is strongly affected by depositional setting within the flood plain, and it is suggested that crevasse splay, overbank flood and relatively extensive lacustrine deposits be sampled to obtain the most representative measure of regional floodplain floral diversity. Similarity coefficients calculated between floras indicate that depositional environment, and not just stratigraphic level is important in determining the composition of, and similarities between floras. Comparison of the diversity of floras collected from a variety of depositional environments and from different stratigraphic levels is not recommended because of the biases that taphonomic processes can produce.
FIGURE 5.343A Morphotype diversity curve KSD 91 20.0A

FIGURE 5.343B Morphotype diversity curve KSD 91 20.0B
FIGURE 5.343C Morphotype diversity curve KSD 9122.0A

FIGURE 5.343D Morphotype diversity curve KSD 9122.0B
KEY TO GRAPHS: DEPOSITIONAL ENVIRONMENTS

- Crevasse splay
- Cut-off lake
- Lake (extensive)
- Channel
- Lake (small scale)
- Swamp/marsh
- Overbank

These symbols relate graphs drawn to show diversity and climatic trends throughout the early Palaeocene (figures 5.35A, 5.35B, 6.311A, 6.311B, 6.311C, 6.311D, 6.313A, 6.313B, 6.321A, 6.321B). They indicate from which particular depositional environment the flora providing the data was derived.

STRATIGRAPHIC CORRELATIONS

Raton Basin: between zero and ten metres above the boundary (KSD 91 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0) sites are vertically measured from the boundary, although correlation between sites is not possible. For sites higher up in the Palaeocene within the Barren Series (KSD 91 3.0, 4.0 and 5.0), correlation is by palynologic zonation (after Fleming, pers. comm. 1991), together with height above boundary. For sites more than 200m above the boundary (KSD 91 1.0 and 2.0) correlation is lithologic between sites, and by reference to core data provided by York Canyon Mine (R. Pillmore, pers. comm. 1991) for stratigraphic position relative to other sites. See also section 3.21 for a fuller explanation.

Williston Basin: between zero and two metres above the boundary, sites are lithologically correlated. Above this they are positioned stratigraphically from their relationship to the alphabetically named sequence of coals within the Tullock Formation together with reference to data from U.S.G.S. field note books. See also section 3.21 for a fuller explanation.
FIGURE 5.35A
Raton Basin: Floral diversity throughout the early Palaeocene

FIGURE 5.35B
Williston Basin: Floral diversity throughout the early Palaeocene
CHAPTER SIX

CLIMATE
CHAPTER SIX

CLIMATE

6.1 USING FOSSIL FLORAS TO DETERMINE PALAEOCLIMATES

6.11 The links between flora and climate
Leaves have a direct link with the earth's atmosphere, through the gaseous exchange that occurs during photosynthesis. A delicate balance between maximising photosynthesis, through increased leaf area, and minimising water loss, through a decreased area is advantageous. In an environment where sunshine and moisture are plentiful, leaves are large because they don't have to cope with water stress. However, in a desert environment leaves are small, because although sunshine is copious, water stresses are high, so a plant minimises water loss through a decreased leaf area. It is this phenomenon that is utilised by palaeobotanists when determining palaeoclimates. The development of other leaf physiognomic features are also determined to a greater or lesser extent by prevailing climatic variables. Wolfe (1990) estimated that more than 70% of physiognomic variation in leaves corresponds to moisture and temperature variables. Physical characteristics of vegetation living under comparable climatic conditions, from widely separated regions, are also similar (Wolfe 1978).

Bailey and Sinnot (1915) were the first to point out the relationships of leaf margin and size with temperature and precipitation levels. They stated that leaves and leaflets with entire margins predominated in warm, dry
environments, and those with non-entire margins were numerous in moist, temperate, seasonal regions; additionally large leaves occurred where moisture was abundant but where it was restricted, leaf size decreased.

6.12 Physiognomic versus 'nearest living relative' studies

Although vegetation that occupies similar climatic zones in widely separated regions has comparable morphology, the regions may have only a few taxa in common. This is because historical and evolutionary factors can result in floristically different compositions of plants from similar climates and environments, but with similar physiognomic characters, in different areas (Wolfe 1978). This suggests that an analysis of physiognomic characteristics of a fossil leaf assemblage provides a more direct and reliable means of determining palaeovegetation type and climate than does floristic composition (Richards 1952). It seems that it is not desirable to assign fossil leaves to modern species and genera, because in doing so inferences are made about genetic histories and taxonomic relationships, for which there is insubstantial evidence. Using such a 'nearest living relative' (N.L.R.) approach also presumes that there has not been a change of habitat preference of a group over time, and necessitates an estimation of the palaeoclimate from the range of habitats in which the N.L.R. now grows (Dolph and Dilcher 1979). If fossil floras are to be used to gain an insight into palaeoclimates, then it is therefore valid to divide them into morphotypes for analysis, with recognition based solely on physiognomic features, independent of any taxonomic affiliations.

6.13 Problems of determining palaeoclimates from leaf physiognomy

Reliability of the climate signal from floras depends on the vegetation being from a climax community (Spicer 1990). If vegetation is successional then it is
not necessarily completely in equilibrium with its environment, and therefore may yield erroneous climatic data. This may have important implications for post K-T boundary floras which have been perceived as successional on an evolutionary time scale (Wolfe and Upchurch 1986, section 4.41) and therefore may give inaccurate palaeoclimatic results upon analysis.

There is a non-random distribution of species within a community, therefore the climatic signal for two contemporaneous floras in the same region may be significantly different, because leaf forms may vary drastically over a short distance (Dolph and Dilcher 1979, section 5.3). This tends to be true of small fossil assemblages. Large assemblages are considered to reflect a wider range of terrestrial microenvironments, because stream transport causes taxonomic mixing of leaves from different microclimatic regimes (Christophel and Johnson 1990).

Almost all described North American early Palaeocene floras represent flood plain vegetation, which is essentially a low diversity type, not generally sensitive to temperature (Wolfe 1985), with leaf margin characteristics that do not necessarily reflect accurately that of the regional vegetation. This arises from the concentration of non entire-margined species in the stream and lakeside vegetation relative to the slope and interfluve regions (Wolfe 1971). In an ideal situation, this indicates that to obtain useful palaeoclimatic information from fossil leaf physiognomy, multiple samples from different depositional environments at the same stratigraphic levels should be obtained (Burnham 1989). However, although all samples collected for this study were from flood plain environments, floras with over 80% entire margins were recognised. This indicates that some flood plain depositional
environments may reflect the regional flora when climatic conditions produce distinctive enough leaf physiognomies to override taphonomic biases.

6.14 Other factors affecting leaf physiognomy

Leaf form can also be influenced by soil moisture, relative humidity, light intensity, air speed, direction of air flow over a plant, air temperature, soil nutrient availability, soil pH, vertical position of leaves in a forest, interactions with other organisms in an ecosystem, latitude, altitude, seasonality and diurnal variation. Ultimately, however, it is prevailing moisture and temperature conditions that, to a large extent, will determine physiognomy.

6.2 METHODS OF DETERMINING PALAEOCLIMATES FROM LEAF PHYSIOGNOMIC DATA

6.21 Introduction

From initial observations by Bailey and Sinnot (1915) qualitative methods assigning fossil floras to phytogeographic groups on the basis of their physiognomy, specifically leaf margin and size, were employed in palaeoclimatic determinations. A quantitative method (leaf margin analysis) was subsequently developed by Wolfe (1979) using margin characteristics of a flora to give an estimate of palaeotemperature (see section 6.22). This was somewhat more objective, but still did not integrate all the physiognomic data from a flora to elucidate palaeoclimates, and was not suitable for use with fossil floras that grew where water had been a growth limiting factor. The CLAMP technique was developed in an attempt to overcome such shortcomings (Wolfe in press, see section 6.23).
6.22 Leaf margin analysis (L.M.A.)

6.221 Methodology of L.M.A. and its drawbacks

Wolfe (1979) observed a relationship between the percentage of entire margined leaf species in living south east Asian floras, and the mean annual temperature regime in which they grew. He quantified the relationship as a 3% change in percent of entire margin species for every 1°C change in mean annual temperature (Wolfe 1979). This can be applied graphically to fossil floras in an attempt to elucidate palaeotemperatures (Fig. 6.221a and b).

The link between leaf margins and palaeotemperature was based on a study of vegetation from south-eastern Asia, and this may not be applicable to all global vegetation types. Inherent differences in vegetation structure of the southern hemisphere means that a 4% rather than 3% change in the ratio of dentate to entire margins signifies a 1°C change in M.A.T. (Wolfe 1979, Spicer 1990). As all data for this study was obtained for the northern hemisphere then this was not considered to be a problem. Plants growing under climatic regimes characterised by seasonal and low rainfall show a varying margin to M.A.T. relationship (Wing and Greenwood 1993) and an analysis of non-coniferous leaf margins in forests where conifers are dominant reveals that they do not show a distinct relationship to M.A.T. at all (Wolfe 1979). In this study it is only the seasonality of rainfall which may slightly affect the margin to M.A.T. relationship.

It is not just prevailing climate that influences the form of leaf margins found in a fossil flora. It is well documented (MacGinitie 1974, Dolph and Dilcher 1979, Burnham 1989, Greenwood 1992, Wing and Greenwood 1993) that leaf production, post abscission transportation, preservation of canopy versus non-canopy leaves and leaves of streamside versus climax vegetation also
affect the proportion of entire margin leaves in a fossil flora and result in a misrepresentation of the regional flora and climate (see section 3.7). Thus the palaeotemperature determinations derived from leaf margin analysis become less accurate. Wolfe himself (1985) states that such an analysis should only be carried out on floras with more than thirty species and that multiple sampling from the same area should be practised in order to counteract these problems. Floras collected and analysed in this study do not exhibit such diversities. This means that absolute figures may not be entirely accurate but trends, where comparisons are made between climatic results obtained from fossil floras, are still important.

6.23 Climate leaf analysis multivariate programme (CLAMP)

6.23.1 A brief explanation of CLAMP

CLAMP or Climate Leaf Analysis Multivariate Program is a method of integrating all physiognomic information from a leaf assemblage to estimate palaeoclimatic variables. It employs correspondence analysis, using the statistical package M.V.S.P (Kovach 1990), to infer patterns of correlation between the physiognomic characters of a flora, and climatic variables derived from modern day meteorological data (Wolfe 1990).

6.23.2 CLAMP methodology

Before a flora can be analysed using the program it has to be 'scored'. Physiognomic characters sensitive to climatic parameters are assessed quantitatively by noting their presence or absence and leaf size is calculated and categorised (fig. 6.232a). Divisions within a physiognomic category define the nature of the feature (see fig. 6.232b). This scoring process is carried out for all morphotypes within a flora, and the scores for each feature added together.
These total scores are then represented as a percentage of total possibilities defined for feature variability. It is this percentage that is utilised in the analysis. Such a method does not take the abundance of a morphotype into account, only the features of that morphotype. A sample score sheet and scoring for leaf megafloras in this study can be found in Appendix F.

Axis one and two represent the axes of greatest variability in the analysis. Because leaf morphological characters indicative of similar climates plot close together, when they are placed on a plot of axis one against axis two the spread of points define two vectors which can be related to mean annual temperature and precipitation, (fig. 6.232c). The vector associated with axis one predominantly represents the temperature dependent features and that associated with axis two, the precipitation. Scores for climatic data from modern meteorological stations can be superimposed on the same plot. Those stations with similar climate plot near to one another, and to the floral physiognomic features common to that climate (6.232d). From the position of a fossil flora in the framework, defined by the modern climatic data, it is possible to estimate the palaeoclimatic conditions under which the fossil flora grew.

The current approach that Wolfe uses for this estimation (Wolfe, in press) involves orthogonally projecting the vector derived from a sample score onto calibrated mean annual temperature and precipitation vectors related to axis one and two respectively. He uses the following argument for this method. Axis one doesn't itself represent mean annual temperature, positioning of cool megathermal desert samples higher on axis one than warm megathermal samples implies that a vector representing M.A.T. would be inclined to the left of the positive part of axis one. In accordance with this,
when M.A.T.s for samples are treated as a physiognomic character state, the score for these determines a vector in such a position. If sample scores are projected orthogonally to this M.A.T. vector, relative positioning of projected samples approximates M.A.T. This positioning could form the basis for moderately accurate estimates of M.A.T., but inspection of the positioning indicates that drier samples generally have lower relative positions than wetter samples of approximately the same M.A.T. Therefore, a vector that is a compromise between the orientations of the M.A.T. and axis one might order the samples more accurately, so this is what is utilised. From the relative position of a fossil flora within this ordination its M.A.T. is determined.

Because the positioning of the M.A.T. vector as described above, is to some extent, subjective I have chosen the more straightforward and reproducible approach, in this study, of using the simple regression of axis one score against M.A.T., even though this method is less accurate. Thus M.A.T.s derived in this study, are obtained by projecting the axis one score for a fossil flora onto the regression line relating axis one score to M.A.T. (as defined by living vegetation) and reading off the appropriate M.A.T. from the y-axis (figure 6.232e). The same method is employed for determining M.A.P., except that axis two scores against M.A.P. together with a regression line relating axis two scores to M.A.P. are used.

6.233 Advantages of CLAMP over other methods

There are a number of reasons why this method has been used over other statistical techniques:

1) Correspondence analysis is robust to non-normality in data sets. Palaeoecological variables such as leaf morphology do not necessarily show a
normal Gaussian distribution, so this robustness is desirable. Other statistical methods, such as multiple regression analysis, assume normality.

2) Principal component and regression analysis give bunching, as they have a bias towards the abundance or rarity of a character. Correspondence analysis is not affected in this way.

3) Correspondence analysis (C.A.) provides two plots, one relates to variables (leaf characteristics) and the other to samples (sites with known climate details). As C.A. is a reciprocal process the two plots are directly compatible. Other techniques need transformation or manipulation of the data to do this. However there may be problems with comparing bounded and unbounded variables (see Wing and Greenwood (1993) for full explanation).

4) Multiple regression analysis allows correlation between the variables (leaf characters) and this eases problems with redundancy. However for fossil floras the element of redundancy, inherent in CLAMP, is desirable as many leaf characteristics are 'lost' during the process of fossilisation (see section 6.24).

6.234 Accuracy of CLAMP

Multiple regression analysis has the advantage that the programme is not affected by the addition of a fossil site. Correspondence analysis does not have this advantage, but because of the number of modern floras now incorporated in to CLAMP, it is quite robust to such affects. Considerable work is currently in progress to determine the accuracy of CLAMP compared to other statistical methods of determining palaeoclimates (Gregory and Chase 1992, Wing and Greenwood 1993, Povey et al, in press) but for the purpose of this study, where
trends in temperature rather than absolute values were deemed more valuable, the original CLAMP technique (Wolfe, in press) has been utilised, although the problems associated with it, as pointed out by other workers, have been considered.

After scoring the angiosperm element of each fossil flora, following the Wolfe method (in press), the CLAMP multivariate statistical programme was applied to determine mean annual temperature and precipitation.

6.24 Testing CLAMP for information loss using an ideal data set

6.241 Problems with incomplete leaf physiological data sets

When collecting leaf fossils it is often the case that a specimen will be incomplete, either because of the taphonomic processes it experienced prior to deposition, poor preservation or the extraction techniques used. This means that morphological details required to score leaf specimens for use in CLAMP can be readily lost. To test the validity of CLAMP when used for these data sets lacking in certain morphological information, an 'ideal' data set was defined. This comprised a flora of thirty morphotypes chosen randomly from Raton Basin complete morphotypes. Real morphotypes taken from a basin that had been worked on in this study were used, because it was felt that the results that they produced would be more relevant to those obtained from the floras collected and used in palaeoclimatic determinations. In the ideal state (flora A) these morphotypes had all their morphological features present so that CLAMP scoring was complete. This provided the ideal mean annual temperature and precipitation estimates to which non-complete data (floras B-S), from the same flora, could be compared. Non-ideality was achieved systematically by randomly extracting one third, two thirds and all of the data for each of the CLAMP scoring categories - margin, size, apex, base, length to
width ratio and shape. This meant that in total there were nineteen variations of the synthetic flora.

**Table 6.241: Ideal CLAMP floras**

<table>
<thead>
<tr>
<th>FLORA NAME</th>
<th>CHARACTERISTIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>IDEAL A</td>
<td>COMPLETE FLORA</td>
</tr>
<tr>
<td>IDEAL B</td>
<td>-33% MARGIN DATA</td>
</tr>
<tr>
<td>IDEAL C</td>
<td>-66% MARGIN DATA</td>
</tr>
<tr>
<td>IDEAL D</td>
<td>-100% MARGIN DATA</td>
</tr>
<tr>
<td>IDEAL E</td>
<td>-33% SIZE DATA</td>
</tr>
<tr>
<td>IDEAL F</td>
<td>-66% SIZE DATA</td>
</tr>
<tr>
<td>IDEAL G</td>
<td>-100% SIZE DATA</td>
</tr>
<tr>
<td>IDEAL H</td>
<td>-33% APEX DATA</td>
</tr>
<tr>
<td>IDEAL I</td>
<td>-66% APEX DATA</td>
</tr>
<tr>
<td>IDEAL J</td>
<td>-100% APEX DATA</td>
</tr>
<tr>
<td>IDEAL K</td>
<td>-33% BASE DATA</td>
</tr>
<tr>
<td>IDEAL L</td>
<td>-66% BASE DATA</td>
</tr>
<tr>
<td>IDEAL M</td>
<td>-100% BASE DATA</td>
</tr>
<tr>
<td>IDEAL N</td>
<td>-33% L:W DATA</td>
</tr>
<tr>
<td>IDEAL O</td>
<td>-66% L:W DATA</td>
</tr>
<tr>
<td>IDEAL P</td>
<td>-100% L:W DATA</td>
</tr>
<tr>
<td>IDEAL Q</td>
<td>-33% SHAPE DATA</td>
</tr>
<tr>
<td>IDEAL R</td>
<td>-66% SHAPE DATA</td>
</tr>
<tr>
<td>IDEAL S</td>
<td>-100% SHAPE DATA</td>
</tr>
</tbody>
</table>

The very essence of CLAMP implies that the loss of some or all morphological data from a specific physiognomic feature of morphotypes in a flora should not have a disastrous overall affect on the mean annual palaeotemperature and palaeoprecipitation estimates derived from it. The multivariate nature of the programme should minimise inaccurate estimates derived from a non complete data set because it integrates data from all physiognomic features, and is not just dependant on one or two specific
features. These ideal runs were able to test this robustness of CLAMP to information loss.

