

Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis

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ABSTRACT

The warmest global temperatures of the Cenozoic Era occurred in early Eocene time, following a warming trend that started in late Paleocene time. The greater Green River Basin of southwestern Wyoming is one of the best areas in the Rocky Mountains for paleobotanical investigation of the Paleocene-Eocene climatic transition. Intensive sampling has resulted in the recovery of an estimated 189 species of plant macrofossils from the Tiffanian, Clarkforkian, Wasatchian, and Bridgerian land mammal “ages.” The leaf morphologies and taxonomic affinities of these fossils were used in combination with other indicators to evaluate Paleocene-Eocene climates. Following cool humid conditions in the Tiffanian, the Clarkforkian was humid and subtropical, and several plant families with modern tropical affinities appeared. However, as in the Tiffanian, Clarkforkian floras had low diversity and were dominated by a single species in the birch family. Mean annual temperature (MAT) rose from an estimated 12 °C in the Tiffanian to 19 °C in the Clarkforkian, while mean annual precipitation (MAP) for the Tiffanian and Clarkforkian is estimated to have been 130–150 cm. Little fossil plant material is preserved from the latest Clarkforkian or the earliest Wasatchian, which is thought to have contained an interval of cooling and drying followed by renewed warming. By the middle Wasatchian, the time of the Cenozoic thermal maximum, the inferred MAT was about 21 °C, and the MAP was near 140 cm. A second influx of plant families with tropical affinities appeared in the area, and diversity increased significantly, but most plant families known from

the Clarkforkian persisted. Species turnover from the Clarkforkian to the Wasatchian was greater than 80%. A second turnover of more than 80% of species (but not families) from the Wasatchian to the early Bridgerian accompanied drying and increased seasonality of precipitation. The early Bridgerian MAT is inferred to have been near 20 °C and the MAP to have been about 80 cm. Except for the Tiffanian and possibly portions of the early Wasatchian, paleoclimates during the study interval were predominantly frost free. Although the moderating influence of the Green River lake system has been suggested as a possible explanation for mild Eocene winters in Wyoming, this study shows that virtually frost-free climates existed in the area prior to and independent of significant lake development.

INTRODUCTION

The geologic record provides the only documentation of the effects of long-term climate change. One of the most instructive time periods for understanding the processes and effects of global warming is the early Eocene, the warmest interval of the Cenozoic, which followed a warming trend that started in late Paleocene time (Corfield and Cartledge, 1992; Zachos et al., 1994; Corfield and Norris, 1998; Wing et al., 1999). Classic indicators of Eocene global warmth include alligators on Ellesmere Island (Dawson et al., 1976; Estes and Hutchison, 1980), *Nothofagus* (Southern Beech) forests in Antarctica (Case, 1988), and kaolinite deposition off Antarctica (Robert and Chamley, 1991; Robert and Kennett, 1992). The Paleocene-Eocene interval is especially useful for investigating global warming because its biota was more closely related to living organisms than the biota of previous warm intervals of the Mesozoic, and continental positions were not greatly different from those of today.

Most of what is known about the Paleocene-

Eocene transition on a fine temporal scale comes from marine cores (e.g., Kennett and Stott, 1991; Zachos et al., 1994; Bralower et al., 1995, 1997). Nearly all fine-scale continental data, especially paleobotanical data, are derived from a single area, the Bighorn Basin of northwestern Wyoming (Hickey, 1980; Wing and Bown, 1985; Wing et al., 1991, 1995, 1999; Bown et al., 1994; Wing, 1998). The relative lack of data from other regions, even from other areas in the Rocky Mountains (Hickey, 1977), makes it difficult to place events observed in the Bighorn Basin into a broader context.

The present study is of a region located ~300 km south of the southern Bighorn Basin. Plant macrofossils in the greater Green River Basin of southwestern Wyoming (Fig. 1) are well preserved and abundant in the late Paleocene–early Eocene interval. A combination of previous lithostratigraphic work, mammalian biostratigraphy, and radiometric dating provides a well-resolved stratigraphic context, which is updated here (Fig. 2). The study area is also the subject of a recent climate modeling study by Sloan (1994), which examined the possibility that the mid-early to middle Eocene Green River lake system had a moderating effect on Wyoming climates. Climate modeling studies of the early Eocene have generated freezing winters in the Western Interior, contradicting paleontological evidence of predominantly frost-free climates (Sloan and Barron, 1992; Sloan, 1994; Sloan and Rea, 1995; Greenwood and Wing, 1995). In the study area, abundant fossil plants are preserved from sediments below the first lake deposits, and additional fossil floras predate the expanded lake phases (Fig. 2; Roehler, 1993). Roehler (1993, p. 68) considered the maximum lake expansion (Fig. 2; LaCledde Bed) to represent the peak of Eocene warmth and rainfall in the region.

This first paleobotanical field study of the Paleocene-Eocene transition in southern Wyoming

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Data Repository item 200014 contains additional material related to this article.