6.242 Results of 'ideal CLAMP' test

Table 6.242: Results of ideal CLAMP

<table>
<thead>
<tr>
<th>FLORA NAME</th>
<th>M.A.T./°C</th>
<th>DEVIATION</th>
<th>M.A.P./cm.</th>
<th>DEVIATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>14.3</td>
<td>IDEAL VALUE</td>
<td>205</td>
<td>IDEAL VALUE</td>
</tr>
<tr>
<td>B</td>
<td>15.8</td>
<td>+1.5</td>
<td>220</td>
<td>+15</td>
</tr>
<tr>
<td>C</td>
<td>15.9</td>
<td>+1.6</td>
<td>222</td>
<td>+17</td>
</tr>
<tr>
<td>D</td>
<td>14</td>
<td>-0.3</td>
<td>240</td>
<td>+35</td>
</tr>
<tr>
<td>E</td>
<td>14.8</td>
<td>+0.5</td>
<td>200</td>
<td>-5</td>
</tr>
<tr>
<td>F</td>
<td>14.7</td>
<td>+0.4</td>
<td>200</td>
<td>-5</td>
</tr>
<tr>
<td>G</td>
<td>16</td>
<td>+1.7</td>
<td>140</td>
<td>-65</td>
</tr>
<tr>
<td>H</td>
<td>14.3</td>
<td>0</td>
<td>210</td>
<td>+5</td>
</tr>
<tr>
<td>I</td>
<td>14.3</td>
<td>0</td>
<td>210</td>
<td>+5</td>
</tr>
<tr>
<td>J</td>
<td>16</td>
<td>+1.7</td>
<td>218</td>
<td>+13</td>
</tr>
<tr>
<td>K</td>
<td>14.7</td>
<td>+0.4</td>
<td>208</td>
<td>+3</td>
</tr>
<tr>
<td>L</td>
<td>14.9</td>
<td>+0.6</td>
<td>216</td>
<td>+11</td>
</tr>
<tr>
<td>M</td>
<td>13</td>
<td>-1.3</td>
<td>203</td>
<td>-2</td>
</tr>
<tr>
<td>N</td>
<td>14.7</td>
<td>+0.4</td>
<td>210</td>
<td>+5</td>
</tr>
<tr>
<td>O</td>
<td>14.8</td>
<td>+0.5</td>
<td>217</td>
<td>+12</td>
</tr>
<tr>
<td>P</td>
<td>21.5</td>
<td>+7.2</td>
<td>209</td>
<td>+4</td>
</tr>
<tr>
<td>Q</td>
<td>13.5</td>
<td>-0.8</td>
<td>222</td>
<td>+17</td>
</tr>
<tr>
<td>R</td>
<td>14.6</td>
<td>+0.3</td>
<td>209</td>
<td>+4</td>
</tr>
<tr>
<td>S</td>
<td>14.1</td>
<td>-0.2</td>
<td>230</td>
<td>+25</td>
</tr>
</tbody>
</table>

There is an overall tendency for temperature and precipitation estimates to be increased when data is lost, although this is not really significant unless all information about a particular physiognomic feature of a flora is absent,
which in reality is an extremely rare situation. Different features seem to have more bearing on either the temperature or precipitation estimates. Loss of information on base shape, length-to-width ratio and apex shape most affect temperature estimates, whereas that lost for margin type and leaf shape most affect precipitation estimates. Data loss for leaf size and margin type affect estimates of both, and are therefore inferred to be the most important physiognomic variables in determining palaeoclimates. It is interesting to note that a 66% loss of information for margin type causes an overestimate of temperature of 1.6°C whereas 100% loss yields an underestimate of only 0.3°C.

From the results of this analysis, it seems viable to use the CLAMP method for palaeoclimatic determinations from fossil floras which have some morphological information absent, and in reality it is often the only option that is available.
### 6.3 RESULTS OF LEAF PHYSIOGNOMIC ANALYSES

#### 6.3.1 Clamp results

**TABLE 6.31: Results of CLAMP palaeoclimatic determinations**

<table>
<thead>
<tr>
<th>SITE</th>
<th>M.A.T. /°C</th>
<th>M.A.P. /cm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>KSD 1.0</td>
<td>14</td>
<td>340</td>
</tr>
<tr>
<td>KSD 2.0</td>
<td>10.5</td>
<td>290</td>
</tr>
<tr>
<td>KSD 3.0</td>
<td>14</td>
<td>360</td>
</tr>
<tr>
<td>KSD 4.0</td>
<td>13</td>
<td>250</td>
</tr>
<tr>
<td>KSD 5.0</td>
<td>7.5</td>
<td>210</td>
</tr>
<tr>
<td>KSD 7.0</td>
<td>13.5</td>
<td>270</td>
</tr>
<tr>
<td>KSD 8.0</td>
<td>10</td>
<td>275</td>
</tr>
<tr>
<td>KSD 9.0</td>
<td>14</td>
<td>370</td>
</tr>
<tr>
<td>KSD 10.0</td>
<td>7.5</td>
<td>160</td>
</tr>
<tr>
<td>KSD 11.0</td>
<td>17</td>
<td>390</td>
</tr>
<tr>
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6.311 Raton Basin

CLAMP applied to post boundary floras indicates general mean annual temperatures of between 10-14°C although there is variation from 7-17°C (Figure 6.311a/c). These levels remain similar throughout the barren series and the upper coal zone, with average mean annual palaeotemperatures of 12°C (Figure 6.311a). There is distinct dissimilarity between these results and the CLAMP estimates obtained by Wolfe (1990), which suggest a M.A.T. 5-6°C higher than those of the late Cretaceous, when M.A.T.s were within the megathermal climatic regime of greater than 20°C (Wolfe and Upchurch 1987c), and a 10°C increase following the boundary event.

Two estimates for latest Cretaceous M.A.T.s gave widely varying results but these calculations are based on very low diversity floras (7 and 3 morphotypes) which may explain this. The latest Cretaceous appeared to be relatively dry (Wolfe and Upchurch 1987b & site KSD 15.0 - 170cm/yr), and it is proposed that floras from climatic regimes with low mean annual rainfall have very variable entire leaf margin to M.A.T. ratios (Wing and Greenwood 1993) which could also account for this.

Estimates for mean annual precipitation are also variable, although they appear to be much greater than for the latest Cretaceous. Post boundary levels vary from 270-390 cm./yr (Figure 6.311b/d), although site KSD 91 10.0 (Clear Creek North) records a significantly lower level of 160 cm./yr. Throughout the rest of the early Palaeocene, levels remain high at between 200-350 cm./yr (Figure 6.311b/d), with a slight decline during the barren series, followed by a rebound to higher levels in the upper coal zone, although this is still not as high as is seen immediately after the boundary event.
6.312 Powder River Basin
The sole mean annual palaeotemperature estimate for this region is 12°C with precipitation of 230cm./yr.

6.313 Williston Basin
Mean annual temperatures from the very earliest Palaeocene floras (Uppermost Hell Creek Formation) average at around 10°C, approximately analogous to the mesothermal-microthermal boundary, and remain steady into the Tullock Formation (figure 6.313a). Estimates can be as high as 13°C, but there is one which is anomalously low at 4.5°C (KSD 91 25.0, Last Day Bluff). However, this site has a flora with only five morphotypes which is derived from a restricted depositional channel environment. This would explain the anomaly, as it is known that floras derived directly from channel deposits do not yield reliable palaeoclimatic results (Burnham 1987). Precipitation levels remain constant throughout the early Palaeocene, at around 160-190cm./yr with no discernible trends (Figure 6.313b). There are two anomalous results, one is associated with the low diversity flora of KSD 91 25.0, described above, and the other is also associated with a low diversity flora (KSD 91 22.0C, 9 morphotypes), and suggests an M.A.P. of 280cm./yr. It also records a slightly higher mean annual temperature than other floras.

6.32 L.M.A. results
Graphic methods were used to determine palaeotemperatures following the temperature entire-margin relationship derived by Wolfe (1979), and utilised by Wing and Greenwood (1993) (figures 6.221 A & B). Although Wolfe (1979) and Wing and Greenwood (1993) use the same graphic relationship between the percentage of entire-margined leaves and temperature to determine palaeotemperatures, the equation for this relationship is not published, so the
gradients of the linear relationship derived from each plot had to be used. Using the two gradients ensures that results were reproducible and errors were kept to a minimum. The second method (Wing and Greenwood 1993) yields slightly higher results, but this is attributed to the graphic reproduction.
**TABLE 6.32: RESULTS FROM L.M.A. ANALYSIS**

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6.321 Raton Basin

L.M.A. suggests that climates in the Raton Basin throughout the early Palaeocene are broadly subtropical, verging on a megathermal climatic regime, with mean annual temperatures between 15-20°C (Figure 6.321a). The six post boundary floras suggest high temperatures of around 20°C, apart from site KSD 91 8.0 (Berwind Canyon road section) which yields an inferred temperature of only 13-14°C. The majority of these floras are of low diversity (all under twenty morphotypes bar one) which will have affected the results. However, the two floras collected from the same stratigraphic level but at different lateral positions at site KSD 91 9.0 (Starkville south), gave very similar palaeotemperature estimates of 21/22°C and 23/24°C, despite their different diversities of fourteen and twenty one morphotypes. Temperatures remain high, approaching 20°C, at the top of the lower coal series and into the barren series, although the uppermost site within this group of floras (KSD 5.0 Potato Canyon Rd) yields an apparently anomalously low figure of 9°C. The lack of collecting sites within the barren series means that it is difficult to infer whether this is a real temperature low at this time or just an anomalous result due to depositional setting. The fact that this site is the most diverse within this uppermost lower coal zone/barren series group of floras may be significant. Floras from sites in the upper coal zone again yield mean annual palaeotemperatures of between 15-20°C, indicating continuing subtropical conditions at this latitude of 45°N.

Late Cretaceous temperatures are highly disparate. This is probably due to low precipitation levels causing irregular relationships between leaf margin and mean annual temperature (for full explanation see section 6.221).
6.322 Powder River Basin

The only M.A.T. derived from L.M.A. is from site KSD 91 17.0, and it suggests a palaeotemperature of 15.5/16.5°C, cooler than the more southerly Raton Basin.

6.323 Williston Basin

M.A.T. estimates from leaf margin analysis are significantly lower for floras of the Williston Basin than they are for those of the Raton Basin, with a predominant mesothermal climate. In the uppermost Hell Creek Formation (earliest Palaeocene), mean annual temperatures are around 10°C (Figure 6.321b) but then a distinct drop is observed, to mean annual temperatures as low as 3-4°C for floras with diversities of around twenty morphotypes. This seems unlikely considering the other palaeoclimatic evidence from this time, such as the presence of large, ectothermic animals (Nichols et al. 1989) and palms, which indicates higher temperatures. Within the lower Tullock Formation mean annual temperatures are of levels similar to those of the earliest Palaeocene, in the region of around 10°C, although the low diversity flora (5 morphotypes) from KSD 91 25.0 infers one of 1°C which appears to be erroneous and similar to that obtained from CLAMP.

Considering that Wolfe (1985) stated that L.M.A. should ideally be carried out on floras with 30 or more species/morphotypes the validity of these results, which were obtained from floras with a maximum number of twenty six morphotypes but generally lower than this, is put into some doubt. Estimates seem to be better for floras from the warmer, southerly Raton Basin than the more northerly Williston Basin. Burnham (1987a) has suggested that L.M.A. is particularly effective for predicting M.A.T. from floras with high
proportions of entire margined leaves, so this could be related to the greater proportion of entire margined leaves present in floras from the Raton Basin.

**6.33 Comparison of CLAMP and L.M.A. results**

Temperatures derived from CLAMP analysis are significantly different from those derived from leaf margin analysis, although exactly the same data set was used for both. In the Raton Basin CLAMP mean annual temperature estimates are consistently lower than those obtained by leaf margin analysis by up to 8°C. In the more northerly Williston Basin temperatures derived from CLAMP are consistently higher than those obtained from leaf margin analysis by up to 8°C, although generally differences are somewhat smaller. In both cases the same overall trends are observed, and the variance between the two differently derived temperatures remains constant. The number of morphotypes in a flora bears little relationship to the disparities between the determined palaeotemperatures, so they cannot be explained by unreliable results obtained from low diversity floras.

Consistently lower temperatures derived from leaf margin analysis of Williston Basin floras may be associated with a selection for deciduousness at the boundary (Wolfe 1987 and section 4.5), causing margin characteristics to be out of equilibrium with prevailing climatic conditions. The multivariate nature of CLAMP dampens such affects, giving possibly more realistic estimates of palaeotemperature. The low palaeotemperatures derived for the Williston Basin are, however, in keeping with those described by Upchurch (1989) for the northern region of the western interior.

A preference for deciduous species following the boundary event, however, can not explain the discrepancy between temperature estimates derived from
floras of the Raton Basin. The relatively high proportion of entire margined leaves in the earliest Palaeocene would imply that there was no such preference at these lower latitudes, a conclusion that is in contrast to that of Wolfe (1987). The increase of deciduous species could also be related to a general increased seasonality in climate following the boundary event (see sections 6.63 and 6.64).

Wing and Greenwood (1993) used both a multiple regression approach based on CLAMP, with a reduced number of predictor variables, and L.M.A. to determine Eocene palaeoclimates from palaeobotanical data and found that there was a general agreement between results from the two methods. They concluded that this was because margin configuration is the most important floral indicator of palaeoclimatic variables. The modifications they used may improve the reliability of CLAMP as it reduces the disparity between results obtained using the two different methods in this study.

6.4 CLIMATE OF THE LATE CRETACEOUS

6.41 General late Cretaceous climate

There is much evidence to suggest that the climate of the Late Cretaceous was far more equable (Smit and Van der Kaas 1984) and warmer, than that experienced today. Here, equability is used in the sense of similar climates experienced over broad latitudinal areas. The apparent lack of permanent ice at the poles and configuration and topography of land masses implies that temperatures were higher than that of the present (Barron and Washington 1984, Spicer and Parrish 1990). Latitudinal temperature gradients were lower than the present day and have been estimated as between 0.3°C/1° latitude
from North American terrestrial evidence (Wolfe and Upchurch 1987) to 0.14°C/1° latitude from marine evidence (Spicer and Corfield 1992). There also appears to have been minimal seasonality in climate at high latitudes in the northern hemisphere (Spicer 1989).

6.42 Late Cretaceous 'Greenhouse condition'

It has been proposed that these late Cretaceous high temperatures were caused by raised atmospheric CO₂ (Hansen 1990), causing a 'greenhouse condition'. Horrell (1991) provides a review of the evidence for such conditions which comes from the sedimentological, palaeobotanical and geochemical records. A number of theories have been described to explain this 'greenhouse warming'. McLean (1978a) considers that deep ocean waters were triggered in to releasing vast amounts of CO₂ in to the atmosphere in a chain reaction of climate warming and carbon dioxide expulsion, but the source of that initial trigger is problematic. He also suggests (1978b) that the widespread regression of epeiric seas at this time would result in an increase of total world primary productivity, and that this in turn would affect carbon dioxide variability. Intense late Cretaceous volcanism, particularly the extrusion of the Deccan Traps, has also been cited to explain CO₂ increases (Herman 1985). The Deccan Traps were extruded over a time span of 500,000 years across the Cretaceous-Tertiary boundary (Courtillot et al 1990), and would have added to atmospheric carbon dioxide levels, exacerbating the greenhouse conditions (see section 2.9). It is evident, however that by the latest Cretaceous there is some breakdown of the 'Greenhouse condition' and deterioration of equability and climate as a whole (Savin 1972, Hickey 1981, Spicer 1990 and see section 6.5), is experienced.
6.5 NON-FOSSIL ANGIOSPERM EVIDENCE FOR CLIMATE ACROSS THE CRETACEOUS TERTIARY BOUNDARY

6.5.1 Cretaceous-Tertiary climates from palynology

In general palynological studies do not support theories for sudden, wide-ranging climatic changes throughout the late Cretaceous and early Tertiary (Jarzen 1977, Tschudy 1984, Nichols et al 1986). Instead, they tend to imply more gradual climate change, but it is possible that a brief period of climatic perturbation occurred at the boundary which was of such a short time scale that it does not leave any evidence in the palynological record. The palynological record may tend to smooth out climatic signals that appear more sudden from palaeobotanical studies. This is because pollen and spores are more enduring than fossil leaves and may therefore remain within an ecosystem far longer, before being secured in the rock record. They also exhibit less physiognomic change to climate than do megafossils and are susceptible to syn-depositional reworking.

Nichols et al (1986) have discovered pollen of palms and screw pines (Pandanus) throughout boundary sections in Saskatchewan in accordance with hypotheses of an overall warm, equable climate. However, there are a number of conflicting palynological observations that suggest climatic changes at this time. Frederiksen (1989) analysed pollen from the late Cretaceous and early Tertiary of New England and found evidence to suggest warmer and more moist conditions following the boundary, whereas a drop in the number of pollen species across the boundary period in eastern Montana (Hall and Norton 1967) and a shift from angiosperm to gymnosperm domination in the pollen record of the same area (Nichols et al 1986) have been attributed to a temperature drop. Hickey (1984) describes an
increased severity of angiosperm extinction towards the north in the *Aquilapollenites* province and has suggested that this was due to climatic deterioration, accompanied by a steepened temperature gradient from the south to north at the end of the Cretaceous, coincident with deterioration of the 'greenhouse condition'. A trend for increased proportions of pollen adjusted to wind pollination following the Cretaceous-Tertiary boundary is observed in Canadian sections (Jarzen 1977) which is seen as an adaptation to increased dry/wet, and cool/warm seasonality.

### 6.52 Cretaceous/Tertiary boundary climates from marine isotopic evidence

Marine oxygen isotopes suggest that there was global cooling throughout the Late Cretaceous from Albian times (Spicer and Corfield 1992), both in equatorial and polar regions, and this appears to correlate with declining atmospheric CO₂. Savin (1972) reports that the temperature minimum was in the early Maastrichtian, although there may also have been a temperature drop prior to the boundary itself. In the early Palaeocene, evidence points to a warming of surface waters (D’Hondt and Lindinger 1988), with temperature gradients still low and tropical-subtropical species forming significant proportions of nannoplankton assemblages poleward of 30°N (Wolfe and Poore 1986). Oceans are somewhat buffered to temperature change and therefore the likely affects of a proposed short post-impact cool period may not be experienced, or recorded as strongly as in terrestrial environments.

### 6.53 Climatic inferences from sedimentary evidence

Sedimentological evidence indicates that the amount of standing water on land increased dramatically in the earliest Palaeocene (Favstovsky 1987) of North America, and it has even been suggested that there was extensive flooding during the Cretaceous-Tertiary transition period (Favstovsky *et al*
1989). This is commensurate with the abundance of water plants observed at and just above the boundary in the northern great plains (see section 4.43). Gley soils observed in the northern area of the Western Interior at this time do not only indicate abundance of water but also seasonality (Favstovsky and McSweeney 1987). Impure coal horizons of the uppermost Hell Creek Formation also indicate seasonally dry swamps. Palaeosols, containing dispersed carbonate, from the same section as the coals, suggest a subhumid climate. Both are evidence of waterlogging (Retallack et al. 1987). In the overlying Tullock Formation, thick coal horizons and fossilised trunks (also found at McGuire Creek), are indicative of permanently waterlogged swamps and high humidity (Retallack et al. 1987). Most sedimentologic evidence points to prevailing humid, slightly cooler conditions than the Late Cretaceous in the early Palaeocene, with increased climatic seasonality.

6.6 K-T BOUNDARY CLIMATIC DETERMINATIONS FROM FOSSIL FLORAS:

6.6.1 Cretaceous-Tertiary climates form non North American floral evidence
There is little data for palaeoclimatic interpretations based on terrestrial evidence from outside North America. There is however, some from Asia and high latitude regions, mainly Alaska.

Floras from Eastern Asia suggest that there was a rise in temperature up until the Campanian and that this was then followed by minor cooling in the Coniacian and subsequent deterioration of climate throughout the boundary period, culminating in the late Danian (Krassilov 1975).
In both of the earth's polar regions a gradual cooling trend is observed during the latest Cretaceous (Askin 1988, Spicer and Parrish 1990), such that cool temperate climates occurred above palaeolatitudes of 75° in the late Cretaceous and early Tertiary. Tree ring data from the North Slope of Alaska indicates distinct seasonality at this time (Spicer 1990) with dark, cool winters (Clemens and Nelms 1992), when temperatures seldom dropped below freezing in coastal areas, but where winter freezing probably occurred in continental areas (Spicer and Parrish 1990). Parrish and Spicer (1988) recognise an increase in temperature from the Cenomanian to the Coniacian, followed by a decline from the Campanian to Maastrichtian on the Alaskan North Slope, with the temperature maximum near the middle of the late Cretaceous (Spicer and Parrish 1988). The late Cretaceous Arctic coastal plain vegetation experienced M.A.T.s of 6-13°C whereas Palaeocene estimates are lower, at MAT 6-7°C. (Spicer and Chapman 1990). High diversity in southern Alaska Palaeocene floras has been related to renewed global warming (Spicer et al 1987), but this must have been short lived because although floras from the early Palaeocene of south east Alaska have 50% entire margins, later in the Palaeocene this has decreased by 10%, with increasing deciduoussness implying cooling form the early to late Palaeocene (Wolfe 1972). The climate became more irregular and unfavourable for high latitude plants at this time (Spicer and Chapman 1990).

The Palaeocene Agatdalen flora of Western Greenland is suggestive of mesothermal climates with M.A.T. > 13°C but < 20°C (Wolfe 1980). In north-eastern Siberia, floras from the Rarytkinian Formation (Late Maastrichtian-Danian) indicate cooling and humidization, as is seen in North American floras, but this apparently occurs prior to the boundary event, at the base of the upper Maastrichtian (Golovneva, in press).
6.62 Latest Cretaceous climates from fossil floras of North America

Palaeobotanical evidence from the Late Cretaceous of North America indicates a temperature increase from the Cenomanian to Santonian, a slight decline into the Campanian, further decline in the early Maastrichtian then a rebound to Santonian levels by the late Maastrichtian (Wolfe and Upchurch 1987, Upchurch 1989). Johnson et al. (1989) also suggested late Cretaceous climatic warming using palaeobotanical evidence from N. Dakota but Hickey (1977) implied late Cretaceous through to early Palaeocene cooling accompanied by increased continentality and seasonality (Hickey 1981), from megafloral evidence in mid to high latitudes.

Wolfe and Upchurch (1987c) summarise late Cretaceous precipitation patterns. Low-moderate rainfall was experienced at low latitudes moderately increasing at palaeolatitudes from 40-50°N, and this was evenly distributed throughout the year. Mesothermal regimes between 50-65°N experienced mild seasonality and variable annual precipitation. Equability meant that late Cretaceous isotherms were displaced northwards with the mega-mesothermal boundary (20°C) at 40-50°N and the meso-microthermal boundary (13°C) at 65-75°N. (Upchurch 1989).

6.63 Early Palaeocene palaeoclimates from non-angiosperm plants of North America

6.631 Palms

Palms grow under very specific conditions and will not tolerate temperatures much less than freezing. Their preference is for mild climates, with rare frosts, and cold month means greater than 5°C. This means that, presuming these tolerances have not changed through time, the presence of palms in the fossil record of the early Palaeocene is useful in inferring palaeoclimates.
Palms have been found at most sites in the Raton Basin, occurring from a couple of metres above the boundary, through the barren series and in to the upper coal series. There appear to be no palms preserved just above the boundary within the upper most part of the lower coal series. Palaeoclimatic determinations (sections 6.31 and 6.32) suggests that temperatures were high enough at this time to support the widespread growth of palms in the area so their absence may be an artefact relating to a brief, cold, impact winter which temporarily saw the exclusion of palms in the area. If this is true then there must have been refugia enabling recolonisation of the area by palms, by the time deposition of the barren series was initiated.

In the southern Powder River Basin (KSD 93 1.0) palms are found within a couple of metres of the boundary, but are rare within the Williston Basin suggesting that winter temperatures at this higher latitude (55°N) only bordered on those high enough to support palms. This does not necessarily mean long periods of low temperatures, occasional hard freezes would facilitate this.

6.632 Water plants

An abundance of water plants allied to *Nelumbo, Paranympheae* and *Azolla* are found in the earliest Palaeocene of sites in the McGuire Creek area of the Williston Basin (sites KSD 91 20.0 & 21.0) and at Teapot Dome (sites KSD 93) in the southern Powder River Basin. This suggests that there were significant amounts of standing water at this time in the north-central area of the North American continent following the Cretaceous-Tertiary boundary. Ponds of small lateral extent were widespread on floodplains, and were permanent enough to allow the development of abundant water plants. In turn, this suggests that levels of precipitation and water tables were higher in the early
Palaeocene than they were in the Late Cretaceous, when water plants were not so abundant, implying that precipitation levels increased across the Cretaceous-Tertiary boundary.

6.633 Conifers

Conifers allied to *Glyptostrobus*, *Taxodium* and *Metasequoia* are absent in the Raton and Powder River Basins, but are observed at a number of sites within the Williston Basin (KSD 91 22.0, 23.0 and 24.0). Their presence suggests more temperate, meso-microthermal conditions. *Metasequoia* is also indicative of relatively wet conditions (Burnham 1987).

6.64 Earliest Palaeocene palaeoclimates from fossil floras of North America

Wolfe & Upchurch (1987a) see no overall climatic difference between the latest Cretaceous and earliest Palaeocene from paleobotanical evidence. Nichols *et al* (1989) also propose that the presence of large, ectothermic reptiles across the boundary period in the northern Western Interior indicates that there was no general climatic deterioration from the late Maastrichtian to the early Palaeocene, conditions remaining mesothermal. Results from this study are not in agreement with this and indicate that temperatures were slightly lower across the American continent than has previously been suggested at this time (see section 6.3), and certainly lower than those previously suggested for the latest Cretaceous (Wolfe and Upchurch 1987a).

This trend, however, is in approximate accordance with Upchurch (1989) who suggests a temperature decline in the northern Great Plains; but it is not of the same magnitude that he suggests, which is up to 10°C with a mean cold month temperature below freezing. The low occurrence of palms in the Williston Basin (see section 6.631) may suggest periodic winter freezing, and
temperatures derived from L.M.A./CLAMP analyses (tables 6.31 and 6.32) place the region on the microthermal/mesothermal boundary, with M.A.T. at around 12°C, but with a post-boundary colder spell.

The Raton Basin consistently has temperatures approaching megathermal, at around or just below 20°C. Limited results from the Powder River Basin suggest an earliest Palaeocene climatic regime just within mesothermal temperature regime, with mean annual temperatures around 13-14°C. Palaeocene floras from S.E. U.S.A. suggest cooling throughout the Palaeocene period (Wolfe 1978). Wolfe and Upchurch (1987b) propose that in Lance/Tullock time the megathermal/mesothermal ecotone (20°C isotherm) lay in the south part of Powder River Basin. They suggest (Wolfe and Upchurch 1987a) that megathermal conditions were predominant in the Raton Basin throughout the whole of this period, with temperatures greater than 20°C, but estimates from this study (section 6.31 and 6.32) imply that mean annual temperatures in the Raton Basin, in the earliest Palaeocene, were around the 20°C level (figure 6.31la & 6.321a), which is at the megathermal/mesothermal boundary point. This suggests that the megathermal/mesothermal ecotone lies nearer to the Raton Basin at around 45°N palaeolatitude.

The mesothermal/microthermal boundary (13°C) appears to lie in the south of the Williston Basin at around 55°N, although anomalous results for palaeotemperatures (see section 6.32) may mean that it was located at a more northerly position. The position of the mega-mesothermal boundary is displaced slightly north to that suggested for the late Cretaceous by Wolfe and Upchurch (1987c), but the meso-microthermal boundary appears to be displaced distinctly northwards from its late Cretaceous position, indicating
that although there was continuing significant poleward displacement of major isotherms (Upchurch 1989) and temperature gradients were still less than 1°C/1°pl., conditions of climatic equability were decreasing into the Palaeocene.

It has been suggested that observed vegetational changes following the boundary event may be attributed to a brief, cold 'impact winter' of one to two months duration (Wolfe and Upchurch 1986) which caused a selection for deciduous species, better adapted to the onset of a sudden harsh climate. Evidence for such a sudden post-boundary cold period has been observed by Wolfe (1991) who identified structures in the cuticles of fossil water lilies as being formed by rapid freezing caused by the effects of an impact-derived dust cloud. If such an event did occur, then floral physiognomy following this may have consequently been out of step with climate causing inaccurate climatic determinations. Anomalously low temperatures are obtained from L.M.A. at sites in the Williston Basin (section 6.323) and this correlates with Wolfe's analysis of the Brownie Butte (Williston Basin) assemblage (1990) where 27% entire margins implied MAT of 10°C but CLAMP indicated higher temperatures. Analysing entire margin data from boundary floras, Wolfe (1990) inferred a gradual temperature decrease across the boundary, but other correlations he carried out (Wolfe 1990) indicated that there was no overall temperature change. This all intimates that a sudden but brief post-boundary cold spell could have caused a selection for deciduous life habits. However, from work in this study, it seems that such a selection was not uniform over the whole of North America. Percentage of entire leaf margins are relatively high within the Raton Basin for the early Palaeocene, and L.M.A. suggests megathermal temperatures. Apparently, leaf margins were not drastically affected. There is also considerable evidence for an increase in seasonality in
the early Palaeocene (section 7.6) which would also have caused an increased proportion of deciduous (non entire-margined) leaf forms

Wolfe (1990) inferred a four fold precipitation increase at the boundary, from CLAMP analysis of Western Interior floras, with levels persisting for 0.5-1.0 million years after the event, then decreasing to three times late Cretaceous levels. Nichols et al. (1989) suggest a similar pattern from work on the Powder River Basin with precipitation increasing from the late Maastrichtian into the early Palaeocene, then moderately declining into the time of deposition of the Lebo member of the Fort Union Formation. Increased precipitation in the early Palaeocene is supposedly most pronounced south of 48°N. (Upchurch 1989). This correlates well with CLAMP determinations of this study (section 6.31) which indicate very high levels of precipitation in the earliest Palaeocene throughout the Western Interior. Precipitation is particularly pronounced in the Raton Basin where mean annual precipitation estimates are approximately 100cm. greater, at between 270-390 cm/yr, than for floras from the Williston Basin. Mean annual precipitation levels remained at between 160-190 cm/yr throughout the early Palaeocene in the Williston Basin, but were higher at around 230 cm/yr in the more southerly Powder River Basin (tables 6.31 and 6.32, figs 6.311b/d & 6.313b). It seems a gradation can be identified across the Western Interior, from high levels of precipitation in the warm, more southerly Raton Basin through to lower levels in the cooler, Williston Basin, although levels in all areas are still considerably higher than those suggested for the latest Cretaceous (Wolfe and Upchurch 1987c). A trend for a slight decrease in precipitation levels in the early Palaeocene, following the initial peak, is observed in the barren series of the Raton Basin. This is succeeded in the upper coal series by a rebound to mean annual precipitations nearly as high as post-boundary levels (figs 6.311b/d).
Similar trends are not easily discernible in the Williston and Powder River Basins. It may be that precipitation was even higher than has been suggested here, because Greenwood (1993) has stated that fossil floras preserve consistently smaller leaves than those present in their source flora due to taphonomic processes. If this is the case, then systematically lower estimates for mean annual precipitation estimates will be derived from physiognomic analyses of fossil floras.

It is possible that the increase of angiosperm leaves of deciduous aspect can be related to an increased aseasonality of early Palaeocene climates, and that a selection for deciduousness is not a survival mechanism in response to a brief impact-related cold period at the Cretaceous-Tertiary boundary. Gley soils and thin, impure coal seams (section 6.53) abundant in the northern Great Plains in the earliest Palaeocene (Favstovsky and McSweeney 1987) indicate increased seasonality, as does fossil wood (Wheeler and Baas 1991). Other evidence for seasonal climatic regimes comes from the sections studied at Tea Pot Dome (KSD 93 2.0, section 4.51) which suggest periodic leaf abscission, probably associated with deciduousness and seasonal leaf loss.

**6.7 CONCLUSIONS**

Results of an experiment to test the validity of using CLAMP for floras which do not retain all morphological characters, indicated that loss of foliar physiognomic information does not considerably alter palaeoclimatic determinations, so it is recommended that CLAMP can be viably used under such circumstances. The experiment also revealed that CLAMP estimates are most sensitive to loss of information about leaf margin and size which implies that these characters are the most important in determining palaeoclimates. The comparison of CLAMP and L.M.A. estimates for
palaeotemperature in this study indicate that in megathermal climatic regimes L.M.A. gives consistently higher figures than CLAMP, but for mesothermal climatic regimes, figures are consistently lower. It is suggested that this is due to higher proportions of entire-margined leaves in megathermal regimes, affording greater accuracy to L.M.A. estimations.

Temperature estimates and trends derived from CLAMP and L.M.A. in this study show that in the early Palaeocene of North America, temperatures decreased slightly from their late Cretaceous levels, particularly in the northern part of the region, although no evidence was found for an 'impact winter'. Temperature decreases across the continent caused a shift southwards of climatic zones from their positions in the latest Cretaceous, together with a steepened north-south temperature gradient. In the Raton Basin megathermal conditions prevailed with the megathermal-mesothermal border located just to the north of the basin. In the Williston Basin mild, mesothermal climates existed with the mesothermal-microthermal boundary located to the north of the basin. CLAMP determinations show that precipitation increased significantly everywhere across the North American continent following the boundary event, but was particularly pronounced in the south. Precipitation levels decreased somewhat after this initial peak, but remained high throughout the early Palaeocene. Varying evidence both from this study and analysis of previous work suggests that seasonality increased from the Late Cretaceous into the Palaeocene, but was more pronounced in central and northerly areas of the North American continent.
L.M.A. GRAPH (from Wolfe '79)

\[ y = 1.0000 + 0.30000x \quad R^2 = 1.000 \]

L.M.A. GRAPH (From Wing and Greenwood '93)

\[ y = 1.0524 + 0.30995x \quad R^2 = 0.999 \]

FIGURES 6.221A & B: L.M.A. GRAPHS USED TO DETERMINE PALAEOTEMPERATURE
LEAF SIZES IN SQUARE mm

<table>
<thead>
<tr>
<th>CATEGORY</th>
<th>SIZE/mm</th>
<th>CATEGORY</th>
<th>SIZE/mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepto I</td>
<td>0-25</td>
<td>Micro III</td>
<td>1325-3550</td>
</tr>
<tr>
<td>Lepto II</td>
<td>25-80</td>
<td>Meso I</td>
<td>3550-6180</td>
</tr>
<tr>
<td>Micro I</td>
<td>80-400</td>
<td>Meso II</td>
<td>6180-9590</td>
</tr>
<tr>
<td>Micro II</td>
<td>400-1325</td>
<td>Meso III</td>
<td>9590-14420</td>
</tr>
</tbody>
</table>

FIGURE 6.232A: CLAMP LEAF SIZE CATEGORIES
APEX
EMARGINATE: Most apical part of leaf convexly curves towards base
ROUNDED: Smooth arc across apex
ACUTE: Straight margins in apical third of leaf
ATTENUATE: margins change from linear/convex to concave in apical fourth of leaf. This extends for 1cm

BASE
CORDATE: Leaf base embayed in a sinus whose sides are straight-concave
ROUNDED: Margins form smooth convex arc across base
ACUTE: Straight to convex margins in basal fourth of leaf

SHAPE

OBOVATE
Axis of greatest width intersecting long axis of leaf in its apical third

ELLiptical
Axis of greatest width perpendicular to midpoint of leaf axis

OVATE
Axis of greatest width intersecting long axis of leaf in its basal third

MARGIN

LOBED: Line drawn through the sinuses parallels midrib
NO TEETH: Entire margin

Tth ROUND: Basal and apical flanks of tooth are convex and convexity extends to tip of tooth
Tth COMPOUND: Tooth has smaller teeth on (typically) basal flank
Tth ACUTE: Apical and basal flanks of tooth form a sharp point
Tth CLOSE: Basal flank of tooth is 3x or less than that of apical flank
Tth REGULAR: Interval between corresponding points on teeth varies by no more than 30%

Information about leaf size scoring can be found in figure 6.232A

FIGURE 6.232B: AN EXPLANATION OF CLAMP SCORING CATEGORIES
(after Wolfe (in press))
FIGURE 6.232C: CLAMP axis 1 against axis 2
with selected physiognomic characters plotted

FIGURE 6.232D: CLAMP axis 1 against axis 2
with selected areas of vegetation plotted
(Not included in CLAMP data set used in analysis)
FIGURE 6.232e: EXAMPLE OF CLAMP AXIS ONE vs M.A.T. PLOT WITH REGRESSION USED TO DETERMINE M.A.T.
FIGURE 6.311a: RATON BASIN: M.A.T. vs STRATIGRAPHIC POSITION

FIGURE 6.311b: RATON BASIN: M.A.P. vs STRATIGRAPHIC POSITION
**KEY TO GRAPHS: DEPOSITIONAL ENVIRONMENTS**

- △ Crevasse splay
- △ Cut-off lake
- △ Lake (extensive)
- △ Channel
- △ Lake (small scale)
- △ Swamp/marsh
- △ Overbank

These symbols relate graphs drawn to show diversity and climatic trends throughout the early Palaeocene (figures 5.35A, 5.35B, 6.311A, 6.311B, 6.311C, 6.311D, 6.313A, 6.313B, 6.321A, 6.321B). They indicate from which particular depositional environment the flora providing the data was derived.

**STRATIGRAPHIC CORRELATIONS**

**Raton Basin:** between zero and ten metres above the boundary (KSD 91 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0) sites are vertically measured from the boundary, although correlation between sites is not possible. For sites higher up in the Palaeocene within the Barren Series (KSD 91 3.0, 4.0 and 5.0), correlation is by palynologic zonation (after Fleming, pers. comm. 1991), together with height above boundary. For sites more than 200m above the boundary (KSD 91 1.0 and 2.0) correlation is lithologic between sites, and by reference to core data provided by York Canyon Mine (R. Pillmore, pers. comm. 1991) for stratigraphic position relative to other sites. See also section 3.21 for a fuller explanation.