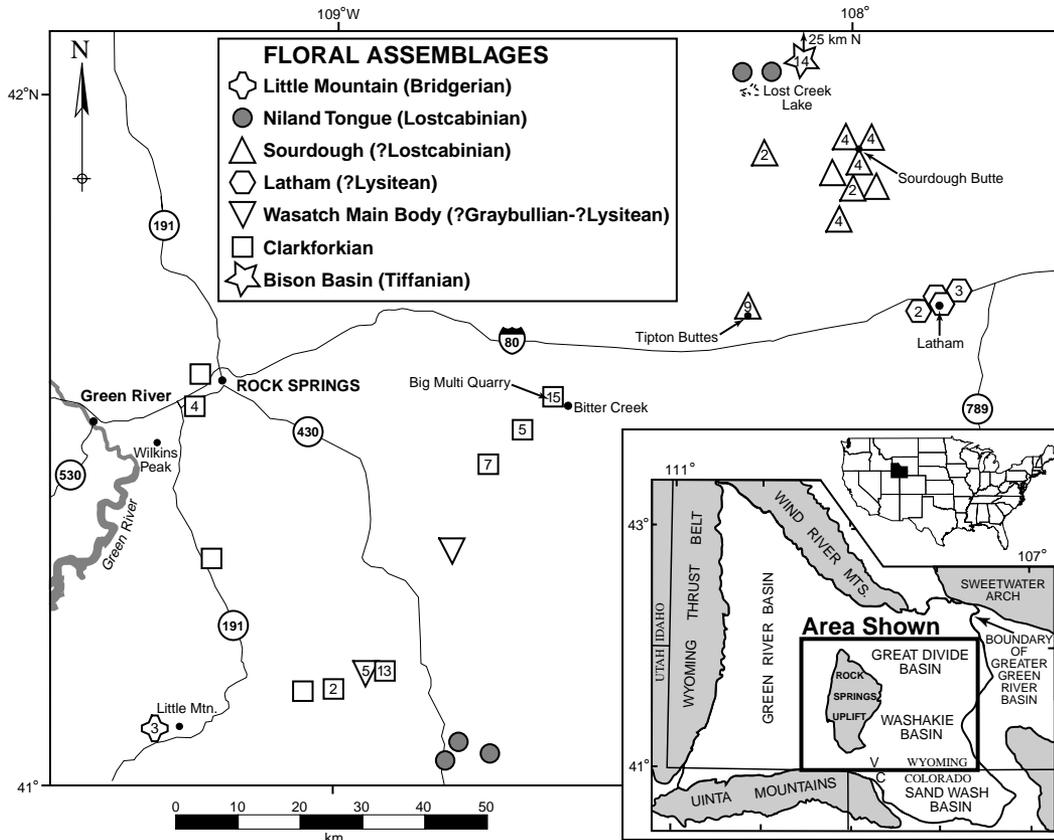


Figure 1. Setting. The inset shows the greater Green River Basin, redrawn after Roehler (1993), showing boundary and principal subbasins: the Green River Basin proper and the Great Divide, Sand Wash, Vermilion Creek (V and C), and Washakie Basins. Uplifts are shown in gray. The main figure shows the locations of the fossil plant quarries within the seven sampling intervals (Table 2; Fig. 2). Symbols representing more than one locality in close proximity bear the number of localities; symbols are not to scale.

investigates the following: (1) climatic changes that occurred in this area in late Paleocene and early Eocene time; (2) the responses of ancient floras to these changes in terms of turnover and diversity; (3) the patterns of climatic and floristic change compared with those known from the Bighorn Basin; and (4) whether warm, humid, and frost-free conditions existed independent of the Green River lakes.

SETTING AND PREVIOUS WORK

The greater Green River Basin, comprising most of southwestern Wyoming and portions of Colorado and Utah, exposes ~5 km of Late Cretaceous–middle Eocene continental rocks, including 3 km of Eocene section (Fig. 1; Roehler, 1985, 1992a, 1992b, 1992c). Today this area is an arid high desert (Knight, 1994). Late Paleocene and early Eocene time is primarily represented by the fluvial Paleocene Fort Union Formation, the fluvial, primarily early Eocene Wasatch Formation, and the lacustrine early and middle Eocene Green River Formation, which interfingers with the Wasatch and subsequent fluvial formations (Fig. 2). The majority of the plant fossils recovered for this study were found in the Fort Union Formation of the Washakie, Great Divide, and Green River Basins, the Wasatch Formation of the Great Divide Basin, and the Green River Formation of

the Green River Basin proper (Figs. 1 and 2). A summary of previous paleoclimatic analyses is shown in Table 1. Several papers on plant macrofossils have addressed the systematics and paleoecology of portions of the paleoflora (Brown, 1962; MacGinitie, 1969; Manchester and Dilcher, 1982, 1997; Wing and Hickey, 1984; Manchester, 1987; Manchester and Zavada, 1987; Herendeen et al., 1990; Herendeen and Dilcher, 1991; Manchester and Chen, 1996; Gemmill and Johnson, 1997; Wilf et al., 1998a; Wilf and Labandeira, 1999). Extended discussion of previous work and stratigraphy, descriptions and photographs of many of the fossil plant species, and locality and lithologic data can be found in Wilf (1998). A complete occurrence matrix has been placed in the GSA Data Repository¹.

STRATIGRAPHY

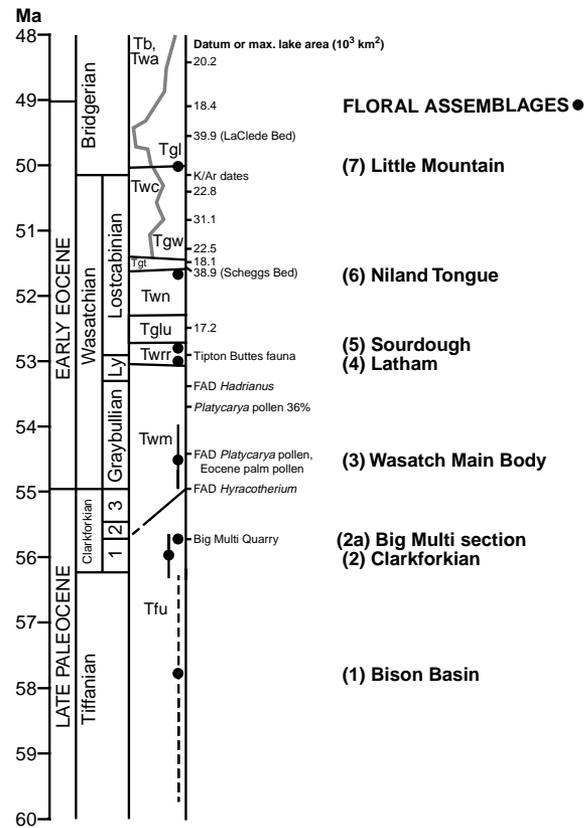
Fossil floras were grouped into seven samples for analysis (Figs. 1 and 2; Table 2). Samples 1–6 are from alluvial environments, and sample 7 is lacustrine. Only samples 2 and 3 are significantly

time averaged. The samples are: (1) the Tiffanian Bison Basin assemblage from the Fort Union Formation of the northern Great Divide Basin, first reported by Gemmill and Johnson (1997); (2) floras from the uppermost Fort Union and lowest Wasatch Formations, known or inferred to be Clarkforkian, including the flora of an 18 m stratigraphic section through Big Multi Quarry (early Clarkforkian; Wilf et al., 1998a; Figs. 1 and 2); (3) floras from the Main Body of the Wasatch Formation, probably Graybullian to Lysitean; (4) the flora of the Latham coal zone, Ramsey Ranch Member of the Wasatch Formation, from a single horizon that is possibly Lysitean; (5) the flora of the Sourdough and Monument coal zones of the Ramsey Ranch Member, probably earliest Lostcabinian; (6) the flora of the uppermost Niland Tongue of the Wasatch Formation, known to be Lostcabinian; and (7) the early Bridgerian flora from the southwest slope of Little Mountain (Fig. 1), found in the uppermost Wilkins Peak and lowermost Laney Members of the Green River Formation.

The oldest sample in this study consists of 14 quarries from a single stratigraphic level in the Bison Basin (Gemmill and Johnson, 1997). Revised identifications, based on examination of the voucher collections at the Denver Museum of Natural History (DMNH), are used here. Fossil mammals found in the Bison Basin have been as-

¹GSA Data Repository item 200014, supplemental data tables, is available on the Web at <http://www.geosociety.org/pubs/drpint.htm>. Requests may also be sent to Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301; e-mail: editing@geosociety.org.