**Williston Basin:** between zero and two metres above the boundary, sites are lithologically correlated. Above this they are positioned stratigraphically from their relationship to the alphabetically named sequence of coals within the Tullock Formation together with reference to data from U.S.G.S. field note books. See also section 3.21 for a fuller explanation.
Figure 6.311a: Raton Basin: M.A.T. vs Stratigraphic Position

Figure 6.311b: Raton Basin: M.A.P. vs Stratigraphic Position

0-10m above K-T Boundary (KSD 91 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0): sites vertically measured from the boundary, although correlation between sites is not possible. 10-200m above K-T Boundary (KSD 91 3.0, 4.0 and 5.0): site correlation is by palynologic zonation (after Fleming, pers. comm. 1991), together with height above boundary. 200m or more above K-T Boundary (KSD 91 1.0 and 2.0): correlation is lithologic between sites, and by reference to core data provided by York Canyon Mine (R. Pillmore, pers. comm. 1991) for stratigraphic position relative to other sites.
0-10m above K-T Boundary (KSD 91 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0): sites vertically measured from the boundary, although correlation between sites is not possible. 10-200m above K-T Boundary (KSD 91 3.0, 4.0 and 5.0): site correlation is by palynologic zonation (after Fleming, pers. comm. 1991), together with height above boundary.
0-2m above K-T Boundary (KSD 91 20.0 & 22.0) sites lithologically correlated.
2m or more above K-T Boundary (KSD 91 19.0, 24.0, 25.0) sites stratigraphically positioned from their relationship to the alphabetically named sequence of coals within the Tullock Formation together with reference to data from U.S.G.S. field note books.
0-10m above K-T Boundary (KSD 91 7.0, 8.0, 9.0, 10.0, 11.0, 12.0, 13.0): sites vertically measured from the boundary, although correlation between sites is not possible. 10-200m above K-T Boundary (KSD 91 3.0, 4.0 and 5.0): site correlation is by palynologic zonation (after Fleming, pers. comm. 1991), together with height above boundary. 200m or more above K-T Boundary (KSD 91 1.0 and 2.0): correlation is lithologic between sites, and by reference to core data provided by York Canyon Mine (R. Pillmore, pers. comm. 1991) for stratigraphic position relative to other sites.
FIGURE 6.321b
WILLISTON BASIN: M.A.T. (L.M.A.) vs STRAT. POSITION

Stratigraphic position above KTB in metres

WILLISTON BASIN: M.A.T. (L.M.A.2) vs STRAT POSITION

Stratigraphic position above KTB in metres

0-2m above K-T Boundary (KSD 91 20.0 & 22.0) sites lithologically correlated.
2m or more above K-T Boundary (KSD 91 19.0, 24.0, 25.0) sites stratigraphically positioned from their relationship to the alphabetically named sequence of coals within the Tullock Formation together with reference to data from U.S.G.S. field note books.
CHAPTER SEVEN

DISCUSSION
CHAPTER SEVEN

DISCUSSION

7.1 GENERAL EARLY PALAEOCENE ENVIRONMENT

The general early Palaeocene environment in the Western Interior of North America, appears to have been rather homogeneous with floral diversity relatively low, although not as low as has previously been suggested. In the Williston Basin low-lying swamps, facilitating the build up of thin coal bands, and small lakes, inhabited by aquatic plants, were interspersed with raised areas with a more diverse vegetation. Sites in the Powder River Basin record extensive lacustrine and swampy conditions at this time, but these are interspersed with better drained flood plain and channel environments. Although morphological analysis of vegetation implies that precipitation levels were higher in the more southerly Raton Basin, swamps were not predominant here in the earliest Palaeocene. Instead, meandering rivers on a broad flood plain were the predominant depositional environment. Soon after the boundary event, coarser grained deposits dominated and this has been related to increased tectonism in the source area (Flores 1987), but the increase in precipitation may have exacerbated the effect, by causing enhanced run off and erosion. This influx of coarse grained sediments is also observed at Tea Pot Dome, some 20m above the boundary, and in the Williston Basin with the onset of deposition of the Tullock Member of the Fort Union Formation.
7.2 TAPHONOMIC BIASES WITHIN FLORAS

Comparing diversities, composition and similarities of floras collected from the range of depositional environments described above, revealed that floras often preserved taphonomic biases dependent on their original depositional setting on the flood plain. Floral similarities were often observed between floras from different stratigraphic levels, but similar depositional environments, and differences seen between floras from the same stratigraphic level, but different depositional environments. These taphonomic effects can mask diversity and morphological changes in floras and this had to be taken into account when determining climatic variables and floral change through time. It was found that those depositional environments which had a transportational element to them, enabling the preservation of leaves from more distal areas of the flood plain and hinterland, as well as the ability to preserve leaves that had abscised directly on to the flood plain, best represented the regional vegetation. In effect, these environments were crevasse splays, areas of overbank floods and relatively extensive lakes.

7.3 VEGETATION

Assessing the flora of the Northern Great Plains, Brown (1962) states that "The overall pattern....in the Lower Palaeocene is that of platanophylls dominating near channel stream deposits, a diverse mix of compound and simple leaved angiosperms of archaic and modern affinities on levees and crevasse splays and a mix of archaic and modern conifers in backswamps", moreover he perceives it as essentially lowland, and not easily distinguished from that of the Late Cretaceous. This is in accordance with the observations of Johnson and Hickey for floral turnover prior to the boundary from the
northern Great Plains (1990), and with evidence from the Russian continent (Golovneva, in press). Palynofloras from the North American continent also appear to be, in part, transitionary across the boundary period (section 4.7). Together with this study they all point to floral turnover being gradual in nature, although possibly punctuated by the boundary event.

Floral changes that are observed across the boundary, are essentially in response to climatic variation. The loss of thermophilic characters from more southerly floras; adaptations, such as drip tips, for greater levels of moisture throughout floras from the region and the increased proportion of dentate-margined leaf types, associated with deciduousness, are all observed. These are essentially adaptations to a wetter and cooler climate, with an increased element of seasonality.

Although extinctions of up to 70% have been detected across the boundary period in the northern Great Plains (Johnson and Hickey 1990), it is difficult to attribute this solely to the affects of a meteorite impact. A post-impact winter, together with acid rain-out, would have killed off vegetation, but not seed stocks. This is because seeds are able to survive periods of harsh climatic and environmental conditions, and their life can actually be prolonged by exposure to low temperatures (Spicer, pers. comm. 1993). Following abatement of the 'impact winter' in the earliest Palaeocene (see section 2.6), vegetation would have regenerated from these seed stocks, so it is highly unlikely that it would have been significantly different to that of the Late Cretaceous. If it did have any affect on floras, the boundary event itself merely exacerbated the turnover caused by more long term changes, such as deterioration of greenhouse conditions. It may also have contributed to the
suppression of floral diversity levels throughout the early Palaeocene, which remain low, with no one flora comprising more than thirty morphotypes.

There is a problem in identifying short term ecological effects versus longer term evolutionary effects on boundary floras. Because angiosperms are generalists, it is more likely that the longer term climatic changes occurring across the boundary period would have had an evolutionary affect on them, as opposed to the brief 'short sharp shock' of an 'impact winter' situation, which would have had a relatively short term ecological affect.

7.4 DIVERSITY AND SUCCESSION

The suggestion by Wolfe and Upchurch (1987), that floral succession following the boundary event was on an evolutionary time scale, over a period of a few million years, seems to be refuted by evidence from this study. Soon after the boundary event, floras containing relatively abundant angiosperm megafossils are widespread in the Western Interior. Graphs of floral assemblage diversities throughout the early Palaeocene (figures 5.35A/B) reveal that floras with diversities of twenty two morphotypes occur within approximately a metre of the boundary (KSD 91 22.0) in the Williston Basin (table 5.3) and of twenty one morphotypes, at a similar stratigraphic level, in the Raton Basin (KSD 92 9.0). This stratigraphic level falls within Wolfe and Upchurch's 'phase three' of ecological succession following the boundary event (1987 & section 4.41), where recolonization by angiosperms, and dominance of early successional stream side species, is described.

At sites studied from Tea Pot Dome (KSD 93 1.0 and 2.0), floras from beds 2.5 metres above the boundary are more diverse than those that are
stratigraphically higher, which also have a 'more disturbed' aspect to their overall leaf physiognomy. The stratigraphically lower floras are from a different depositional setting to those above, which suggests that floral diversity changes in the earliest Palaeocene are not simply related to post-boundary recovery and that taphonomic considerations may have equal, if not more, bearing on floral diversity and leaf physiognomy. Johnson and Nichols (1987) also detect a facies change at the Cretaceous-Tertiary boundary in some parts of North Dakota, which obscures the pattern of megafloral turnover there. Perturbation of environmental conditions at the K-T boundary, affecting flora and vegetation, followed by ecosuccession, as is evidenced by fern dominance succeeded by initially low diversity angiosperm floras, can be detected, but it appears to be on a shorter time scale than has previously been suggested. It is also complicated by taphonomic biases inherent in floras derived from differing depositional environments.

7.5 CLIMATE

Early Palaeocene climate, as determined from North American data, and other studies from the rest of the world, can not be explained simply. The affects of a boundary event merely appear to have exacerbated the stresses imposed by a globally changing climate commensurate with the deterioration of the Cretaceous 'global greenhouse' condition. The non-uniform climatic changes observed across the North American continent are better explained by general climate change occurring throughout the Mesozoic to Cenozoic transition.

Evidence for decreased climatic equability, accompanied by increased seasonality across the boundary period in North America, was originally
ascribed to the withdrawal of the mid-Cretaceous seaway (Srivastava 1970), as its tempering influence on climate was removed. But this would not be applicable elsewhere in the world, where climatic deterioration is indicated at this time (see section 6.5). However, a proposed increase in seasonality (Srivastava 1970) is interesting in the light of observations made on leaf physiognomy of North American floras. Leaf margin analyses, which give mean annual temperatures of below freezing for Western Interior floras, have been interpreted as evidence for a selection for deciduousness following a post boundary cold spell (Wolfe 1987). Although mean annual temperatures derived from leaf margin analyses and multivariate analyses of leaf physiognomy in this study (section 3.61 and 3.62), were lower than those of the latest Cretaceous, and of those previously suggested for the early Palaeocene (Wolfe 1990), they are not below freezing, and are realistic if early Palaeocene cooling is invoked due to overall deterioration in climatic equability and breakdown of the Late Cretaceous 'greenhouse condition'.

The analysis of fossil wood can often yield information on seasonality. Unfortunately, the record of fossil wood in the Palaeocene is rare, although distinct changes in its structure are observed across the boundary period. These have partially been attributed to the emergence of angiosperms as large trees coincident with the development of multi-stratal forests. However, Wheeler and Baas (1991) conclude that although North American Palaeocene climates appear tropical, they also had a seasonal element and certain features, indicating climatic equability that were widespread in Cretaceous woods, such as the absence of marginal parenchyma, are not observed in their Palaeocene counterparts. The paucity of fossil wood at this time makes it impossible to determine whether these changes were sudden or not (Wheeler and Baas 1991). They need not necessarily have been connected with the
boundary event and could, instead, have been due to more long term changes in climatic conditions. If woody features, indicating an increased seasonality, can be attributed to long term climatic change then it is possible that the increased proportion of angiosperm leaves of deciduous aspect could also be, so that a selection for deciduousness is not necessarily a survival mechanism in response to a brief impact-related cold period at the Cretaceous-Tertiary boundary.

Further evidence for seasonality of climates in the early Palaeocene comes from gley soils and thin, impure coal seams (section 6.53) which are abundant in the northern Great Plains at this time (Favstovsky and McSweeney 1987). These features form in response to wet/dry and cool/warm seasonality. Other evidence for seasonal climatic regimes comes from a section studied at Tea Pot Dome (KSD 93 2.0) which suggests periodic leaf abscission from the presence of repeated thin leaf beds of similar leaf forms, preserved at fine stratigraphic intervals. This is indicative of periodic leaf abscission, which is associated with deciduousness and seasonal leaf loss. Not every season's leaf fall may be preserved in the section. Only those leaf falls that occurred when depositional regimes were conducive to sedimentation, such as periods of extensive overbank flooding, facilitating deposition of coarser sediments on to a muddy flood plain, would have been preserved. From this combined evidence for an increased seasonality of climates in the early Palaeocene of North America, it is probable, that the increase in deciduous leaf forms can at least, in part, be attributed to enhanced climatic seasonality at this time and not necessarily to a selection for such forms induced by a brief impact winter.

Evidence for an impact winter following the boundary impact is difficult to detect, in that unambiguous evidence that it would have produced is unlikely
to have been preserved in the sedimentological and fossil records. From climatic determinations in this study, there appear to be no drastically low mean annual temperatures following the K-T boundary, although in more northerly areas of the Great Plains temperatures are generally at their lowest in the early Palaeocene, directly after the boundary event. In general, mean annual temperatures of the early Palaeocene for the Western Interior of North America were somewhat lower than those of the Late Cretaceous, and indicate a southerly shift of climatic zones, together with decreased latitudinal climatic equability across the continent.

Mean annual precipitation was at considerably higher levels in the early Palaeocene than it had been in the Late Cretaceous. This was observed throughout the continent, but was most pronounced at more southerly latitudes. Although the peak in precipitation observed directly after the boundary event drops off somewhat later in the early Palaeocene, precipitation levels remain relatively high throughout this period. It has been suggested that low levels of precipitation in the Late Cretaceous may have been caused by raised levels of atmospheric carbon dioxide (Wolfe and Upchurch 1987b). The deterioration of the greenhouse condition in the latest Cretaceous may then account for the raised levels of precipitation observed in the earliest Palaeocene. Another explanation for this, directly related to the boundary event, may have been the presence of a dust cloud inducing precipitation through the high density of condensation nuclei in the atmosphere. However, these affects are likely to be extremely short term, with little evolutionary affect on angiosperms, and again it is difficult to say whether they would have been preserved in the palaeobotanical record.
7.6 FLORAL ZONES

Megafloral zones of the late Cretaceous and early Tertiary of North America were largely defined by climate, and it is interesting to note that these zones were about 20° north of their equivalents today, indicating the prevailing equability, although this equability decreased distinctly from the Late Cretaceous in to the early Palaeocene. The megathermal zone extended up to about 45°N, including the Raton Basin, the mesothermal zone from approximately 45°N to 55°N, including the Powder River and Williston Basins and the microthermal zone north of palaeolatitude 55°N, extending north from the northern part of the Williston Basin.

Inferences about regional climatic and floral zones come from the study of specific floras to build up an overall picture across a region. When discussing such broad biogeographic zones it is also important to remember the unstable 'boundary environment' in which they existed. Shifting coastlines, tectonism, climatic change and altering animal herbivory all had a bearing on the prevailing flora, and their affects might not necessarily have been uniform across the North American continent. Broad assumptions are made from small areas. This might mean that a specific sampled flora was adapted to a more localised environment, which can not be applied in a regional context. Therefore it is essential that floras from a number of regions are studied if conclusions are to be drawn about zonal characteristics of floras.

On a broader scale, flora from the northern great Plains of the U.S.A. appears to be correlatable with that of north-eastern Siberia (Golovneva, in press), which would suggest broad latitudinally defined zones in the northern hemisphere unlike those of Crane (1987), which show divisions between the American and Asiatic continents.
7.7 THE BOUNDARY 'SNAP SHOT'

The Cretaceous-Tertiary boundary claystone and its associated phenomena have been observed in only certain depositional environments. This means that in effect only 'snap shots' of the events of that brief period are preserved in the geological record. These can be pieced together to give a general picture, but it is impossible to detect what happened in those environments that are not represented. The majority of terrestrial boundary sites are preserved in flood plain sediments of the Western Interior of the United States, there are no records of the boundary from montane areas of this time. Although artifacts of montane vegetation may be transported to low lying areas and preserved in the palaeontological record, along with the prevailing vegetation, their individual characteristics will become diluted in the more abundant flood plain vegetation. Marginal marine areas did not preserve sediments from this time, but deeper marine environments did. This may be allied to widespread regression of seas, but again means that a component of the global picture at the Cretaceous-Tertiary boundary is missing.

Cretaceous-Tertiary boundary sites are not only confined to certain depositional environments, but also to certain areas of the world. The majority, as has been pointed out previously, are found in the Western Interior of the United States. This immediately introduces a bias to interpretations. Sites in other parts of the world show some of the phenomena and extinction patterns associated with boundary sites in North America, but generally the evidence they provide is much less clear. This immediately suggests that the event or events at the boundary were not necessarily globally encompassing, but were felt more forcefully on the North American continent.
7.8 SHIFTING ENVIRONMENTS AND VEGETATION

Even after the initial sudden affects of the boundary event had abated, the prevailing conditions within terrestrial environments did not return to those of the Late Cretaceous in North America. The combination of long term, ongoing climatic and tectonic changes, together with the residual affects of boundary perturbations, irreversibly altered environmental conditions. Across the Western Interior, temperatures became somewhat cooler, precipitation increased, the biota was irreversibly changed and the general character of the environments of deposition changed. This change varied from north to south with a tendency for northern waterlogged swamps and sluggish rivers, and southern meandering rivers on broad flood plains. Soon after the boundary event, however, there is a trend for coarser grained sedimentation throughout the Western Interior which can be related to increased tectonism in the source area of the Rocky Mountains, as well as greater levels of precipitation.

The morphological plasticity of the angiosperms and their preference for disturbed habitats meant that they were able to consolidate their hold on this changing terrestrial environment in the early Palaeocene, and ultimately dominate vegetation throughout the rest of the Tertiary. A high peak in species turnover is witnessed amongst angiosperms in the late Palaeocene to early Eocene, and Tiffney (1981) suggests that this is perhaps some lag effect occurring well after the boundary event, but it is difficult to envisage how such a short term event took millions of years to manifest itself in the palaeobotanical record. Environmental and climatic perturbations at the boundary might well have temporarily halted the expansion of the angiosperms but ultimately may have assured their dominance in floras by virtue of their morphological plasticity.
Global evidence suggests that the latest Cretaceous and early Palaeocene were times of climatic and ecological change, both in marine and terrestrial environments. Conversely, evidence for a global catastrophe at the Cretaceous-Tertiary boundary, is primarily derived from the terrestrial environment of the North American continent, and even here it is not conclusive. A review of all the trends observed world-wide at the Cretaceous-Tertiary boundary reveals that the changes observed in biota and climate at this time, can not simply be related to the impact of a bolide, and its associated phenomena. Instead, they reflect the more global and wide ranging changes of the period that were punctuated and exacerbated by this brief deleterious event.

7.91 CONCLUSIONS
There are a number of important points raised or challenged by this thesis. Of primary importance is the fact that taphonomic biases have previously been overlooked in discussions of boundary and early Palaeocene floras. This study has shown that taphonomy has a significant bearing on floral diversity and composition in the early Palaeocene, often masking the character of regional vegetation. This can affect palaeoclimatic determinations from leaf physiognomies and has strong implications for previous theories regarding 'eco-succession' following the boundary event. The floras that preserve least taphonomic bias, and therefore are the most accurate representations of regional floras, are those from crevasse splay, overbank and lacustrine environments which all have an element of transportation and mixing of leaves in their formation.
Climatic determinations from CLAMP and L.M.A. analyses carried out in this study reveal that following the boundary event there was a marked increase in precipitation across the American continent, although this was most intense in the south. This was accompanied by a slight drop in temperature, although no evidence was discovered for an 'impact winter'. Equability across the American continent decreased causing a shift southwards of climatic and vegetational zones and seasonality increased. This study shows that it is possible for floral change across the boundary period to be solely attributed to ongoing climatic change throughout the boundary period and suggests that plants, as generalists, are more susceptible to long term changes on an evolutionary time scale as opposed to short term ecological changes such as those observed at the Cretaceous-Tertiary boundary.

Finally, comparisons between this study and work from other regions of the world at this time reveals that the North American continent was most drastically affected by the Cretaceous-Tertiary boundary event and the conclusion is made that the events at the Cretaceous-Tertiary boundary were not the cause of global devastation, as has previously been suggested.
CONCLUSIONS
CONCLUSION

The environment of the early Palaeocene across the Western Interior of North America appears to have been fairly homogeneous. River systems draining the eastern flank of the newly emerging Rocky Mountains spread out onto flood plains, where deposition in a variety of environments, from braided streams through to meandering rivers, swamps and ponds, facilitated the fossilisation of leaf megafloras. Sediments generally consisted of relatively finer grained deposits directly after the boundary event, followed by a shift to deposition of coarser grained material early in the Palaeocene. This is observed throughout the continent, approximately synchronously and could be due to increased precipitation or tectonic activity, but is probably a combination of the two phenomena.

Composition of fossil floras varies between the three areas studied, and appears to be a function of their latitudinal position and consequent prevailing climatic conditions. Changes observed in their overall physiognomy across the boundary period, are essentially adaptations in response to ongoing climatic changes, with increased proportions of features related to high levels of precipitation and increased seasonality. In all areas, floral diversity is low throughout the early Palaeocene, although it apparently recovers from the affects of the boundary event more rapidly than has previously been suggested. More southerly areas appear to have suffered most in this respect. Intrabasinal variations in diversity and composition of fossil floras from similar stratigraphic levels, but different alluvial depositional environments, are noticeable. This has been attributed to taphonomic processes specific to particular microenvironments within a general flood plain environment. These also cause similarities between fossil floras from
the same depositional settings, at different stratigraphic levels. Comparing diversities and compositions of floras from different depositional environments and stratigraphic settings can therefore yield erroneous results. These taphonomic constraints may also mask climatic signals derived from leaf physiognomy.

Global climate was already in a state of flux prior to the Cretaceous-Tertiary boundary event, with the deterioration of 'greenhouse conditions'. Determination of mean annual temperatures and precipitation from earliest Palaeocene floras collected in this study, suggest that change continued throughout this time with raised precipitation, especially directly after the K-T boundary, slightly lower temperatures and a shift southwards of climatic zones in North America, from their positions in the latest Cretaceous. This is commensurate with decreased climatic latitudinal equability. Palaeobotanical and sedimentological evidence suggests that these conditions were accompanied by an increase in seasonality. An increase in climatic seasonality could explain the rise in proportion of deciduous leaf types observed in North American floras, at this time, without a need for selection of such forms induced by the deleterious effects of the boundary event.

As data in this study were only collected from North America these climatic interpretations can only be applied to this area. Whether climatic changes are due to the boundary event and impact of a meteorite alone is debatable. Other factors such as regression of the epicontinental Western Interior sea, tectonic uplift of the Rocky Mountains and ongoing breakdown of greenhouse conditions would also have substantially affected climate. However, the affects of an impact may be responsible for geologically brief climatic changes observed, such as the dramatic rise in precipitation following the boundary.
No conclusive evidence was found to support the theory of an 'impact winter' although such an event may have been too brief to have been recorded in the geological record.

Evidence suggests that the effects of a bolide impact at the Cretaceous-Tertiary boundary have previously been overstated, and that it was not the prime cause of global catastrophe. Palaeobotanical data from areas away from the North American continent indicates little change at the boundary itself and climatic data from these regions is indicative of gradual humidization and cooling, together with decreased latitudinal equability. The most indicting evidence for ecological devastation caused by the impact of an extra-terrestrial body at the Cretaceous-Tertiary boundary is from North America and even here, as is shown in this study, evidence can be ambiguous and signals masked by more long term climatic and environmental changes, as well as variations in local depositional settings.

From data currently available, it appears that floral extinctions, ecological trauma within terrestrial environments and climatic change at the Cretaceous-Tertiary boundary in North America can, in part, be attributed to the boundary event, but in other parts of the world its affects were less, and even minimal when compared with the more wide scale and ongoing changes occurring throughout the Late Cretaceous and early Tertiary transition.
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APPENDIX A

LOCATION OF FIELD SITES
APPENDIX A

LOCATION OF FIELD SITES

**KSD 91 1.0 & 2.0 YORK CANYON MINE**

KSD 91 1.0 (36°51'57" N. 104°55'29" W. CASA GRANDE 7.5" quad) and KSD 91 2.0 (36°51'57"N. 104°55'31" W. CASA GRANDE 7.5" quad) were in York Canyon P & M open cast coal mine, which is located at the end of the 555 road, south of the town of Raton, New Mexico. KSD 91 2.0 comprised a hard wall cut approximately 115m above the main coal seam, 400m above the Cretaceous-Tertiary boundary, just above the 'K' seam (pers. comm. R. Pillmore). KSD 91 1.0 was on the bench directly below KSD 91 2.0 (approximately 380 m above the boundary), so that the two collection sites were approximately 20m. apart stratigraphically.

**KSD 91 3.0, 4.0 AND 5.0 POTATO CANYON ROAD**

Sites KSD 91 3.0 (36°53'42"N. 104°35'49"W. TIN PAN CANYON 7.5"quad), 4.0 (36°53'42"N. 104°35'49"W. TIN PAN CANYON 7.5" quad) and 5.0 (36°52'52"N. 104°39'50"W. TIN PAN CANYON 7.5" quad) were located along Potato Canyon road 555, which is the road that leads from the town of Raton to York Canyon Mine. At its eastern end, the road passes close to a known K/T boundary site (now inaccessible as the land is owned by Vermejo Park nature reserve) and road cuts from here to the mine afford a good section through the early Paleocene. Three such road cuts with good leaf fossils were selected as collection sites. These corresponded to sites worked on by Fleming (pers. comm.) in the construction of palynologic zones of the early Palaeocene in the Raton basin. Thus, the sites had a strong stratigraphic control and, respectively, were 140, 200 and 250 metres above the boundary.

**KSD 91 6.0 OLD RATON PASS**

KSD 91 6.0 (36°54'22"N. 104°27'10"W. RATON 7.5" quad) was located on the north east side of the Old Raton Pass road, just below the mesa summit. No leaf megafossils from the early Palaeocene were found.
KSD 91 7.0 BERWIND CANYON STREAM SECTION
KSD 91 7.0 was located in the stream section at Berwind Canyon (west of the Ludlow exit on Interstate [I] 25), to the south of the dirt road. Leaf fossils were collected from the unit immediately above the boundary (40-100cm above the boundary). On a return trip to this locality further collection was made on a unit approximately 2m above the boundary.

KSD 91 8.0 BERWIND CANYON ROAD SECTION
KSD 91 8.0 is almost directly opposite KSD 91 7.0, on the opposite side of the road, which follows the same course as the stream at this point. The boundary can be found towards the base of the outcrop, which has been excavated by previous workers. Leaf megafossils were collected from a unit 15cm above the boundary. Organic material was also collected from 1.3m above the boundary.

KSD 91 9.0 STARKVILLE SOUTH
KSD 91 9.0 (37°06'00"N. 104°31'10"W. STARKVILLE 7.5 quad) corresponds to the Starkville south road cut on the east side of Interstate 25. This road cut extends for over 100m but collection was confined to a trench that had been dug by previous workers exposing a bed yielding abundant leaf fossils. This unit was approximately 1m above an easily identifiable boundary claystone.

KSD 91 10.0 CLEAR CREEK NORTH
Locality KSD 91 10.0 (37°05'02"N. 104°31'05"W. STARKVILLE 7.5" quad) corresponds to the road cut at Clear Creek North on the north east side of I 25. Organic material occurs 15cm above the boundary (few angiosperms) as well as in Cretaceous sediments.

KSD 91 11.0 CLEAR CREEK SOUTH
KSD 91 11.0 (37°04'42"N. 104°29'59"W. STARKVILLE 7.5 quad) corresponds to Clear Creek south which, again, is a road cut on the east side of I 25. This site yielded some organic material just above the boundary (few dicots) and had a well defined boundary claystone.

KSD 91 12.0 GALLINAS JUNCTION NORTH
KSD 91 12.0 (37°03'43"N. 104°31'15"W. STARKVILLE 7.5 quad) corresponds to the road cut on the east of I 25, to the south of the Gallinas Junction interchange. To the south of this outcrop there is a large low
angle reverse fault, but collection was done to the north. The collecting site is just above the 'bench cut' and the boundary appears to be just below the 'bench cut', although this is inaccessible.

**KSD 91 13.0 GALLINAS JUNCTION SOUTH**
Locality KSD 91 13.0 (37°04'10"N. 104°31'27"W. STARKVILLE 7.5 quad) is at Gallinas Junction South, in a road cut on the east side of I 25, 0.75 miles to the north of KSD 91 12.0. There are two fossil bearing units here, a couple of metres above the boundary. They are of different lithologies, although stratigraphically at the same level.

**KSD 91 14.0 & 15.0 MADRID EAST AND WEST**
These are located to the west of the basin, on the south side of the Purgatoire River and main railroad line, approximately 0.5 miles west of the distinctive yellow bridge in the hamlet of Tijeras. KSD 91 14.0 (37°07'12"N. 104°38'51"W. VALDEZ 7.5 quad) is the farthest west of these and here the boundary is well exposed. This site represents the only latest Cretaceous flora (from approximately 70cm below the boundary) sampled in the Raton basin. KSD 91 15.0 (37°07'15"N. 104°38'32"W. VALDEZ 7.5" quad) provided very few dicot. leaf fossils.

**POWDER RIVER BASIN**

**KSD 91 16.0 POINTY HILL, LANCE CREEK**
Locality KSD 91 16.0 (43°17'31"N. 104°40'48"W. DIXON RANCH 7.5 quad) is known locally and in the literature as 'Pointy Hill', on the Dixon Ranch. Exposure was poor, with overburden that had to be removed. Only reedy monocots and finely disseminated organic matter were found at this locality, in sediments within 15m of the boundary.

**KSD 91 17.0**
Locality KSD 91 17.0 (43°17'21"N. 104°41'15"W. DIXON RANCH 7.5 quad) was on the opposite, south side of the creek and consisted of a small resistant sandstone ridge topping less resistant sediments which form 'Pointy Hill'. Although initial inspections looked promising few leaf fossils were found here.

**KSD 91 18.0 POINTY HILL, LANCE CREEK**
KSD 91.18.0 {43°.17'31"N. 104°.40'40"W. DIXON RANCH 7.5 quad}, proved to be the only locality in the area with identifiable dicotyledonous remains. This was on the east side of 'Pointy Hill'. It was necessary to dig back some way to find relatively unweathered leaf fossils, although these tended to be fragmented. The trench which was dug, was vertically contiguous with the log drawn at KSD 91.16.0 and contained the K/T boundary claystone, although this was a lot less easy to distinguish than it had been in the Raton basin. A series of small trenches were dug at lower levels in the sequence to ensure that the boundary had been correctly identified. The leaf flora collected was from approximately 2m above the boundary.

KSD 93.1.0 AND 2.0 TEA POT DOME
KSD 93.1.0 and 2.0 were to the west of Pine Ridge {approximately 43°.15'02" N. 106°.00'10" W.} Two contiguous trenches were dug, the lower containing the boundary claystone package. Leaf megafossils came from two sections, one from each trench. In the lower trench (which contained the boundary claystone) a flora was collected from the base and top of a 1.5m thick unit which had a base 1m above the boundary claystone. In the stratigraphically higher trench, leaf megafossils were sampled from a sequence of thin beds 3.5-4m above the boundary.

WILLISTON BASIN

KSD 91.19.0 RICK’S PLACE
Locality KSD 91 19.0 {47°.31'50"N. 107°.00'40"W. TRUMBO RANCH 7.5" quad}, known as Rick's Place (8504, U.S.G.S. locality), had angiosperm leaf fossils at a level approximately 4m. above the boundary. The boundary here was difficult to locate due to the large amount of overburden.

KSD 91.20.0 & 22.0 MCGUIRE CREEK
The McGuire Creek area is approximately 50 miles to the east of KSD 91 19.0. KSD 91 20.0 (47°37'50"N. 106°10'08"W. BUG CREEK 7.5" quad), known as McGuire Creek swamp, yielded many well preserved leaf fossils from just below the 'Z' coal but above the lowest coal in the 'Z' coal complex. There was relatively little overburden and no discernible boundary claystone at this locality.
KSD 91 22.0 [47°37'48"N. 106°10'10"W. BUG CREEK 7.5 quad] was again located at McGuire Creek swamp but refers to a bluff (barbed wire bluff) a couple of hundred metres to the south of KSD 91 20.0. Very well preserved leaf fossils came from a level approximately 3m. below the 'Z' coal but just above the lowest coal of the 'Z' coal complex.

KSD 91 21.0 NELSON CREEK
KSD 91 21.0 was located south of McGuire Creek, off a dirt track to the east of the McCone county '24' road, at Nelson Creek. The site was known as 'Toni's Turtle' because of the excellent turtle remains found there. Again collecting was from just below the 'Z' coal (3m. below). This site may be of late Cretaceous age.

KSD 91 23.0 OLD COUNTY ROAD, GARFIELD COUNTY
The first of these localities, KSD 91 23.0, was located along the cut on the Old County Road in Garfield Co. It yielded only a few dicots. A lot of overburden made excavation difficult.

KSD 91 24.0 & 25.0 BISCUIT BUTTE
Locality KSD 91 24.0 [47°29'30"N. 106°W. BISCUIT BUTTE 7.5 quad], Cottonwood Sheep Canyon related to Hickey's site 788 and Archibald's log S14. Many well preserved dicot. leaves were found there, in two different lithologies. Collection was carried out at two different sites at a similar stratigraphic level on opposite sides of the canyon. This level was above the 'Y' and below the 'X' coal, approximately analogous in age to the collections made from York Canyon Mine.

KSD 91 25.0, relates to another of Hickey's localities. It is on a bearing of 070 degrees from Biscuit Butte [BISCUIT BUTTE 7.5 quad], approximately 0.5 miles from the Old County Road. The outcrop of the fossil bearing lithology is very weathered and it is highly likely that this collecting locality will no longer yield any fossil material. It is of a similar age to KSD 91 24.0.
APPENDIX B

SEDIMENTARY LOGS
KEY TO SEDIMENTARY LOGS

Sandstone
Siltstone
Claystone
Shale
Carbonaceous shale
Coal
Laminations
Lenses
Tabular cross bedding
Trough cross bedding
Convoluted bedding
Sideritic concretions

Angiosperms
Fossil wood/bark
Fragmented organic material
Roots
Stringers
Fusain

Insect cocoons (poss.)
Fossil fish

Logs were not drawn at sites where fossil angiosperms were not present
(KSD 91 6.0 & 23.0)
Lustrous, blocky coal

Carbonaceous laminations

Organic-rich shale with fragmented leaves

Organic-rich laminations

Angiosperm megafossils in laminations

Few organic-rich laminations

Fossil wood and bark impressions

Carbonaceous shale with laminations of lustrous, high grade coal

Fragmented organic material forms mats which define laminations

Angiosperm leaves and fragmented organics form mats
KSD 91 2.0 YORK CANYON MINE

COMMENTS:

- Low grade coal laminations in carbonaceous shale
- Angiosperm megafossils
- Coal-rich carbonaceous shale
- Diverse angiosperm megafossils
- Organic-rich laminations
- Matted and fragmented organic material

Scale: 1cm: 100cm
KSD 91 3.0 POTATO CYN ROAD

COMMENTS:

Carbonaceous and coal-rich near base
Laterally continuous coal

Coal lenses

Twigs and fragmented organic matter
Fragmented organic matter

Undulatory, discontinuous laminations
due to organic material

Palms common
Well preserved angiosperms rare

Scale 1cm: 50cm
KSD 91 4.0 POTATO CYN ROAD

COMMENTS:

Scoured base

Angiosperm leaf fossils in laminated mudrocks

Scale: 1cm: 200cm
KSD 91 5.0 POTATO CYN ROAD

COMMENTS:

Coaly intercalations

Undulatory, discontinuous laminations related to carbonaceous material and angiosperm megafossils

Organic-rich

Scale: 1cm: 50cm
KSD 91 7.0 BERWIND CANYON STREAM SECTION

COMMENTS:

Soured base

Streaks of coaly material

Fragmented organic material and few angiosperm leaf fossils

Lenses of coarser grained sediment

Angiosperm megafossils randomly oriented

Angiosperm leaf fossils

Laterally heterogeneous bed

Twigs and fragmented angiosperm leaves occur at bedding planes of harder, basal part of bed

Coaly streaks and abundant organic material

KTB

Organic material forming mats at bedding planes

Scale: 1cm:10cm
KSD 91 8.0 BERWIND CANYON ROAD

COMMENTS:

Palms

Sideritic

Angiosperm leaf fossils and fragmented organic material
Finely laminated
Sideritic concretions

Laterally heterogeneous bedding

Angiosperm leaf fossils on bedding planes
KTB

Scale 1cm: 50cm
COMMENTS:

Laterally heterogeneous, bedded near base

Palms present

Discontinuous laminations defined by fragmented organic material

Organic rich bed

Finely disseminated organic matter at bedding planes

Fragmented organic material defines bedding planes.

Abundant angiosperm megafossils

Lustrous, blocky and brittle coal

Organic material forms mats at bedding planes

Organic matter defines discontinuous laminations and forms mats

KTB

*Figures next to log relate to gaps in the section
KSD 91 10.0 CLEAR CREEK NORTH

COMMENTS:

Bedded near top, laterally varying in thickness

Fossil palms, *Equisitum* twigs

Few angiosperm leaf fossils towards top of bed but distribution very laterally heterogeneous

KTB

Increasingly carbonaceous near top of bed

Scale 1 cm: 20 cm
KSD 91 11.0 CLEAR CREEK SOUTH

COMMENTS:

Carbonaceous at top of bed with fragmented organic material

Fragmented organic material

Discontinuous, undulatory laminations defined by carbonaceous material. Angiosperm fossils where bed more consolidated

Lustrous and blocky coal

Coal streaks and mats of plant material

Fragmented organic material concentrated near base of bed

KTB
Angiosperm leaf megafossils
Sideritic nodules

Scale: 1cm: 100cm
Swaley laminations defined by fragmented carbonaceous material

Fossil palms
Rare angiosperm megafossils
Laterally discontinuous unit

Fragmented organic material
Leaf meagafossils at base
Thin, dense layers of organic material at bedding planes
Roots
Coaly streaks

Scale 1 cm: 20 cm
Scoured base
Sideritic nodules
K-T boundary
Coal lenses, thin mats of dense organic material

Leaf megafoils

Coal lenses
Dense, thin mats of organic material at bedding planes

Scale: 1cm: 20cm
COMMENTS:

Poorly preserved leaf megafossils occur higher in section within continuation of uppermost bed of log (to 15m above KTB)

Well bedded in parts (variable throughout bed)

KTB Claystone

Scree

Laterally discontinuous beds

SCALE: 1cm: 20cm
KSD 91 16.0 POINTY HILL

COMMENTS:

Weathered organic material

Fragmented leaf (mainly monocotyledonous) & woody material

Fragmented organic material and monocots

Monocotyledonous and fragmented organic material

Organic material associated with silty intercalations

Monocots of laterally variable distribution

Disseminated organic material and monocots in abundance

Monocots, fragmented organics and few angiosperms as mats on bedding planes

Low grade coal in parts

Scale: 1cm: 50cm
KSD 91 18.0 POINTY HILL

COMMENTS:

- Fragmented organic material
- Rooted horizons
  Monocotyledous material
  Roots perpendicular to bedding
- Sandy intercalations preserving few angiosperms at upper interface with claystone
- Abundant angiosperms, often not bedding parallel
- Abundant angiosperms
- Monocotyledous debris
- Fragmented organic material
  Monocotyledous fossils
- Fragmented organic material
  Coaly in parts

Scale: 1cm: 10cm
COMMENTS:

'Salt and pepper sandstone'

Coaly
Abundant angiosperm leaf fossils on bedding planes

Isolated angiosperm leaf fossils

Isolated leaf fossils, randomly orientated

Scale: 1:10
KSD 91 20.0 McGuire Creek Swamp

Comments:

- Coal of variable grade
- Fractures parallel to bedding
- Parallel layers of monocotyledonous and other organic material
- Low grade coal
- Small (2cm.) lenses of coaly material
- Coalified twigs, non bedding parallel
  Laterally discontinuous clay laminations
- Coal lenses
  Monocotyledonous material
- Woody fragments non bedding parallel
  Monocotyledonous fossils
- Clay lenses in more consolidated base of bed
- Monocotyledonous material
- Angiosperm leaf fossils near base
- Low grade coal
  Coal stringers
  Angiosperm leaf fossil horizons at top of bed
- Azolla in unlaminated basal part of bed
  Rooted horizons perturbing underlying laminations
- Angiosperm leaf fossils

Scale: 1cm:10cm
KSD 91 21.0 TONI'S TURTLE, NELSON CREEK

COMMENTS:

Abundant angiosperm leaf fossils
Fusain lenses
Monocotyledonous material

Lenses of fine grained sandstone
Angiosperm leaf fossils parallel to bedding
Rare monocots

Scale: 1cm: 10cm
COMMENTS:

Fusain
Angiosperm leaf fossils and fragmented organic material

Lignite with some fusain

Abundant angiosperm leaf fossils

Monocots and other macerated plant material on bedding planes

Carbonaceous shale trending to coal, not laterally heterogeneous and with stringers below

Angiosperm leaf fossils

Angiosperm leaf and coniferous fossils

Small scale cross bedding defined by clay drapes

Scale: 1cm: 10cm
KSD 91 24.0 COTTONWOOD SHEEP CANYON

COMMENTS:

Abundant angiosperm leaf megafossils

Fossil conifers and angiosperm debris

1cm: 10cm

Basal units of logs are stratigraphically equivalent across canyon

Abundant leaf megafossils

Abundant angiosperm leaf megafossils plus fern and conifer fossils

Small leaf megafossils

1cm: 10cm
KSD 93 1.0 TEA POT DOME

COMMENTS:
Woody material
Angiosperm fossils

Palm debris

Large angiosperm megafossils

Angiosperm fossils
Monocots
Three seed types
Fan palms

Fossil water plants
K-T boundary
Rootlets and possible rhizomes

Scale: 1cm:10cm
Homogeneous sediments, rooted throughout

Abundant rooted horizons

Low diversity stenophyllous leaf megafossils, laterally heterogeneous

Stenophyllous leaf megafossils

Twigs and stenophyllous leaf megafossils, forming mat

Datum level, laterally equivalent to uppermost unit of KSD 93 1.0 log. Twigs and leaf megafossils

Scale 1cm: 20cm
APPENDIX C

LEAF FOSSIL MORPHOTYPES (PLATES)
APPENDIX C

LEAF FOSSIL MORPHOTYPES (PLATES)

NOTES FOR FOSSIL LEAF MORPHOTYPE PLATES

Where there appear to be morphotypes missing from the sequence, that is where there are gaps in the numeric sequence, this is because these were merged with other morphotypic groups after the initial numbering.