Figure 2. Stratigraphic framework for the seven floral assemblages (filled circles). Land mammal “age” (see Prothero, 1995, for use of quotations) and subage boundaries are after Wing et al. (1999), except the Wasatchian-Bridgerian boundary (after Krishtalka et al., 1987). The Paleocene-Eocene boundary, currently unresolved (Berggren et al., 1997), is set here to the Clarkforkian-Wasatchian boundary. The early–middle Eocene boundary is after Cande and Kent (1992, 1995). Solid vertical line—estimated stratigraphic lumping; dashed vertical line—age uncertainty; Tfu—Fort Union Formation (fluvial); Tw—Wasatch Formation (fluvial); Twm—Main Body, events interpolated using Roehler (1992c) and Hutchison (1980); Twrr—Ramsey Ranch Member; Twn—Niland Tongue; Twc—Cathedral Bluffs Tongue. Tg—Green River Formation (lacustrine); Tglu—Luman Tongue; Tgt—Tipton Shale Member; Tgw—Wilkins Peak Member; Tgl—Laney Member. Tb—Bridger Formation (fluvial). Twa—Washakie Formation (fluvial). Ly—Lysitean. Numbers along right side of column indicate maximum areal extents of indicated phases of Green River lakes, in thousands of square kilometers, from Roehler (1993).



signed to several Tiffanian zones (Ti2, Ti3, and Ti5; Gazin, 1956; Archibald et al., 1987), and the fossil plant horizon has not been correlated to a specific mammal quarry. A range of possible ages for sample 1 is therefore indicated, from ca. 60 to 56.2 Ma (Prothero, 1995).

For the Clarkforkian, the principal biostratigraphic tiepoint for southern Wyoming is Big Multi Quarry, in the northwestern Washakie Basin (Figs. 1 and 2; Rose, 1981a; Dawson and Beard, 1996; Wilf et al., 1998a). The mammalian fauna of Big Multi Quarry is early but not earliest Clarkforkian (Wilf et al., 1998a). As an approximation, the quarry is shown in Figure 2 at the Cf1-Cf2 boundary, placed in the latest calibrations of the Bighorn Basin sequence ca. 55.7 Ma (Wing et al., 1999). The 15 quarries reported by Wilf et al. (1998a) from the Big Multi section are included in sample 2, with a single new taxon, and also considered separately as sample 2a because they are biostratigraphically well constrained. Of the remaining 34 localities in sample 2, many are known to be Clarkforkian on the basis of mammalian occurrences. The others are placed in sample 2 on the basis of high stratigraphic position in the Fort Union Formation, floristic and lithologic similarity to known Clarkforkian strata in the area, palynological data, and/or a megafloreal zonation established in the Bighorn Basin (Hickey, 1980; Wing, 1998).

Sample 2 is estimated to be time averaged over Cf1 and possibly the latest Tiffanian because none of the localities appears to be much younger than Big Multi Quarry (Fig. 2).

Plant fossils from the Main Body of the Wasatch Formation, sample 3, are rare, and the species richness of the sample is very low (Table 2). Lithologies are sandy and frequently oxidized, and the occasional carbonaceous deposits are highly weathered. Part of the basal Wasatch Formation on the west side of the Rock Springs uplift is palynologically determined to be Paleocene (Kirschbaum, 1987; Kirschbaum and Nelson, 1988). However, the base of the Wasatch Formation contains diagnostic Wasatchian mammals on the southeast side of the uplift, closer to the plant localities in sample 3 (Roehler, 1992c; Fig. 2). Sample 3 is most likely to be Graybullian to Lysitean.

Samples 4–6 were found in the Ramsey Ranch Member and Niland Tongue of the Wasatch Formation in the Great Divide Basin (Fig. 2; Pipiringos, 1961; Masursky, 1962; Roehler, 1987, 1991, 1992b, 1993). The lowest productive level was sample 4, a tabular carbonaceous shale layer immediately above the Latham 4 coal (Masursky, 1962; Figs. 1 and 2). Preservation was fair to poor. However, the fossiliferous units were fine grained, indicating little transport of plant material. Preliminary faunal lists from new excava-

tions of the Tipton Buttes faunal locality, ~48 m above the Latham assemblage (Figs. 1 and 2), indicate a Lysitean or Lostcabinian assignment (Pipiringos, 1961, Table 3; R. Anemone, 1998, personal commun.).

Sample 5, herein called the Sourdough assemblage, was recovered from the uppermost Ramsey Ranch Member in roof strata of the Sourdough and Monument coal zones (Pipiringos, 1961; Masursky, 1962). These units are grouped together for analysis because levels that bear fossil plants are minimally separated stratigraphically (0–20 m) and because nearly all of the plant species recovered can be found within a single extensive layer above the Sourdough 2 coal. The Sourdough 2 coal, 42 m above the Tipton Buttes faunal locality, appears to be of similar age to the 621 m level of the Elk Creek section in the Bighorn Basin, where a laterally extensive carbonaceous shale deposit occurs that is also rich in fossil plants (e.g., Davies-Vollum and Wing, 1998). The latter is earliest Lostcabinian and has been calibrated to 52.8 Ma (Wing et al., 1999). This tentative interbasinal correlation is based primarily on high floristic similarity (discussed later), and also on the Lysitean-Lostcabinian affinities of the underlying Tipton Buttes fauna.

Nearly all of the species recovered for sample 6 were found at two previously known localities in the upper 27 m of the Niland Tongue in the

TABLE 1. PREVIOUS PALEOCLIMATIC INTERPRETATIONS

Author(s)	Study area	Interpretation	Evidence
Early Bridgerian (Wilkins Peak Member of Green River Formation)			
Wolfe et al., 1998	Little Mountain	MAT~17.2 °C*	Leaf physiognomy
Roehler, 1993, and references therein	Greater Green River Basin	Cyclically hot arid and warm temperate	Sediments, plants, vertebrates
Herendeen et al., 1990; Herendeen and Dilcher, 1991	Little Mountain	Subtropical/tropical	Legumes and hornworts: living relatives
MacGinitie, 1969; Leopold and MacGinitie, 1972	Little Mountain	Seasonally dry subtropical	Pollen and plant macrofossils: living relatives and leaf physiognomy
Wasatchian			
Grande, 1994	Fossil Lake (Lostcabinian)	Subtropical to tropical	Reptiles and fish: living relatives
Nichols, 1987	Vermilion Creek Basin (Lostcabinian)	Subtropical/tropical with abundant rainfall	Pollen: living relatives
Roehler, 1993	Greater Green River Basin	Warm temperate, warming to subtropical in Lostcabinian	Sediments, plants, vertebrates
Clarkforkian			
Wilf et al., 1998a	Big Multi Quarry, northwest Washakie Basin	Humid subtropical; MAT ~19.5 °C, MAP~137 cm	Plants: leaf physiognomy and living relatives; vertebrates: cenogram analysis, living relatives, functional analogues; sediments
Roehler, 1979	Northwest Washakie Basin	Humid subtropical	Sediments, vertebrates, plants

Notes: MAT—mean annual temperature; MAP—mean annual precipitation.

*This estimate was based on MacGinitie's (1969) original Little Mountain collections, a subset of the Little Mountain assemblage of this study.

northern Great Divide Basin (Fig. 1) (see Phipps, 1961; Wing and Hickey, 1984, Table 3). The Niland Tongue is Lostcabinian (Gazin, 1965; Roehler, 1987; Krishtalka et al., 1987). The base of the Lostcabinian is currently placed at 52.9 Ma (Wing et al., 1999), and the end, the Wasatchian-Bridgerian boundary, is estimated to be 50.1–50.2 Ma based on recalibrated K/Ar dates (Fig. 2; Mauger, 1977; Krishtalka et al., 1987; Clyde et al., 1997). Stratigraphic interpolation using the

Tipton Buttes fauna as the base of the Lostcabinian gives an approximated age for sample 6 of 51.7 Ma (Fig. 2).

The highest stratigraphic level studied here is represented by the Little Mountain flora, sample 7 (Fig. 1), first collected by MacGinitie (1969) for the University of California Museum of Paleontology (UCMP). Although it has not been possible to relocate MacGinitie's original quarry, two new collections have been made in the same area for

the Florida Museum of Natural History (UF) and for the National Museum of Natural History (USNM), approximately quadrupling the number of species. The USNM specimens and the majority of the UCMP material are from the uppermost Wilkins Peak Member, and the remainder is from the lowermost Laney Member. Recent examination of field photographs of the UF locality shows that it probably is in the lower 30 m of the Laney Member. No significant differences have been detected yet in floristic composition or leaf physiognomy between the Wilkins Peak and Laney material, so all of the Little Mountain collections are treated here as sample 7. The recalibrated K-Ar dates of 50.1 and 50.2 Ma, mentioned here, are from the Wilkins Peak Member in the Green River Basin, and one is from the upper third of the member. On the basis of the calibration of the Wasatchian-Bridgerian boundary using these dates by Krishtalka et al. (1987, p. 93) and the presence of Bridgerian mammals in fluvial rocks coeval to the Wilkins Peak Member (Krishtalka et al., 1987), sample 7 dates from ca. 50 Ma and is early Bridgerian and late early Eocene (Cande and Kent, 1992; new radiometric dates are needed for improved calibration).

METHODS

The majority of the voucher collections, which I made in the 1994–1996 and 1998 field seasons, are housed in the Department of Paleobiology, National Museum of Natural History, accession no. 420051. Collections examined from other institutions were: (1) the Bison Basin sample (DMNH); (2) UF and DMNH collections from three Paleocene sites on the west side of the Rock

TABLE 2. SAMPLING, CLIMATIC, AND DIVERSITY DATA

Sample	(1) BB	(2) Cf	(2a) BM	(3) WM	(4) La	(5) Sd	(6) NT	(7) LM	Totals
#Quarries	14	49	15	6	7	31	5	3	115
#Morphotypes	39	58	35	14	19	74	26	87	252
#Species	29	48	29	13	17	61	24	59	189
#Woody dicots	26	37	21	9	12	44	14	49	155
#Reproductive	10	10	6	1	2	14	2	29	65
<i>P</i>	0.346	0.432	0.571	-	0.500	0.659	0.714	0.602	
LMAT, °C	11.7	14.4	18.6	-	16.4	21.3	23.0	19.6	
σ(LMAT), °C	2.9	2.5	3.3	-	4.4	2.2	3.7	2.1	
MI _{NA}	7.71	7.58	7.46	-	7.23	7.62	7.01	6.52	
L _{MAP} , cm	147	137	129	-	113	140	100	76.9	
se+(L _{MAP}), cm	63.6	59.2	55.5	-	48.9	60.5	43.4	33.2	
se-(L _{MAP}), cm	44.4	41.3	38.8	-	34.2	42.2	30.3	23.2	
<i>N</i> _{mean}	9.9	5.1	6.4	2.5	4.4	6.7	7.0	28	
<i>N</i> _{dev}	3.7	3.6	4.2	1.4	3.4	6.7	6.8	17.6	
<i>N</i> _{max}	15	17	15	4	12	33	16	48	
<i>D</i> _{mean}	0.48	0.25	0.34	-	-	0.46	-	-	
<i>D</i> _{max}	0.57	0.61	0.61	-	-	0.73	-	-	
<i>D</i> _{cum}	0.56	0.57	0.51	-	0.66	0.79	-	0.87	
<i>H</i> _{mean}	0.87	0.51	0.63	-	-	1.0	-	-	
<i>H</i> _{max}	1.1	1.2	1.2	-	-	1.7	-	-	
<i>H</i> _{cum}	1.0	1.3	1.1	-	1.5	2.0	-	2.8	

Notes: BB—Bison Basin; Cf—Clarkforkian; BM—Big Multi section; WM—Wasatch Main Body; La—Latham; Sd—Sourdough; NT—Niland Tongue; LM—Little Mountain; #Woody dicots—number of dicot leaf types used for paleoclimate analyses; *P*—proportion of woody dicots with untoothed margins; LMAT—estimated mean annual temperature from leaf-margin analysis; σ(LMAT)—sampling error (Wilf, 1997: Equation 4); MI_{NA}—mean natural log leaf area; L_{MAP}—estimated mean annual precipitation from leaf-area analysis; se—standard error; *N*—#species/quarry; *D*—Simpson's Index, *H*—Shannon-Wiener index, as in Rose (1981b); dev—1 standard deviation; cum—all quarries in sample combined. All diversity indices based on dicot leaves only (Tables A1 and A2). La and LM cumulative diversity indices are from drawer counts of all localities (226 and 271 specimens, respectively). - = data not available or not applicable.

Springs uplift; (3) the aforementioned UCMP and UF collections from Little Mountain.

The 115 quarries were each localized, generally consisting of 1–2 m³ of sediment. Most of the quarries were in fine-grained rocks, predominantly carbonaceous shales and siltstones of distal backswamps and oxbows, but also fine-grained to occasionally medium-grained near-channel or lake margin sandstones. Plants were preserved exclusively as compressions and impressions. Leaf assemblages from late Paleocene and early Eocene carbonaceous shales of the Bighorn Basin are considered to be minimally transported and to represent 2000 yr or less of deposition (Davies-Vollum and Wing, 1998). The carbonaceous shale and siltstone beds from samples 2–6 are similar in general features to those in the Bighorn Basin and are also considered to represent rapid deposition from a small source area (supporting criteria of Wilf et al., 1998a). Lacustrine assemblages, such as the Little Mountain sample, are thought to represent wider time windows than fluvial assemblages and to be derived from a larger source area (e.g., Wing and DiMichele, 1995). The Bison Basin assemblage may also reflect relatively greater spatial mixing from deposition in a pond-like environment (Gemmill and Johnson, 1997). Field censuses of dicot leaves were taken for quarries with abundant identifiable material, found in samples 2 and 5, to assess relative dominance and evenness (Table 2; Tables A1 and A2; Burnham et al., 1992; Davies-Vollum and Wing, 1998; Wilf et al., 1998a). For Bison Basin, Gemmill and Johnson (1997) reported data from 10 field censuses, which are used here with revised identifications.