Photos shown here are the best representations of each morphotypic group, but do not necessarily show all the physiognomic characters stated in the morphotypic descriptions of Appendix D. This is because these descriptions are derived from the study of all specimens in each morphotypic group, together with referral to published monographs, which may reveal characters not apparent in even the most representative example of the morphotype.

On film overlays to photos, bold lines (——) represent features present in the photograph, short dashed lines (----) represent broken/lost edges to leaves and long dashed lines (——) represent features not present in the underlying photograph but common to that particular leaf morphotype.
PLATE R1: Raton Basin morphotype 1
PLATE R1: Raton Basin morphotype 1

PLATE R1a Raton Basin morphotype 1a
PLATE R2: Raton Basin morphotype 2

PLATE R2a: Raton Basin morphotype 2a
PLATE R3: Raton Basin morphotype 3

PLATE R3a: Raton Basin morphotype 3a
PLATE R3: Raton Basin morphotype 3

PLATE R3a: Raton Basin morphotype 3a
PLATE R4: Raton Basin morphotype 4

PLATE R4a: Raton Basin morphotype 4a
PLATE R6: Raton Basin morphotype 6

PLATE R6a Raton Basin morphotype 6a
PLATE R7: Raton Basin morphotype 7

PLATE R7a: Raton Basin morphotype 7a
PLATE R9: Raton Basin morphotype 9

PLATE R9a: Raton Basin morphotype 9a
PLATE R9: Raton Basin morphotype 9

PLATE R9a: Raton Basin morphotype 9a
PLATE R10: Raton Basin morphotype 10

PLATE R11: Raton Basin morphotype 11
PLATE R13: Raton Basin morphotype 13

PLATE R13a: Raton Basin morphotype 13a
PLATE R14: Raton Basin morphotype 14

PLATE R15: Raton Basin morphotype 15
PLATE R26: Raton Basin morphotype 26

PLATE R27: Raton Basin morphotype 27
PLATE R26: Raton Basin morphotype 26

PLATE R27: Raton Basin morphotype 27
PLATE R28: Raton Basin morphotype 28

PLATE R29: Raton Basin morphotype 29
PLATE R34: Raton Basin morphotype 34

PLATE R35: Raton Basin morphotype 35
PLATE R34: Raton Basin morphotype 34

PLATE R35: Raton Basin morphotype 35
PLATE R36: Raton Basin morphotype 36

PLATE R37: Raton Basin morphotype 37
PLATE R38: Raton Basin morphotype 38

PLATE R40: Raton Basin morphotype 40
PLATE R38: Raton Basin morphotype 38

PLATE R40: Raton Basin morphotype 40
PLATE R41: Raton Basin morphotype 41

PLATE R42: Raton Basin morphotype 42
PLATE R48: Raton Basin morphotype 48

PLATE R49: Raton Basin morphotype 49
PLATE W1: Williston Basin morphotype 1

PLATE W3: Williston Basin morphotype 3
PLATE W4: Williston Basin morphotype 4

PLATE W5: Williston Basin morphotype 5
PLATE W6: Williston Basin morphotype 6

PLATE W7: Williston Basin morphotype 7
PLATE W8: Williston Basin morphotype 8

PLATE W9: Williston Basin morphotype 9
PLATE W8: Williston Basin morphotype 8

PLATE W9: Williston Basin morphotype 9
PLATE W12: Williston Basin morphotype 12

PLATE W13: Williston Basin morphotype 13
PLATE W12: Williston Basin morphotype 12

PLATE W13: Williston Basin morphotype 13
PLATE W14: Williston Basin morphotype 14

PLATE W15: Williston Basin morphotype 15
PLATE W16: Williston Basin morphotype 16

PLATE W17: Williston Basin morphotype 17
PLATE W18: Williston Basin morphotype 18

PLATE W19: Williston Basin morphotype 19
PLATE W20: Williston Basin morphotype 20

PLATE W21: Williston Basin morphotype 21
PLATE W20: Williston Basin morphotype 20

PLATE W21: Williston Basin morphotype 21
PLATE W22: Williston Basin morphotype 22

PLATE W23: Williston Basin morphotype 23
PLATE W26: Williston Basin morphotype 26

PLATE W27: Williston Basin morphotype 27
PLATE W28: Williston Basin morphotype 28

PLATE W36: Williston Basin morphotype 36
PLATE W28: Williston Basin morphotype 28

PLATE W36: Williston Basin morphotype 36
PLATE W40: Williston Basin morphotype 40

PLATE W41: Williston Basin morphotype 41
PLATE W40: Williston Basin morphotype 40

PLATE W41: Williston Basin morphotype 41
PLATE W42: Williston Basin morphotype 42

PLATE W43: Williston Basin morphotype 43
PLATE W44: Williston Basin morphotype 44

PLATE W45: Williston Basin morphotype 45
PLATE W46: Williston Basin morphotype 46

PLATE W47: Williston Basin morphotype 47
PLATE W50: Williston Basin morphotype 50

PLATE W51: Williston Basin morphotype 51
PLATE W52: Williston Basin morphotype 52

PLATE W53: Williston Basin morphotype 53
APPENDIX D

LEAF FOSSIL MORPHOTYPES (DESCRIPTIONS)
APPENDIX D

LEAF MORPHOTYPE DESCRIPTIONS

For future reference the likely repository for these specimens will be the University of Oxford Museum.

RATON BASIN 1
Shape ovate; size: micro 11-1-meso 1; l:w:1-2:1; base: round; apex: acute with possibly rounded tip; margin: crenate with small distant rounded 'teeth'; venation: semi-craspedodromous, primary veins straight and medial, secondary veins opposite with angle of divergence of approximately 45 degrees initially straight but curving strongly near to margin where they form loops; aff. Juglans taurina (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 1: KSD 91 5.149, KSD 91 10.111, KSD 91 10.115, KSD 91 10.112, KSD 91 5.95, KSD 91 5.131, KSD 91 5.61, KSD 91

RATON BASIN 1A
Shape: elliptic; size: micro 111-meso 1-11; l:w: 2-3:1; base: ?;apex: acute; margin: serrate, mainly entire but some small serrations with acute sinuses; venation: semi-craspedodromous; secondaries alternate with large angle of divergence forming large but weak loops near margin.
SPECIMENS IDENTIFIED AS RATON BASIN 1A: KSD 91 13.34, KSD 91 13.23, KSD 91 13.12, KSD 91 3.16, KSD 91 2.48, KSD 91 5.92

RATON BASIN 2
Shape: wide ovate; size: micro II-III; l:w: 1-2:1; base: round; apex: acute; margin: irregularly dentate with close, sharp teeth and round sinuses, some compound; venation: craspedodromous, primary veins thin and straight, secondaries opposite becoming more alternate near to the apex with low angle of divergence terminating at teeth, tertiary veins branch from basal secondary (poss. pectinal primary ?) and from other secondaries near to the margin; aff. Viburnum asperum
SPECIMENS IDENTIFIED AS RATON BASIN 2: KSD 91 5.121, KSD 91 5.81, KSD 91 5.91, KSD 91 5.90, KSD 91 5.41
RATON BASIN 2A
Shape: elliptic-narrow elliptic; size: micro II; l:w: 2-3:1; base: acute; apex: acute; margin: entire; venation: camptodromous, primary mid veins straight and weak, secondary veins slightly alternate with a large angle of divergence terminating far from the margin.
SPECIMENS IDENTIFIED AS RATON BASIN 2A: KSD 91 9.50, KSD 91 11.10, KSD 91 11.3, KSD 91 2.83, KSD 91 7.31, KSD 91 2.9, KSD 91 8.51, KSD 91 8.35

RATON BASIN 3
Shape suborbiculate; size: micro III; l:w: 1-2:1; base: decurrent, acute; apex: round ?; margin: teeth sharp and regular with sharp sinuses; venation: palmate, primary veins number three with two curved near base then straight, secondary veins radiate from marginal primaries with wide angle of divergence curving apically and terminating at teeth; aff. Zizyphus (Lee and Knowlton) and Cercidiphyllum (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 3: KSD 91 5.43, KSD 91 10.3, KSD 91 10.101, KSD 91 10.105, KSD 91 10.1, KSD 91 10.109, KSD 91 2.36, KSD 91 2.11, KSD 91 4.30

RATON BASIN 3A
Shape: elliptic; size: micro II-III; l:w: 1-2:1; base: acute but almost obtuse; apex: acute; margin: regularly dentate with sharp sinuses and rounded teeth; craspedodromous; venation: primary veins medial and strong, secondary veins alternate and rare with a 45 degree angle of divergence following initially straight courses but strongly curved apically midway along their length.
SPECIMENS IDENTIFIED AS RATON BASIN 3A: KSD 91 5.128, KSD 91 5.120, KSD 91 5.88, KSD 91 5.67

RATON BASIN 4
Shape: ovate; size: micro III-meso I; l:w: 2-3/3-4:1; base: ?; apex: acute-attenuate; margin: irregular dentate with very small, round teeth; venation: semi-craspedodromous, primary veins thick and medial, secondary veins opposite and initially straight becoming more curved near the margin where they form loops.

RATON BASIN 4A
Shape: oblanceolate; size: micro II-meso I; l:w: 1-2:1/2-3:1; base: acute; apex: missing; margin: entire; venation: brochidodromous, thick medial primary vein, secondary veins slightly alternate with angle of divergence of approx. 45 degrees straight then form large loops close to margin, tertiaries AO; orthogonal areolation.
SPECIMENS IDENTIFIED AS RATON BASIN 4A: KSD 91 9.43, KSD 91 5.105

RATON BASIN 5
Shape: ovate-elliptic; size: micro III-meso I; l:w: 2-3:1; apex ?: base: round-decurrent; margin: irregularly dentate with close-distant sharp teeth; venation: semi-craspedodromous, primary veins thick and medial, secondary veins opposite and fine forming loops near to margin, tertiary veins not visible; aff. Sapindus/Phyllites (Brown)/Quercus Ratonensis (Lee & Knowlton).
RATON BASIN 5A
Shape: narrow ovate; size: micro I-II; l:w: 3-4:1; base: round; apex: acute; margin: regularly dentate, distant teeth with round sinuses and rounded teeth; venation: craspedodromous, primary veins thin, straight and medial, secondary veins with narrow angle of divergence and slightly curved near primary but otherwise straight, terminating at teeth, tertiary veins rare and branch from secondaries, terminating at teeth; aff. *Quercus Greenlandica* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 5A: KSD 91 7.207, KSD 91 14.4

RATON BASIN 6
Shape: ovate but tri-lobed; size: micro II-micro III; l:w: 1-2/2-3:1; base: acute; apex: acute; margin: regularly dentate, sharp teeth with concave-convex sinuses; venation: palmate, primary vein branched so that each branch terminates at the apex of the three lobes, secondary veins are straight with narrow angle of divergence terminating at teeth; aff. *Cissus marginata* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 6: KSD 91 2.68, KSD 91 8.54, KSD 91 1.88, KSD 91 5.79

RATON BASIN 6A
Shape: very narrow elliptic; size: micro III; l:w >4:1; base: missing; apex: ?; margin irregularly dentate ?; venation: craspedodromous, primary veins medial, secondary veins straight with small angle of divergence terminating at teeth; aff. *Dryophyllum, Salix* ?
SPECIMENS IDENTIFIED AS RATON BASIN 6A: KSD 91 14.9

RATON BASIN 7
Shape: elliptic; size: micro III-meso I; l:w: 1-2:1; base acute; apex: acute; margin: dentate with irregular rounded teeth; venation: semi-craspedromous, primary veins thin and straight, secondary veins opposite with a narrow angle of divergence curving apically forming loops just prior to margin, tertiary veins form loops near margin; aff. *Quercus sullyi* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 7: KSD 91 5.120, KSD 91 3.5, KSD 91 3.3, KSD 91 3.2, KSD 91 5.137, KDS 91 5.112, KSD 91 5.24, KSD 91 5.35, KSD 91 5.30, KSD 91 5.51
RATON BASIN 7A
Shape: elliptic-narrow elliptic; size: micro II; l:w: >4:1; base: acute; apex: acute; margin: entire; venation: brochidodromous, primaries thin and medial, secondary veins opposite with acute angle of divergence forming loops (?); near to margin; aff. Rhamnus hirsuta.
SPECIMENS IDENTIFIED AS RATON BASIN 7A: KSD 91 14.6, KSD 91 9.7, KSD 91 14.5

RATON BASIN 8
Shape wide ovate; size: meso I; l:w: 1-2:1; base: round-cordate; apex: acute-acuminate; margin: irregularly dentate with small, close rounded teeth; venation: primary veins thick and medial, secondary veins with wide angle of divergence, initially straight but curved towards margin where they terminate (poss. looped ?), tertiary veins horizontal; aff. Corylus insgnis (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 8: KSD 91 13.6, KSD 91 5.156, KSD 91 9.60, KSD 91 9.34, KSD 91 4.16, KSD 91 5.91, KSD 91 5.4, KSD 91 5.96, KSD 91 5.64, KSD 91 5.47, KSD 91 5.59

RATON BASIN 8A
Shape: wide elliptic; size: micro II-III; l:w: 1-2:1; base: acute; apex: ?; margin: entire; venation: pallinactodromous, primary veins number three one medial and two pectinal, secondary veins branch possibly forming loops near to margin, tertiary veins looped near to margin; aff. Ficus planicosta (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 8A: KSD 91 2.2, KSD 91 3.14

RATON BASIN 9
Shape: elliptic-narrow elliptic; size: micro II; l:w: 1-2:1/2-3:1; base: acute; apex: acute; margin: entire; venation: primary veins thick and medial, secondary veins straight with slight curve towards the margin or terminate before this; aff. Sapindus affinis (Brown)/Magnolia (Lee & Knowlton).

RATON BASIN 9A
Shape: lanceolate; size: micro II; l:w >4:1; base: ?; apex: acuminate; margin: entire; venation: camptodromous, well defined medial primary, secondary
veins faint and terminating prior to margin, randomly alternate to opposite
sometimes decurrent with primary vein; aff. *Quercus phellas* (Lee &
Knowlton).

SPECIMENS IDENTIFIED AS RATON BASIN 9A: KSD 91 1.105

**RATON BASIN 10**

Shape: narrow elliptic-v. narrow elliptic; size: micro II-III; l:w: >4:1; base:
round acute; apex acute-acuminate; venation: entire margin, primary vein
thick and medial, veins of higher order not present; aff. *Salix viminalifolia*
(Lee & Knowlton).

SPECIMENS IDENTIFIED AS RATON BASIN 10: KSD 91 14.2, KSD 91 9.58,
KSD 91 9.31, KSD 91 9.54, KSD 91 9.32, KSD 91 9.0 (SP 2), KSD 91 9.30, KSD 91
14.1, KSD 91 14.11, KSD 91 14.20, KSD 91 7.26, KSD 91 7.37, KSD 91 7.44, KSD 91
7.144, KSD 91 11.14, KSD 91 15.10

**RATON BASIN 11**

Shape: suborbiculate ?; size: micro III-meso I; l:w: 1-2:1; base: round-cordate;
apex: ?; margin: entire possibly crenate; venation: brochidodromous ?;
primary veins thick and medial, secondary veins thick and straight but curve
sharply apically near to margin their angle of divergence much greater nearer
base; aff. *Pterospermites cordatus* (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 11: KSD 91 4.8, KSD 91 13.11,
91 10.114, KSD 91 2.81, KSD 91 4.34, KSD 91 4.11, KSD 91 4.45, KSD 91 5.49, KSD
91 5.110, KSD 91 5.122, KSD 91 5.6, KSD 91 5.150, KSD 91 5.134

**RATON BASIN 11A**

Shape: ovate; size micro II; l:w 1-2:1; base: ?; apex: ?; margin: dentate with
regular, close, sharp teeth and round sinuses; venation: semi-
craspedodromous, primary veins medial and well defined, secondary veins
alternate and strongly curved apically, tertiary veins approximately
horizontal except near margin where they form loops (festooned ?); aff.
*Hicoria glabra*.

SPECIMENS IDENTIFIED AS RATON BASIN 11A: KSD 91 5.60, KSD 91 8.10
**RATON BASIN 12**
Shape ovate-wide ovate; size: micro III; l:w: 2-3:1; base: acute-decurrent; apex: acute; margin: entire; venation: palinactodromous, primary veins number three (one medial and two pectinal), secondary veins branch from pectinal veins and medial primary near apex (poss. from loops near margin); aff. *Zizyphus fibrillosus* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 12: KSD 91 13.46, KSD 91 8.27

**RATON BASIN 13**
Shape: v. wide ovate; Size: micro II-III; l:w: 1-2:1; base: cordate; apex: acute; margin: irregularly denate with close acute-rounded teeth and rounded sinuses, some compound; venation: actinodromous, primary veins number three, medial vein is straight, pectinals are curved briefly near base then follow straight course until near the apex, secondary veins branch from pectinal veins and near top of marginal vein, forming loops; aff. *Cercidiphyllum articum/Vitis olriki* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 13: KSD 91 4.88

**RATON BASIN 13A**
Shape: ovate ?; size micro II; l:w > 4:1; base: ?; apex: acute; margin: entire; venation: camptodromous, primary vein thin and medial, secondary veins random and very faint.
SPECIMENS IDENTIFIED AS RATON BASIN 13A: KSD 91 4.6

**RATON BASIN 14**
Shape: ovate-wide ovate; size: meso I; l:w: 1-2:1; base: acute; apex: acute; margin: regularly dentate with large distant teeth having acute teeth and rounded sinuses; venation: palmate, actinodromous, primary veins number three each terminating at a 'lobe', secondary veins branch from primaries each terminating at a tooth, tertiary veins form 'AA' junctions with secondaries, areolation orthogonal; aff. *Cissus marginata* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 14; KSD 91 5.15

**RATON BASIN 15**
Shape: narrow ovate; Size: micro II-III; l:w: 1-2:1; base: missing; apex: acute; margin dentate with variable distant-close teeth that are sharp-rounded with rounded sinuses; venation: craspedodromous, thin medial primary
sometimes sinuous, secondary veins rare, where visible they are faint and curve apically terminating at teeth.