Fossil plants were differentiated into 252 morphotypes by analysis of leaf architecture (Hickey, 1973, 1979; Hickey and Wolfe, 1975) and the use of comparative fossil and extant material (Table A3). Assignments of the morphotypes to described taxa were made in many cases; ~80% are not known from the Bighorn Basin (Table A3). The minimum number of species is estimated as 189 (Table 2), calculated as the number of nonreproductive morphotypes plus two ("*Sparganium*" and *Ceratophyllum*). For convenience, "species" will be used to refer both to formally described species and to undescribed morphotypes included in the estimated species count. More than half of the species are new records for the region.

Paleoclimate analysis was based on two primary approaches: (1) analysis of the climatic tolerances of the nearest living relatives of extinct organisms; and (2) quantitative analysis of leaf size and shape. The merits and shortcomings of each approach have been examined elsewhere (e.g., Wing and Greenwood, 1993; Herman and Spicer, 1997; Mosbrugger and Utescher, 1997;

Wolfe et al., 1998). The nearest living relative approach is considered most applicable when the fossil organism belongs to a diverse, widespread, extant clade with consistent climatic tolerances; to increase in accuracy as more organisms are analyzed; and to decrease in accuracy with increasing age of the fossils. Many Paleogene plants belong to extant genera or families, and the nearest living relative and leaf-morphologic approaches have shown broad agreement with each other and with other proxies in many studies of Late Cretaceous and Cenozoic climates (Hutchison, 1982; Johnson and Hickey, 1990; Wolfe, 1992; Wing and Greenwood, 1993; Greenwood and Wing, 1995; Wilf et al., 1998a; Wilf et al., 1999).

The two approaches based on leaf size and shape were leaf-margin analysis (Wolfe, 1979; Wing and Greenwood, 1993; Wilf, 1997) and leaf-area analysis (Wilf et al., 1998b). Both methods use only the woody dicotyledons in an assemblage (Table 2). Leaf-margin analysis uses the following linear relationship between mean annual temperature (MAT, in °C) and the proportion *P* of species in a sample with untoothed margins (Wolfe, 1979; Wing and Greenwood, 1993):

$$\text{estimated MAT} = 30.6P + 1.14. \quad (1)$$

The binomial sampling error on this estimate nearly always exceeds the published regression error of 0.8 °C and is used here as a minimum error (Table 2; Wilf, 1997).

Leaf-area analysis is based on the significant relationship between the mean natural logarithm of the leaf areas of the species in a sample (MlnA, where area is measured in square millimeters) and mean annual precipitation (MAP, in centimeters):

$$\ln(\text{estimated MAP}) = 0.548 \text{ MlnA} + 0.768, \\ \text{standard error} = 0.359 \quad (2)$$

Wilf et al., 1998b; see also Givnish, 1984; Jacobs, 1999). The quantity MlnA was based on the percentage of species in a sample found in each of the Raunkiaer-Webb discrete leaf area categories (Webb, 1959), using the formulae of Wilf et al. (1998b). If a species displayed more than one leaf-area category, it received a fractional score for each category, including rangethroughs. Because of the high sensitivity of recovered leaf size to taphonomic processes and hydraulic sorting, paleoprecipitation estimates from leaf-area analysis must be considered approximate at best. However, intensive sampling throughout the section, the minimally transported nature of most plant material, and the abundance of large leaves at many localities all improve the likelihood that a nearly complete size spectrum has been recovered, at least for common species.

TABLE 3. TOP THREE RANKED DOMINANTS BY FLORAL ASSEMBLAGE

(7) Little Mountain (drawer count)
<i>Parvileguminophyllum coloradensis</i>
<i>Lindera varifolia</i>
<i>Rhus nigricans</i>
(6) Niland Tongue (drawer count)
<i>Platycarya castaneopsis</i>
" <i>Dombeya</i> " <i>novi-mundi</i>
<i>Averrhoites affinis</i>
(5) Sourdough (Table A2)
<i>Platycarya americana</i>
<i>Alnus</i> sp.
Apocynaceae sp.
(4) Latham (drawer count)
" <i>Meliosma</i> " <i>longifolia</i>
<i>Cnemidaria magna</i>
<i>Platycarya</i> ? <i>americana</i>
(3) Wasatch Main Body (drawer count)
<i>Metasequoia occidentalis</i>
" <i>Carya</i> " <i>antiquorum</i>
<i>Averrhoites affinis</i>
(2) Clarkforkian (Table A1; Wilf et al., 1998a)
<i>Corylites</i> sp.
<i>Glyptostrobus europaeus</i>
<i>Persites argutus</i>
(1) Bison Basin (Gemmill and Johnson, 1997)
<i>Corylites</i> sp.
" <i>Ampelopsis</i> " <i>acerifolia</i>
<i>Metasequoia occidentalis</i>

CLIMATE CHANGE

Several profound changes in regional climate occurred during the study interval. Summary results from leaf-margin and leaf-area analysis are shown in Figure 3. Also plotted for comparison are previously published leaf-margin data from the Bighorn and northern Wind River Basins of northern Wyoming (Hickey, 1980; Wing et al., 1991, 1999).

The Bison Basin assemblage has no taxa strongly associated with warm conditions but several that indicate wet environments, including horsetails (*Equisetum*; see Lebkuecher, 1997) and the semiaquatic or fully aquatic *Fortuna* cf. *marsilioides* (see McIver and Basinger, 1993). The Bison Basin dicot species have the largest mean leaf area of all seven samples, indicating abundant rainfall (Fig. 3; Table 2). Palms and gingers, diverse groups with limited frost tolerances today, are conspicuously absent. Leaf-margin analysis indicates mean annual temperatures near 11.7 °C (Fig. 3; Table 2).

There is diverse evidence of humid and subtropical conditions in the Clarkforkian (Wilf et al., 1998a). Palms, gingers, and a few dicot families with modern tropical affinities are present (see next section). Palms are taken as evidence of climates with mean annual temperatures >10 °C, cold month mean temperatures >5 °C, and yearly minimum temperature >−10 °C (Greenwood and

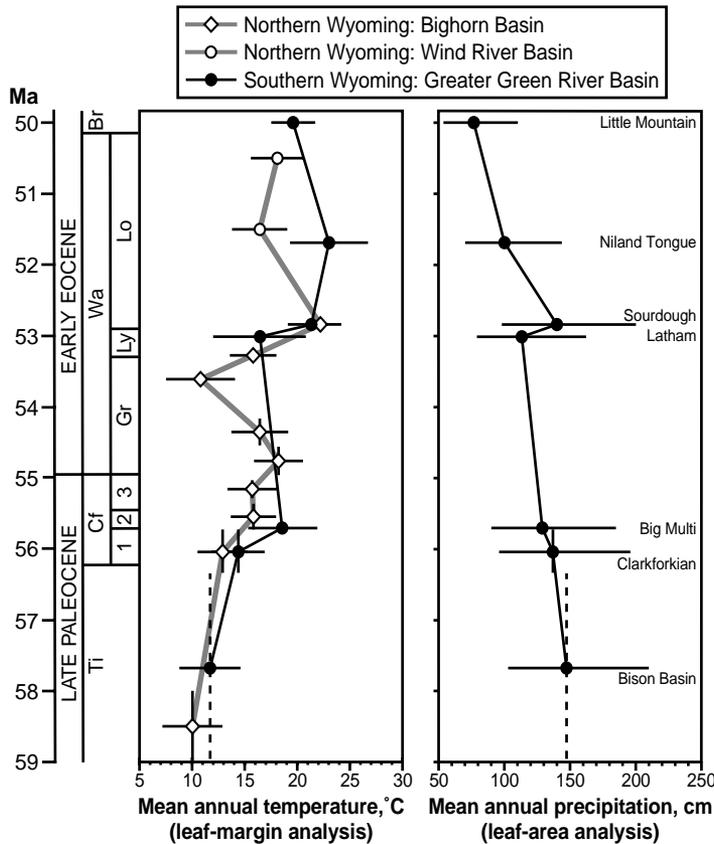


Figure 3. Paleocene-Eocene climate history of southern (Table 2) and northern (Hickey, 1980; Wing et al., 1991, 1999) Wyoming, estimated from leaf-margin and leaf-area analysis. Samples are labeled for the southern Wyoming data. The formulae used for leaf-margin analysis are identical in all data sets shown (Wing and Greenwood, 1993; Wilf, 1997, equation 4 for $\pm 1\sigma$ error bars, which increase with decreasing sample size). Leaf-area analysis as in Wilf et al. (1998b); $\pm 1\sigma$ error bars are asymmetrical because they were converted from logarithmic units. Temporal calibration of northern Wyoming data as in Wing et al. (1991, 1999); see text for calibration of southern Wyoming data. Abbreviations of land mammal zones correspond to Figure 2.

Wing, 1995; see Meyer and Manchester, 1997, for an exception regarding gingers). Two genera of crocodylians as well as champsosaurs have been found at Big Multi Quarry (Rose, 1981a; see also Roehler, 1979). Crocodylians indicate coldest-month mean temperatures >5.5 °C and mean annual temperatures >14.2 °C (Markwick, 1998). Leaf-margin analysis indicates mean annual temperatures near 14.4 °C for the Clarkforkian sample and 18.6 °C for the Big Multi section (Fig. 3; Table 2). Although the error bars overlap, the higher estimated MAT and the higher stratigraphic position of the Big Multi section relative to some of the Clarkforkian localities (Wilf, 1998) are consistent with warming within the Clarkforkian.

Moist, well-forested conditions at Big Multi Quarry have been inferred from several analyses (Wilf et al., 1998a; Table 1). The plant taxa and the reduced lithologies observed at and near Big Multi Quarry are also present throughout the upper Fort Union Formation in the study area. Leaf-area analysis gives essentially identical MAP estimates for the Big Multi section (129 cm) and for the entire Clarkforkian sample (137 cm), indicating the continuation of humid conditions from the Tiffanian.

Changing depositional environments from the

upper Fort Union Formation to the Main Body of the Wasatch Formation are indicated by the rarity of coals in the Main Body and the presence of red beds on the periphery of the greater Green River Basin, contrasted with chloritic green and gray beds in basin centers (Roehler, 1992c, 1993). I have recovered abundant paleosol carbonates from Graybullian red beds in the Main Body of the northwestern Great Divide Basin (site given by Pipiringos, 1961, p. 13). These overlie drab Fort Union deposits, further indicating increased drainage and seasonal moisture deficits on basin margins (e.g., Sobecki and Wilding, 1982). All of these lithologic changes appear to reflect increasing relief and some regional drying as the uplifts of surrounding ranges created rain shadows, so that only the central basins remained waterlogged through most of the year (see also Lillegraven and Ostresh, 1988; Roehler, 1993).

The relatively poor paleobotanical record from the Main Body of the Wasatch Formation suggests continuation of mild conditions, with warming indicated in the upper Main Body. There is no significant gap in the crocodylian record of the Main Body (P. Holroyd, 1998, personal commun.), indicating that severe winters were rare at any time. Leopold and Roehler (*in* Roehler, 1992c) reported palm pollen in the lower Main

Body of the Washakie Basin (Fig. 2). Ginger foliage occurs ~60 m above this pollen sample. The first appearance datum of *Hadrianus*, a large, nonburrowing tortoise and therefore a proxy for warm winters, occurs in the upper Main Body of the Washakie Basin (Hutchison, 1980; Fig. 2). The increase in *Platycarya* pollen abundance in the Main Body mirrors the contemporaneous increase in the Bighorn Basin, which may be related to rising temperatures (Fig. 2; Wing and Hickey, 1984; Roehler, 1992c).

The Latham assemblage indicates warm, mild, and somewhat humid conditions, although the low diversity limits interpretation. Palms and gingers are present, in addition to leaves of the tree fern *Cnemidaria* and the aquatic fern *Salvinia*, both known only from subtropical to tropical climates today. Leaf-margin analysis indicates a MAT near 16.4 °C, similar to Clarkforkian temperatures, although this value is tentative because of the high sampling error (Fig. 3; Table 2). Wet conditions are evident from the presence of three fern species, including *Salvinia*, and the existence of the Latham coal, which reaches 6 m in thickness (Masursky, 1962). Ferns have free-living haploid generations that are highly vulnerable to desiccation and also require aqueous fertilization, and thus the majority of extant fern taxa live

in moist environments. Subsidence and waterlogging in basin centers from continuing tectonic activity may have played a greater role than precipitation in maintaining moist habitats. Leaf sizes are smaller than in the Clarkforkian sample, despite the fine-grained depositional environment, and leaf-area analysis, albeit from a small sample size, indicates a MAP near 113 cm (Fig. 3). Small leaves in the Lysitean have been observed qualitatively in the Bighorn Basin (S. Wing, 1997, personal commun.) and in an assemblage from the San Jose Formation, San Juan Basin, New Mexico, first reported by Tidwell et al. (1981) and recently recollected (S. Wing, P. Wilf, and K. Johnson, 1997, field observations). This combination of evidence supports a somewhat drier regional climate in Latham time, with sufficient rainfall and runoff throughout the year to allow peat formation in the lowest areas of the Great Divide Basin.