SPECIMENS IDENTIFIED AS RATON BASIN 15; KSD 91 4.6, KSD 91 13.56, KSD 91 2.120, KSD 91 5.62, KSD 91 5.72, KSD 91 5.64, KSD 91 5.107

RATON BASIN 16
Shape: narrow ovate-ovate; size: micro III; l:w: 2-3:1; base: acute; apex: ?; margin: entire; venation: brochidodromous, primary vein thick and medial, secondary veins alternate and weak terminating prior to margin or possibly forming weak loops; aff. *Euonymus splendens* (Lee and Knowlton)

SPECIMENS IDENTIFIED AS RATON BASIN 16; KSD 91 8.49

RATON BASIN 17
Shape: wide ovate-very wide ovate; size: micro III-meso I; l:w 1-2:1; base: ?; apex acute; margin: most missing but probably dentate; venation: palmate, primary veins number three or greater, secondary veins branching, terminating at margin ?, tertiary veins link secondaries either horizontally or arched; aff. *Platanus* (Brown).


RATON BASIN 18
Shape: oblanceolate; size: micro III-meso I; l:w: 1-2:1/2-3:1/3-4:1; base: acute; apex: acute; venation: brochidodromous, primary veins strong and straight, secondary veins angle of divergence 45 degrees and straight for most of course then strongly curved near margin where they form loops, tertiary veins are approx. horizontal-AO.

SPECIMENS IDENTIFIED AS RATON BASIN 18: KSD 91 5.43, KSD 91 5.100, KSD 91 13.201, KSD 91 4.38, KSD 91 5.119, KSD 91 5.50, KSD 91 5.47, KSD 91 5.7, KSD 91 5.73, KSD 91 5.104, KSD 91 5.133

RATON BASIN 19
Shape: orbiculate-v. wide ovate; size meso I; l:w 1-2:1; base: cordate-lobate; apex: round; margin: entire possibly slightly crenate; venation: palmate,
primary veins number five terminating at margin, secondary veins branch from primaries, strongly curved and terminating at margin, tertiary veins AA approximately parallel to margin forming concentric pattern; aff. Pterospermites (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 19: KSD 91 13.14, KSD 91 7.101, KSD 91 7.42

**RATON BASIN 20**

Shape; size: micro II-III/meso I; l:w:1-2/2-3:1; elliptic; base: round; apex: missing; margin: irregular dentate with very small sharp teeth and sharp sinuses; venation: semi-craspedodromous, primary vein straight, secondary veins with an angle of divergence of 45 degrees straight then curving strongly close to margin forming loops, tertiary veins AA and festooned forming loops.

SPECIMENS IDENTIFIED AS RATON BASIN 20; KSD 91 4.3, KSD 91 5.37, KSD 91 1.6, KSD 91 1.29, KSD 91 4.20, KSD 91 4.15, KSD 91 5.122, KSD 91 5.117, KSD 91 5.27, KSD 91 5.28, KSD 91 5.134, KSD 91 5.63, KSD 91 5.300, KSD 91 5.68, KSD 91 5.122, KSD 91 5.11, KSD 91 5.4, KSD 91 5.17, KSD 91 5.17, KSD 91 5.54, KSD 91 5.15, KSD 91 5.93, KSD 91 5.148

**RATON BASIN 21**

Shape: narrow-elliptic; size: micro III/ meso I-II; l:w 2-3/3-4/>4:1; base: acute; apex: acute-acuminate sometimes with drip tip; margin: entire; venation: primary veins thick and medial, higher order veins not present.


**RATON BASIN 22**

Shape laceolate-narrow ovate; size: micro II; l:w: >4:1; apex: acute; base: acute; margin: regularly dentate especially near apex with sharp teeth and sinuses; venation: simple craspedodromous, primary veins thin and straight, secondary veins nearly straight terminating at teeth, tertiary veins branching and rare terminating at teeth; aff. Dryophyllum (Brown).

RATON BASIN 23
Shape: oblanceolate; size: micro II-III/meso 1; l:w: 2-3:1/3-4:1; base: acute; apex: missing; margin: entire; Venation: camptodromous, primary vein thick and medial, secondary veins with large angle of divergence, straight but then curved strongly near margin; tertiaries with AO angle of origin; orthogonal areolation; aff. Carya antiquorum (Brown).
KSD 91 2.93, KSD 91 9.83, KSD 91 9.0 (SP 10), KSD 91 13.48, KSD 91 13.32, KSD 91 2.6, KSD 91 1.15, KSD 91 1.22, KSD 91 1.44, KSD 91 1.23A, KSD 91 1.13A, KSD 91 4.31

RATON BASIN 24
Shape: ovate-elliptic; size: micro III-meso I; l:w: 1-2:1/2-3:1; base: acute; apex: acute-acuminate; margin: irregularly dentate with distant, sharp teeth and sharp-round sinuses; venation: craspedodromous, primary veins straight and medial, secondary veins approximately straight and terminating at margin, tertiary veins branch from secondaries near to margin and terminate at margin; aff. Betula (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 24: KSD 91 2.86, KSD 91 5.99, KSD 91 5.109, KSD 91 5.106, KSD 91 3.23, KSD 91 4.2

RATON BASIN 25
Shape: oblanceolate-narrow oblanceolate; size: micro III-meso I-II; l:w: 3-4:1; base: acute; apex: missing; margin: entire; venation: eucamptodromous, primary veins thick and medial, secondary veins alternate and curving apically with an acute angle of divergence terminating prior to the margin, tertiary veins are branching and weak; aff. Magnolia augustifolia (Lee and Knowlton).
SPECIMENS IDENTIFIED AS RATON BASIN 25: KSD 91 2.114, KSD 91 9.57

RATON BASIN 26
Shape wide ovate-orbiculate; Size: micro II; l:w: 1-2:1; base: acute-decurrent; apex: round?; margin: entire near to base but missing near apex probably large distant rounded teeth with sharp sinuses; venation: palmate, primary
veins number three and radiate from base, secondary veins branch from primaries and terminate at margin; aff. *Amelopsis acerifolia* (Newberry).

SPECIMENS IDENTIFIED AS RATON BASIN 26: KSD 91 2.1, KSD 91 15.6, KSD 91 8.35, KSD 91 5.34, KSD 91 5.44, KSD 91 5.15

RATON BASIN 27
Shape: wide-very wide ovate; size: micro III-meso I; l:w: <1:1-2:1; base: round-cordate possibly hastate; apex: acute; margin: lobed with three or five lobes some with teeth, large and rounded sinuses; venation: palmate with one primary vein per lobe terminating at margin, secondary veins are branching, terminating at teeth.


RATON BASIN 28
Shape lanceolate-narrow ovate; size: micro II; l:w >4:1; base: round; apex: acute; margin: entire; venation: eucamptodromous, primary vein thick and medial, secondary veins rare, weak and curved; aff. *Prunus* (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 28: KSD 91 7.41, KSD 91 2.15, KSD 91 7.115, KSD 91 11.4, KSD 91 11.9, KSD 91 10.4, KSD 91 11.25, KSD 91 14.3

RATON BASIN 29
Shape: ovate; size: micro III-meso I; l:w: 1-2:1/2-3:1; base: round; apex: acute; margin: dentate with irregularly spaced sharp teeth and round sinuses; venation: semi-craspedodromous, primary veins straight of variable thickness, secondary veins curving apically from their point of attachment with the primary forming loops close to the margin, tertiary veins are
horizontal and branch from the secondaries near to the margin then terminate at teeth; aff. *Viburnum antiquorum* (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 29; KSD 91 7.142, KSD 91 9.9, KSD 91 13.11, KSD 91 7.201, KSD 91 2.68, KSD 91 5.3, KSD 91 5.201, KSD 91 5.58, KSD 91 5.102, KSD 91 5.26, KSD 91 5.2, KSD 91 5.77, KSD 91 5.147, KSD 91 5.138, KSD 91 5.78, KSD 91 5.12, KSD 91 5.46, KSD 91 5.56, KSD 91 5.53, KSD 91 5.31, KSD 91 5.108

**RATON BASIN 30**
Shape: ovate; size micro III-meso I; l:w 1-2:1; base: acute-round; apex: acute?; margin: crenate with sinuous rounded 'teeth'; venation: craspedodromous, primary veins fairly thick and medial, secondary veins slightly curved (more so closer to primary) with angle of divergence of approx. 45 degrees terminating at teeth, tertiary veins branch from secondaries particularly the basal secondaries.

SPECIMENS IDENTIFIED AS RATON BASIN 30; KSD 91 5.303, KSD 91 9.59, KSD 91 8.36

**RATON BASIN 32**
Shape: narrow oblong; Size: micro III-meso I; l:w: 2-3:1; base: cordate-round; apex: acute; margin: regularly dentate with variable close-distant and rounded teeth (although these aren't visible on all specimens); venation: primary veins thick and medial, secondary veins opposite and straight curving strongly near margin where they form loops, tertiary veins from rare loops on secondaries; aff. *Ulmus rhamnifolia* (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 32: KSD 91 2.12, KSD 91 1.32

**RATON BASIN 34**

SPECIMENS IDENTIFIED AS RATON BASIN 34: KSD 91 2.110, KSD 91 2.102, KSD 91 5.98, KSD 91 5.16, KSD 91 5.10, KSD 91 5.38, KSD 91 5.125

**RATON BASIN 35**

SPECIMENS IDENTIFIED AS RATON BASIN 35: KSD 91 2.3, KSD 91 2.98, KSD 91 2.84

**RATON BASIN 36**

Shape narrow elliptic; size: micro II; l:w: 3-4:1; base: acute; apex: acute?; margin: entire poss crenate; venation: brochidodromous, primary vein thick and medial, secondary veins opposite and decurrent to primary curving apically close to margin to form loops; aff. *Sapindus affinis* (Brown).

SPECIMENS IDENTIFIED AS RATON BASIN 36: KSD 91 1.50, KSD 91 9.35, KSD 91 13.12, KSD 91 4.26

**RATON BASIN 37**

Shape: narrow oblong; size: micro II; l:w: 3-4:1; base: ?; apex: acute ?; margin: entire possibly dentate near apex with sharp irregular teeth; venation: camptodromous, primary veins straight and weak, secondary veins alternate with a variable angle of divergence some more curved than others but all terminate prior to the margin; aff. *Laurus* (Lee and Knowlton).

SPECIMENS IDENTIFIED AS RATON BASIN 37; KSD 91 2.95, KSD 91 3.4

**RATON BASIN 38**

Shape: wide ovate-elliptic; size: micro II; l:w: 1-2:1; base: acute-round; apex: missing; margin: irregularly dentate with sharp teeth and sharp sinuses; venation: semi-craspedodromous, primary veins medial, secondary veins have angle of divergence of approx. 45 degrees and are gently curved towards the margin where they form loops.

SPECIMENS IDENTIFIED AS RATON BASIN 38; KSD 91 9.33, KSD 91 13.3, KSD 91 1.23, KSD 91 1.19, KSD 91 4.14

**RATON BASIN 40**

SPECIMENS IDENTIFIED AS RATON BASIN 40: KSD 91 1.100, KSD 91 9.44, KSD 91 3.20, KSD 91 1.57, KSD 91 1.3, KSD 91 1.37, KSD 91 4.42

RATON BASIN 41
Shape: ovate-narrow ovate; size: micro II-III/meso I; l:w 2-3/3-4:1; base: round; apex: acute-acuminate, some with drip tips; margin: entire; venation: primary veins thick and medial, secondary veins usually absent occasionally a few straight.
SPECIMENS IDENTIFIED AS RATON BASIN 41; KSD 91 4.1, KSD 91 9.3, KSD 91 9.54, KSD 91 13.202, KSD 91 13.51, KSD 91 7.19, KSD 91 7.111, KSD 91 7.1, KSD 91 3.12, KSD 91 2.63, KSD 91 2.8, KSD 91 1.84, KSD 91 1.12, KSD 91 2.46, KSD 91 4.17, KSD 91 4.23

RATON BASIN 42

RATON BASIN 44
Shape: ovate-narrow ovate; size: micro III-meso I; l:w: 2-3:1/3-4:1; base: round-acute; apex: acute-decurrent; margin entire; venation: primary vein thick and medial.

RATON BASIN 45


**RATON BASIN 46**

Shape: wide ovate; size: micro I-II; l:w: 1-2:1 base: ?; apex: acute-decurrent; margin: regularly dentate with close round teeth and sharp sinuses; venation: primary veins thick and medial, secondary veins opposite curved near primary and margin but otherwise straight forming loops near to margin.

SPECIMENS IDENTIFIED AS RATON BASIN 46: KSD 91 5.13, KSD 91 13.23

**RATON BASIN 47**


SPECIMENS IDENTIFIED AS RATON BASIN 47: KSD 91 5.302

**RATON BASIN 48**

Shape: elliptic; size: micro II; l:w 1-2:1; base ?; apex ?; margin: entire; Venation: brochidodromous, primary veins thick and medial, secondary veins fine and sinuous forming loops near margin; aff. *Sapindus affinis* (? (Brown)


**RATON BASIN 49**

Shape: ovate; size micro II-III; l:w 1-2:1/2-3:1; base acute-round; apex ?; margin: irregularly dentate with close, sharp teeth and rounded sinuses; venation: craspedodromous, primary veins straight and medial, secondary veins opposite, curved most near to margin and primary vein terminating at margin ?; aff. *Carpinus* (Lee & Knowlton).

SPECIMENS IDENTIFIED AS RATON BASIN 49: KSD 91 5.80, KSD 91 5.1, KSD 91 5.18, KSD 91 5.45
**Raton Basin 50**
Shape: ovate; size: micro III; l:w 2-3:1 base: acute; apex: acute; margin: entire; venation: brochidodromous, primary veins straight and medial, secondary veins opposite and curved apically forming loops at some distance from the margin; aff. *Nyssa alata* (Brown).
SPECIMENS IDENTIFIED AS RATON BASIN 50: KSD 91 13.38, KSD 91 13.21

**Williston Basin 1**
Shape: elliptic; Size: meso I; l:w 1-2:1; Base: round; Apex: unknown; Margin: dentate, acute teeth, rounded apices; Venation: strong medial primaries, secondaries opposite and apically curved/looped. aff. *Laurus socialis*
SPECIMENS IDENTIFIED AS WILLISTON BASIN 1: KSD 91 22.1B, KSD 91 22.60, KSD 91 21.139, KSD 91 24.73A,

**Williston Basin 3**
Shape: obovate; size: micro III; l:w 2-3:1; base: decurrent; apex: unknown; margin: straight; venation: thick, medial primary, weak straight secondaries.

**Williston Basin 4**

**Williston Basin 5**
Shape: wide ovate; size: meso I, l:w 1-2:1; apex and base unknown; margin: dentate, smooth sinuses, small sharp teeth; venation: palmate with three well defined primaries. aff. *Platanus* (Newberry).
WILLISTON BASIN 6
Shape: oblanceolate; size: micro II-III; l:w 3-4:1; apex and base unknown; margin: entire; venation: secondaries at small angle to primaries and straight terminating at the margin; aff. Carya antiquorum?

WILLISTON BASIN 7
Shape: unknown; size: meso I; base and apex unknown; margin: unknown; venation: straight primaries, secondaries opposite and straight with a narrow angle of divergence from primary.

WILLISTON BASIN 8
Shape: narrow-oblong; size: micro II-III/meso I; l:w 2-3:1; base: round-obtuse; apex: acute; margin: entire (poss. microdentate ?); venation: semi-craspedodromous. aff. Hydrangea artica
SPECIMENS IDENTIFIED AS WILLISTON BASIN 8: KSD 91 21.33, KSD 91 21.10, KSD 91 21.300

WILLISTON BASIN 9
Shape: wide ovate; size: micro II-III; l:w 2-3:1; base: unknown; apex: round; margin: entire; venation: thin primaries, secondaries opposite and decurrent terminating near margin. aff. Cissites (Brown)

WILLISTON BASIN 10
Shape: elliptic; size: micro II; l:w 2-3:1; base: acute; apex: unknown; margin: dentate with acute, regularly spaced and close teeth and acute sinuses; venation: secondaries curved and craspedodromous. aff. Betula.

SPECIMENS IDENTIFIED AS WILLISTON BASIN 10: KSD 91 21.101

WILLISTON BASIN 11

SPECIMENS IDENTIFIED AS WILLISTON BASIN 11: KSD 91 22.178, KSD 91 22.9A, KSD 91 19.1 (BP1), KSD 91 22.20B, KSD 91 22.3B, KSD 91 22.20B,

WILLISTON BASIN 12
Shape: elliptic; size: micro III; base: cuneate, decurrent; apex: unknown; margin: dentate ?; venation: thick primaries, thick straight secondaries; aff. Rhamnus.


WILLISTON BASIN 13
Shape: narrow ovate; size: micro II; l:w 1-2:1; base: acute; apex: unknown; margin: dentate with large, close, regular, rounded teeth and acute sinuses; venation: secondaries branching and curve apically terminating at margin; aff. Quercus (Brown).


WILLISTON BASIN 14

WILLISTON BASIN 15
Shape: narrow oblong; size: micro II-III/meso I; l:w 2-3:1; base: unknown; apex: unknown; margin: dentate with acute, large, regular, close teeth and curved apices; venation: secondaries alternate terminating at margins tertiaries approx. horizontal. aff. Betula (Stevenson).


WILLISTON BASIN 16
Shape: wide ovate; size: micro III/meso I; l:w 1-2:1; base: cordate; apex: unknown; margin: dentate with teeth regular, close and round; venation: secondaries clustered at base curving strongly apically, tertiaries approx. horizontal. aff. Juglans taurina (Brown).


WILLISTON BASIN 17
Shape: oblong-wide ovate; size: micro I-II; l:w: 1-2:1; base: round-decurrent; apex: unknown; margin: dentate with regular, close, rounded teeth and sinuses; venation: primaries curved, secondaries strongly curved.


WILLISTON BASIN 18
Shape: narrow elliptic-narrow ovate; size: micro II-III/meso I; l:w 1-2:1/2-3:1; base: round; apex: acute; margin dentate with regular, close, acute teeth;
venation: secondaries alternate curving apically terminate at margins. aff Acer.


WILLISTON BASIN 19

WILLISTON BASIN 20
Shape: narrow elliptic; size: micro I-II; l:w: 3-4:1; base: unknown; apex: acute; margin: entire; venation: thick medial primary. aff. Prunus coloradensis.
SPECIMENS IDENTIFIED AS WILLISTON BASIN 20: KSD 91 24.85A, KSD 91 19.31, KSD 91 21.18, KSD 91 20.9A

WILLISTON BASIN 21
Shape: suborbiculate-wide ovate; size: micro III; l:w 1-2:1; base: acute-round; apex: round; margin: dentate with regular rounded teeth and sinuses; venation: palmate with three primaries. aff. Platanus raynoldsi. (Newberry).
teeth and rounded sinuses; venation: palmate with three primaries, branching secondaries and tertiaries approx. perpendicular to and linking secondaries. aff. *Cissus marginata*?