The Sourdough assemblage indicates elevated temperatures and the return of humid conditions. A significant influx of dicot families with tropical affinities (next section) and the continuing presence of thermophilic nondicots (palms, gingers, tree ferns, and *Salvinia*) provide floristic evidence for high temperatures. Thick leaves occur on more species than in the Clarkforkian sample, a feature associated today with broad-leaved evergreen forests. However, seasonal light variation at middle latitudes probably precluded fully tropical conditions, reflected by the fact that many abundant taxa were deciduous (alder, poplar, *Platycarya*). Leaf-margin analysis indicates a MAT near 21.3 °C (Fig. 3; Table 2). The Sourdough 2 coal is as much as 3.6 m thick (Masursky, 1962), and claystones at some localities have fine laminae, indicating deposition in standing water. Hydrophilic plants include a water lily, horsetails, and eight species of ferns. Many plant species are represented by large leaves, and leaf-area analysis indicates a MAP near 140 cm.

The megafloora from the Niland Tongue documents the continuation of warm conditions from Sourdough time, following the expansion and retreat of the Luman Lake (Fig. 2). The plant species composition is broadly similar to the Sourdough sample (Table A3), and palynomorphs from the Niland Tongue of the Vermilion Creek Basin (Fig. 1) include many subtropical and tropical forms (Nichols, 1987). Leaf-margin analysis of the 14 dicot species indicates a MAT near 23.0 °C (Fig. 3; Table 2). Analysis of rainfall is less conclusive and is constrained by the low diversity and areal extent of the sample. Several dicot forms consistently have small leaves, so that leaf-area analysis indicates a lower MAP of 100 cm (Fig. 3; Table 2). Coals associated with the species-rich quarries near Lost Creek Lake (Fig. 1)

are <1 m thick (Pipiringos, 1961, p. 47). However, a coal in the upper Niland Tongue of the Vermilion Creek Basin, associated with three other plant quarries (Fig. 1), reaches 3.6 m in thickness (Ellis, 1987). More evidence for moist conditions includes the presence of horsetails and five species of ferns and palynological records from the Vermilion Creek Basin of several aquatic and marsh-dwelling taxa (Nichols, 1987; Table 1). This combination of evidence implies that some drying may have occurred, as indicated by leaf-area analysis. However, swampy conditions continued in low areas, such as the Vermilion Creek Basin, and seasonal, arid climates had not become established.

The lower portion of the superposed Tipton Shale Member of the Green River Formation represents a significant freshwater expansion of Lake Gosiute (Roehler, 1993; Fig. 2). Roehler (1993) considered a sharp and long-lasting change from humid to hot and arid conditions and from fresh to saline lake waters to have occurred higher in the Tipton Shale Member (Rife Bed, Fig. 2; Surdam and Wolfbauer, 1975). Sedimentological data from the succeeding Wilkins Peak Member provide substantial evidence for cyclically arid conditions, such as (1) extensive evaporite deposits, including shortite, halite, and the world's largest known trona reserves (Culbertson, 1971; Roehler, 1993); (2) periodically low lake volume and playa environments, with closed drainage persisting into the overlying Laney Member (McGrew, 1971; Eugster and Hardie, 1975; Surdam and Stanley, 1979; Smoot, 1983; Roehler, 1993); and (3) extensive red beds in portions of the intertonguing, fluvial Cathedral Bluffs Tongue of the Wasatch Formation (e.g., Roehler, 1993). Hot and arid phases alternated as many as 77 times with warm temperate conditions (Roehler, 1993).

The lacustrine Little Mountain assemblage indicates a subtropical, warm climate that was somewhat cooler and had more seasonal rainfall than the middle Wasatchian. Foliar analysis indicates a MAT near 19.6 °C and a MAP near 75.8 cm (Fig. 3; Table 2). These results are consistent with previous work (Table 1). Sufficient water was available to support occasional ferns, horsetails, and the living hornwort species *Ceratophyllum muricatum* (Herendeen et al., 1990), which today inhabits shallow to ephemeral fresh-water environments of tropical and subtropical regions (Les, 1997), and to preserve body fossils of insects, fish skeletons, and the shell of an aquatic turtle (*Echmatemys* sp., P. Holroyd and H. Hutchison, 1999, personal commun.). In addition, increasing deposition of oil shale and decreasing deposition of evaporites occurred through the upper Wilkins Peak Member (Smoot, 1983; Roehler, 1993). These lines of evidence, as well

as the position of the sample at the southern edge of the Green River Basin, indicate that the Little Mountain assemblage was derived from a relatively expanded stage of Lake Gosiute that followed the more evaporitic conditions of the Rife Bed and lower Wilkins Peak Member.

Aridity and increased seasonality are the likely causes of the Wasatchian-Bridgerian floral turnover (next section) and should also be considered as an alternative explanation to high temperatures for observed changes in primate dominance and diversity patterns near the Wasatchian-Bridgerian boundary in southern and northern Wyoming (Beard et al., 1992; Gunnell, 1997).

Discussion

The temperature curves shown in Figure 3 are consistent with each other and with data from other areas, as summarized in the following five points. First, the southern Wyoming temperature means are consistently as warm or warmer than the north. Second, the warming trend in late Paleocene time agrees with data from deep-sea cores (Corfield and Cartlidge, 1992; Zachos et al., 1994). Third, the northern Wyoming data indicate cooling near 54 Ma followed by an abrupt warming trend to 53 Ma; the southern Wyoming data corroborate the warming trend, although the richness of the Main Body sample is too low to evaluate the extent of the preceding cooling. Fourth, both data sets indicate maximum temperatures by the middle of early Eocene time, and the southern Wyoming data indicate that this peak continued further into early Eocene time. This sustained maximum corresponds to the Cenozoic thermal maximum known from marine isotopic data (Miller et al., 1987; Zachos et al., 1994; Bralower et al., 1995). Fifth, the moderate cooling in late early Eocene time is in agreement with the deep-sea record (Zachos et al., 1994; Bralower et al., 1995) and with other proxies, including stable isotope data from late early–early middle Eocene calcite cements in Antarctic fossil wood (Pirrie et al., 1998) and isotopic evidence from mollusks for significant temperature seasonality in the early middle Eocene of the Paris Basin (Andreasson and Schmitz, 1996). All of these results support leaf-margin analysis as a robust methodology for inferring Paleogene continental temperatures.

Davies-Vollum and Wing (1998) noted the absence of tabular carbonaceous shales in the 350–600 m portion of the Willwood Formation in the Bighorn Basin, suggesting a regional drying trend from the early to the late early Eocene as a possible cause. Among other evidence, these authors cited the transition, in southern Wyoming, from the lacustrine Luman Tongue of the Green River Formation to the fluvial Niland Tongue of

the Wasatch Formation and the evaporitic nature of the Wilkins Peak Member of the Green River Formation. If, as suggested here, the Sourdough flora is close in age to the 621 m level of the Willwood Formation, the 350–600 m portion of the Willwood Formation is older than all of the units listed here as well as the humid Sourdough assemblage. The 350–600 m interval appears to correlate with the uppermost Main Body and lower Ramsey Ranch Member of the Wasatch Formation, another possible time of drying in the greater Green River Basin separated from later drying by the wet Sourdough climate (Fig. 3). Early Eocene drying in the Rocky Mountains was not unidirectional, but took place in several pulses and reversals.