**WILLISTON BASIN 26**
Shape: orbiculate- suborbiculate; size: micro II-III; l:w 1-2:1; base: round-decurrent-cordate; apex: obtuse; margin: dentate with irregular acute teeth and rounded sinuses; venation: palmate with five primaries, branching secondaries and tertiaries approx. perpendicular to and linking secondaries. aff. *Cercidiphyllum*.


**WILLISTON BASIN 27**
Shape: orbiculate; size: micro III/meso I; l:w 1-2:1; base: cordate; apex: round; margin: crenate with teeth regularly, close and rounded-acute; venation: palmate with three tertiaries, branching secondaries and tertiaries approx. perpendicular to and linking secondaries. aff. *Cercidiphyllum arcticum*.

WILLISTON BASIN 28
Shape: elliptic; size: micro II-III; l:w:-; base: round, asymmetric; apex: unknown; margin: dentate with small, sharp, irregular teeth; venation: Primaries stout, secondaries opposite, semi-craspedodromous. aff. Cornus nebrascensis (Schimper).
SPECIMENS IDENTIFIED AS WILLISTON BASIN 28: 2.185B, KSD 91 22.16B, KSD 91 22.105B, KSD 91 22.43B, KSD 91 2.98B, KSD 91 22.2B, KSD 91 22.60B, KSD 91 22.10B

WILLISTON BASIN 29
Shape: suborbiculate; size: micro III/meso I l:w 1-2:1; base: cordate; apex: unknown; margin: dentate with regular close rounded-sharp teeth and sharp sinuses; venation: palmate with five primaries, branching craspedodromous secondaries and network of reticulate tertiaries. aff. Vitis.

WILLISTON BASIN 36
Shape: ovate; size: micro II-III; l:w 1-2:1; base: unknown; apex: obtuse ?; margin: dentate irregular round teeth with sharp sinuses; venation: secondaries looped and semi-craspedodromous, tertiaries looped and reticulate. aff. Viburnum
SPECIMENS IDENTIFIED AS WILLISTON BASIN 36: KSD 91 21.106, KSD 91 20.90, KSD 91 22.30B, KSD 91 22.148, KSD 91 22.6, KSD 91 22.5A

WILLISTON BASIN 38


**WILLISTON BASIN 39**

Shape: ovate; size: micro III/meso II; l:w 1-2:1; base: cuneate; apex: acute; margin: dentate with irregular rounded teeth; venation palmate, five primaries, branching secondaries, tertiaries approx perpendicular to and linking primaries and secondaries. aff. *Platanophyllum, Platanus*.


**WILLISTON BASIN 40**


**SPECIMENS IDENTIFIED AS WILLISTON BASIN 40: KSD 91 22.60, KSD 91 20.5A, KSD 91 20.39A**

**WILLISTON BASIN 41**

SPECIMENS IDENTIFIED AS WILLISTON BASIN 41: KSD 91 22.201, KSD 91 20.34A, KD 91 22.76B, KSD 91 2.92

WILLISTON BASIN 42
Shape: ovate; size: micro III; l:w 1-2:1; base: cordate; apex: obtuse; margin: dentate ?; venation: secondaries craspedodromous curved and branching decurrent with primary. aff. Dillenites.

SPECIMENS IDENTIFIED AS WILLISTON BASIN 42: KSD 91 19.61, KSD 91 24.55A, KSD 91 22.122A, KSD 91 25.59

WILLISTON BASIN 43
Shape: ovate; size: micro I; l:w 2-3:1; base: cordate; apex: acute; margin: dentate with regular, close and acute teeth; venation: secondaries craspedodromous straight, tertiaries branch from basal secondary terminating at margin.

SPECIMENS AS WILLISTON BASIN 44: KSD 91 24.50A

WILLISTON BASIN 44
Shape: ovate; size: micro II; l:w 1-2:1; base: acute; apex: acute; margin dentate in upper portion with regular, close, acute teeth and rounded sinuses; venation: secondaries craspedodromous distant and straight. aff. Cissus marginata (Lesquereux) Brown

SPECIMENS IDENTIFIED AS WILLISTON BASIN 44: KSD 91 24.50A

WILLISTON BASIN 45


WILLISTON BASIN 46
Shape: narrow ovate; size: micro III/meso I; l:w 2-3:1; base: unknown; apex: acute; margin: entire; venation: secondaries weak opposite and irregular. aff. Myrrophyllum tirreyi (Lesquereux) Dorf.
SPECIMENS IDENTIFIED AS WILLISTON BASIN 46: KSD 91 24.10B, KSD 91 20.89A

WILLISTON BASIN 47
Shape: narrow oblong; size: meso I; l:w 1-2:1; base and apex unknown; margin: dentate slightly irregular, rounded teeth and sinuses; venation: secondaries camptodromous curving apically. aff. Acer?
SPECIMENS IDENTIFIED AS WILLISTON BASIN 47: KSD 91 21.54, KSD 91 24.64A, KSD 91 21.65

WILLISTON BASIN 48
Shape: orbiculate; size: micro III/meso I up to 12 cm length l:w 1-2:1; base: cordate; apex: rounded; margin: entire near base; venation: palmate with five primaries, secondaries branching form primaries. aff. Menispermites.
SPECIMENS IDENTIFIED AS WILLISTON BASIN 48: KSD 91 24.45A, KSD 91 24.52A, KSD 91 22.21, KSD 91 2.21, KSD 91 21.136

WILLISTON BASIN 49
Shape: narrow-ovate; size: micro III; l:w 1-2:1; base: obtuse-decurrent; apex: unknown; margin: unknown; venation: palmate with three primaries.

WILLISTON BASIN 50
Shape: elliptic; size: micro III/meso I; l:w 2-3:1; base: acute; apex: acute; margin: small, rounded teeth; venation: secondaries alternate and semi-craspedodromous, tertiaries looped. aff. Quercus sullyi/Rhamnus hirsuta?
SPECIMENS IDENTIFIED AS WILLISTON BASIN 50: KSD 91 24.5B, KSD 91 22.172B, KSD 91 22.45B, KSD 91 22.22B, KSD 91 25.81, KSD 91 21.61B

WILLISTON BASIN 51

SPECIMENS IDENTIFIED AS WILISTON BASIN 51: KSD 91 24.40, KSD 91 19.42

**WILISTON BASIN 52**

Shape: elliptic; size: micro III; l:w 2-3:1; base: unknown; apex: acute; margin: dentate with regular, close, round teeth; venation: secondaries semi-crasspedodromous.

SPECIMENS IDENTIFIED AS WILISTON BASIN 52: KSD 91 22.121B

**WILISTON BASIN 53**

Shape: very wide ovate; size: micro II; l:w 1-2:1; base: cuneate; apex: acute ?; margin: dentate/lobate with regular, rounded teeth and three lobes; venation: palmate with three primaries, branching secondaries and reticulate tertiaries. aff. *Cercidiphyllum arcticum* (Heer).

SPECIMENS IDENTIFIED AS WILISTON BASIN 53: KSD 91 24.53B, KSD 91 24.10A, KSD 91 24.64B
APPENDIX E

FLORAL LISTS
APPENDIX E

FLORAL LISTS

RATON BASIN

KSD 91.0 YORK CANYON MINE
R. morph 42
R. morph 21: Laurales
R. morph 44: Laurales
R. morph 41: Laurales
R. morph 17: Platanus
R. morph 9: Magnolia (Lee & Knowlton)
R. morph 40: Laurus socialis (Brown)
R. morph 23: Carya antiquorum (Brown)
R. morph 36: Sapindus affinis (Brown)
R. morph 5: Sapindus/Phyllites (Brown)/Quercus Ratonensis (Lee & Knowlton)
R. morph 38
R. morph 20
R. morph 9A: Quercus phellos (Lee & Knowlton)
R. morph 32
R. morph 4
R. morph 6: Cissus marginata (Brown)

KSD 91.2 YORK CANYON MINE
R. morph 2A
R. morph 42
R. morph 21: Laurales
R. morph 41: Laurales
R. morph 44: Laurales
R. morph 48: Sapindus affinus (Brown)
R. morph 17: Platanus (Brown)
R. morph 37: Laurales
R. morph 28: Prunus (Brown)
R. morph 25: Magnolia augustifolia (Lee & Knowlton)
R. morph 23: Carya antiquorum (Brown)
R. morph. 35: *Persea* (Brown)
R. morph. 34: *Credneria* (Brown)
R. morph. 26: *Amelopsis Acerifolia*
R. morph. 24: *Betula* (Brown)
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 8A: *Ficus planicosta* (Brown)
R. morph 27: *Acer*
R. morph 1A
R. morph. 15: *Cissus marginata*
R. morph. 32: *Ulmus rhamnifolia* (Brown)
R. morph. 6: *Cissus marginata* (Brown)
R. morph. 3: *Zizyphus* (Lee & Knowlton)/*Cercidiphyllum* (Brown)
R. morph. 11: *Pterospermites Cordatus* (Brown)
R. morph. 29: *Viburnum antiquorum* (Brown)

**KSD 91 3.0 POTATO CANYON ROAD**
R. morph. 21: Laurales
R. morph. 41: Laurales
R. morph. 40: *Laurus socialis*
R. morph. 37: Laurales
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 8A: *Ficus planicosta* (Brown)
R. morph. 27: *Acer*
R. morph. 1A
R. morph. 7: *Quercus sullyi*

**KSD 91 4.0 POTATO CANYON ROAD**
R. morph. 42
R. morph 41: Laurales
R. morph. 18: *Pterocarya glabra* (Brown)
R. morph. 44: Laurales
R. morph. 48: *Sapindus affinis* (Brown)
R. morph. 9: *Magnolia* (Lee & Knowlton)
R. morph. 40: *Laurus socialis*
R. morph. 23: *Carya antiquorum*
R. morph. 36: *Sapindus affinis* (Brown)
R. morph. 24: *Betula* (Brown)
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 38
R. morp. 20
R. morph. 27: *Acer*
R. morph. 13A
R. morph. 13: *Cercidiphyllum arcticum/Vitis olriki* (Brown)
R. morph. 15: *Cissus marginata*
R. morph. 8: *Corylus insignis*
R. morph. 3: *Zizyphus* (Lee & Knowlton)/*Cercidiphyllum* (Brown)
R. morph. 11: *Pterospermites cordatus*

**KSD 91 5.0 POTATO CANYON ROAD**
R. morph. 18: *Pterocarya glabra*
R. morph. 34: *Credneria*
R. morph. 42
R. morph. 4A: *Asimina vesperalis*
R. morph. 26: *Amelopsis acerifolia*
R. morph. 24: *Betula*
R. morph. 1: *Juglans taurina*
R. morph. 21: *Laurales*
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 30
R. morph. 49: *Carpinus* (Lee & Knowlton)

**KSD 91 7.0 BERWIND CANYON**
R. morph. 2A
R. morph. 42
R. morph. 21: *Laurales*
R. morph. 41: *Laurales*
R. morph. 44: *Laurales*
R. morph. 10: *Salix viminalifolia* (Lee & Knowlton)
R. morph. 17: *Platanus* (Brown)
R. morph. 28: *Prunus* (Brown)
R. morph. 26: *Amelopsis acerifolia* (Brown)
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 27: *Acer*
R. morph. 19: *Pterospermites* (Brown)
R. morph. 29: *Viburnum antiquum*

**KSD 91 8.0 BERWIND CANYON**
R. morph. 2A
R. morph. 42
R. morph. 48: *Sapindus affinis*
R. morph. 17: *Platanus*
R. morph. 12: *Zizyphus firillosus*
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 30
R. morph. 27: *Acer*
R. morph. 11A: *Hicoria glabra*
R. morph. 44: *Laurus*
R. morph. 26: *Amelopsis acerifolia*
R. morph 16: *Euonymus splendens* (Lee & Knowlton)
R. morph. 6: *Cissus marginata* (Brown)

**KSD 91 9.0 STARKVILLE SOUTH**
R. morph. 2A
R. morph. 7A: *Rhamnus hirsuta* (Brown)
R. morph. 4A: *Asimina vesperalis* (Brown)
R. morph. 42
R. morph. 21: Laurales
R. morph. 41: Laurales
R. morph 44: Laurales
R. morph 48: *Sapindus affinis*
R. morph. 10: *Salix viminalifolia*
R. morph. 9: *Magnolia* (Lee & Knowlton)
R. morph. 40: *Laurus socialis* (Brown)
R. morph. 25: *Magnolia augustifolia* (Lee & Knowlton)
R. morph 23: *Carya antiquorum* (Brown)
R. morph. 36: *Sapindus affinis* (Brown)
R. morph. 5: 
R. morph 30 
R. morph. 38 
R. morph. 27: *Acer*
R. morph. 8: *Corylus insgnis* (Brown)
R. morph. 4 
R. morph. 29: *Viburnum antiquum*

**KSD 91 10.0 CLEAR CREEK NORTH**
R. morph. 28: *Prunus* (Brown)
R. morph. 1: *Juglans taurina*
R. morph. 27: *Acer*
R. morph. 3: *Zizyphus* (Lee & Knowlton)/*Cercidiphyllum* (Brown)
R. morph. 19: *Pterospermites* (Brown)
R. morph. 45: *Porthenocissus ursina* (Brown)
R. morph. 11: *Pterospermites cordatus* (Brown)

**KSD 91 11.0 CLEAR CREEK SOUTH**
R. morph. 2A 
R. morph. 42 
R. morph. 21: Laurales 
R. morph. 10: *Salix viminalifolia* (Lee & Knowlton)
R. morph. 28: *Prunus* (Brown)
R. morph. 5: *Sapindus/Phyllites* (Brown)/*Quercus Ratonensis* (Lee & Knowlton)
R. morph. 11: *Pterospermites cordatus* (Brown)

**KSD 91 13.0 GALLINAS IN SOUTH**
R. morph. 50: *Nyssa alata* (Brown)
R. morph. 42 
R. morph. 21: Laurales 
R. morph. 41: Laurales 
R. morph. 44: Laurales 
R. morph. 17: *Platanus* (Brown)
R. morphr. 23: *Carya antiquorum* (Brown)
R. morph. 36: *Sapindus affinis*
R. morph. 12: *Zizyphus fibrillosus*
R. morph. 5: *Sapindus/Phyllites* (Brown)/ *Quercus Ratonensis* (Lee & Knowlton)
R. morph. 46
R. morph. 38
R. morph. 27: *Acer*
R. morph. 1A
R. morph. 15: *Cissus marginata*
R. morph. 8: *Corylus insignis*
R. morph. 4
R. morph. 19: *Pterospermites* (Brown)
R. morph. 11: *Pterospermites cordatus* (Brown)
R. morph. 29: *Viburnum antiquum*
R. morph. 18: *Pterocarya glabra* (Brown)

**KSD 91 14.0 MADRID WEST**
R. morph. 7A: *Rhamnus hirsuita*
R. morph. 44: Laurales
R. morph. 10: *Salix viminalifolia* (Lee & Knowlton)
R. morph. 28: *Prunus* (Brown)
R. morph. 5A: *Quercus* (Brown)
R. morph. 6A: *Salix*
R. morph. 22: *Dryophyllum*

**KSD 91 15.0 MADRID EAST**
R. morph. 10: *Salix viminalifolia* (Lee & Knowlton)
R. morph. 26: *Amelopsis acerifolia* (Brown)
R. morph. 27: *Acer*

**WILLISTON BASIN**

**KSD 91 19.0 RICK'S PLACE**
W. morph. 1: *Laurus socialis*
W. morph. 3:
W. morph. 5: *Platanus*
W. morph. 7
W. morph. 9: *Cissites*
W. morph. 11: *Eucommia*
W. morph. 13: *Quercus*
W. morph. 15: *Betula*
W. morph. 24: *Amelopsis acerifolia*
W. morph. 38: *Lindera obtusa*
W. morph. 42: *Dillenites*
W. morph. 51: *Robinia wardi*
W. morph. 49
W. morph. 39: *Platanophyllum*
W. morph. 12: *Rhamnus*

**KSD 91 20.0 McGuire CK Swamp**

W. morph. 4: *Sapindus affinis*
W. morph. 6: *Carya antiquorum*
W. morph. 20: *Prunus coloradensis*
W. morph. 22: *Sapindus*
W. morph. 23: *Nyssa/Phyllites*
W. morph. 24: *Amelopsis acerifolia*
W. morph. 29: *Vitis*
W. morph. *Asimina vesperalis."
W. morph. 41
W. morph. 28: *Cornus nebrascensis*

**KSD 91 22 McGuire CK (Barbed Wire Bluff)**

W. morph. 1: *Laurus socialis*
W. morph. 29: *Vitis*
W. morph. 5: *Platanus*
W. morph. 36: *Viburnum*
W. morph. 8: *Hydrangea artica*
W. morph. 38: *Lindera obtusata*
W. morph. 9: *Cissites*
W. morph. 40: *Asimina vesperalis*
W. morph. 11: *Eucommia serrata*
W. morph. 42: *Dillenites*
W. morph. 13: *Quercus*
W. morph. 45: *Zizyphus fibrillosus*
W. morph. 15: *Betula*
W. morph. 48: *Menispermites*
W. morph. 16: *Juglans taurina*
W. morph. 50:
W. morph. 17
W. morph. 52
W. morph. 12: *Rhamnus*
W. morph. 21: *Platanus raynoldsi*
W. morph 49
W. morph. 24: *Amelopsis acerifolia*
W. morph. 39: *Platanophyllum*
W. morph. 27: *Cercidiphyllum arcticum*

**KSD 91 23.0 NELSON CK (TONI'S TURTLE)**
W. morph. 1: *Laurus socialis*
W. morph. 10: *Betula*
W. morph. 24: *Amelopsis acerifolia*
W. morph. 27: *Cercidiphyllum arcticum*
W. morph. 42: *Dillenites*
W. morph. 48: *Menispermites*

**KSD 91 24.0 COTTONWOOD SHEEP CYN. OLD COUNTY RD**
W. morph. 3
W. morph. 24: *Cissus marginata*
W. morph. 5: *Platanus*
W. morph. 26: *Cercidiphyllum*
W. morph. 6: *Carya antiquorum*
W. morph. 27: *Cercidiphyllum arcticum*
W. morph. 11: *Eucommia serrata*
W. morph. 29: *Vitis*
W. morph. 13: *Quercus*
W. morph. 38: *Lindera obtusata*
W. morph. 14: *Hamamelites*
W. morph. 44: *Cissus marginata*
W. morph. 15: *Betula*
W. morph. 46: *Myrtophyllum torreyi*
W. morph. 16: *Juglans taurina*
W. morph. 48: *Menispermites*
W. morph. 17
W. morph. 50: *Quercus sullyi*
W. morph. 19: *Fraxinus eocenia*
W. morph. 53: *Cercidiphyllum*
W. morph 20: *Prunus coloradensis*
W. morph. 54
W. morph. 24: *Amelopsis acerifolia*
W. morph. 12: *Rhamnus*
W. morph 49
W. morph. 39: *Platanophyllum*

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W. morph. 6: *Carya antiquorum*
W. morph. 16: *Juglans taurina*
W. morph. 18: *Acer*
W. morph. 19: *Fraxinus eocenia*
W. morph. 24: *Amelopsis acerifolia*
W. morph. 43: *Dryophyllum*
W. morph 50: *Quercus sullyi*
APPENDIX F

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