The Green River lake system has been suggested as a possible cause of mild winters in southern Wyoming (Sloan, 1994). However, the data presented here indicate that warm and moist climates with minimal frost existed through most of the study interval, independent of lakes. Furthermore, the Green River lakes were areally constricted for much of their history (Fig. 2; Surdam and Wolfbauer, 1975; Surdam and Stanley, 1979; Smoot, 1983; Roehler, 1993). The maximum Wyoming Lake area of 39 900 km² (Fig. 2) was an order of magnitude smaller than a lake the size of the two model grid cells in Sloan's (1994) simulation, 320 000 km². Humid subtropical conditions were already present in the area in the Clarkforkian, when the lake system was confined to the Uinta Basin of Utah (e.g., Grande, 1984). Although a cool interval may have occurred in the Graybullian, virtually frost-free climate returned, as indicated by the Latham assemblage, and predated the first appearance of Lake Gosiute by about 200–300 k.y. (Fig. 2). The first appearance of the Colorado arm of Lake Uinta also did not occur until the Lostcabinian (Kihm, 1984). The Sourdough assemblage, from the Cenozoic thermal maximum, immediately underlies the Luman Tongue of the Green River Formation but predates substantially the Scheggs Bed of the Tipton Shale Member, which was the first significant expansion of the lake (Fig. 2). Maximum lake expansion postdated the entire interval studied here (Fig. 2). Although Roehler (1993) considered the Laney expansion to reflect maximum Eocene warmth and rainfall in the area, this report shows that warmer and moister conditions than he considered to be present during Laney time (about 16 °C and 110 cm MAP) occurred in the middle early Eocene (Fig. 3). The lack of correlation between lake volume and either warmth or rainfall underscores the importance of studies that examine separately the influences of climate and tectonics on lake volume (Love et al., 1963; Colman, 1998; Carroll and Bohacs, 1999) and that investigate other causative mechanisms for

early Eocene continental warmth (Sloan and Morrill, 1998; Sloan and Pollard, 1998).

TURNOVER

Two floral turnovers affecting more than 80% of species are recorded. The first occurred with Clarkforkian–Wasatchian warming. The second took place during the Wasatchian–Bridgerian drying interval. There were several shifts in species dominance, further reflecting reorganization of plant communities (Table 3). However, plant families show low extinction, and three significant influxes of new families occurred, in the Clarkforkian, middle Wasatchian, and early Bridgerian.

Families

The Betulaceae (birch family), Equisetaceae (horsetails), Juglandaceae (walnut family), Platanaceae (sycamore family), and Taxodiaceae (bald cypress family) are present throughout the section. The Betulaceae, Cercidiphyllaceae (katsura family), Cornaceae (dogwood family), Juglandaceae, and Taxodiaceae are conspicuous in the Tiffanian and Clarkforkian samples. These families are well known throughout Paleocene time (e.g., Brown, 1962) and contain mostly deciduous plants with predominantly temperate distributions today, traditionally associating Paleocene time with temperate conditions. In the Clarkforkian, these and other temperate families retained their importance as a number of new groups arrived or reappeared after a hiatus. These families have maximum diversity in the tropics today, giving Clarkforkian vegetation a warmer aspect than the Tiffanian: Arecaceae (palms), Cycadaceae (cycads), Myrtaceae (eucalyptus family), Theaceae (tea family), and Zingiberaceae (ginger family).

The Wasatchian flora of the Great Divide Basin documents the persistence of at least 10 families from the Paleocene, although these were usually represented by new species (Table A4). Examples are the Betulaceae, Cycadaceae, Juglandaceae, Lauraceae, and Myrtaceae. However, a number of families new to the region arrived in the Wasatchian; their living members have tropical centers of distribution. These include the Apocynaceae (periwinkle family), Araceae (arum family), Araliaceae (ivy family), Cyatheaaceae (a family of tropical tree ferns), Elaeocarpaceae (crinodendron family), Euphorbiaceae (spurge family), Leguminosae (legumes), Menispermaceae (moonseed family), Olacaceae (American hog plum family), Salviniaceae (floating fern family), and Sapindaceae (litchi family).

The Bridgerian Little Mountain sample records the persistence of at least 17 families already pre-

sent during and/or before the Wasatchian (Table A3). Families making a first appearance at this level are the Aceraceae (maple family), Anacardiaceae (sumac family), Bignoniaceae (catalpa family), Ceratophyllaceae (hornwort family), Fagaceae (oak family), Hamamelidaceae (witch hazel family), Hydrangeaceae (hydrangea family), Pinaceae (pine family), Simaroubaceae (tree of heaven family), and Tiliaceae (linden family).

Species

Eleven of 29 species, all geographically widespread in the Paleocene (e.g., Brown, 1962), persist from the Bison Basin sample to the Clarkforkian (See (A) in Table A4). This survival of common taxa and the continuing dominance in the Clarkforkian of *Corylites* sp. and "*Ampelopsis*" *acerifolia* (Table 3; see (A) in Table A4) indicate that no marked extinction occurred from the Tiffanian to the Clarkforkian.

Several species with Clarkforkian first appearances or reappearances in the Bighorn Basin (Hickey, 1980; Wing, 1998) also first appear in the Clarkforkian of the study area (see (B) in Table A4). These taxa therefore appear to be useful indicators of Clarkforkian or younger zones throughout Wyoming. Wilf et al. (1998a) noted the contrast of a Tiffanian appearance in southwestern Wyoming and a Clarkforkian appearance in the Bighorn Basin of the dominant leaf genus *Corylites* sp., in association with *Palaeoacarpinus aspinosa* fruits. The Bison Basin sample (*Cornus*) and my preliminary field work in the Tiffanian of the Washakie Basin have revealed four additional species with Clarkforkian first appearances in the Bighorn Basin (see (C) in Table A4; the Washakie Basin occurrences are not listed elsewhere). Two possibilities are that these plants really occurred earlier in southern than northern Wyoming, implying northward migration coincident with warming (Wilf et al., 1998a), or that the late Tiffanian of the Bighorn Basin is undersampled.

The Main Body of the Wasatch Formation contains taxa typical of the Paleocene ("*Carya antiquorum*", *Corylites* sp., and *Metasequoia occidentalis*) and forms that are found both in the Paleocene and Eocene of the area (*Averrhoites affinis* and *Zingiberopsis isonervosa*). As poor as the record is from the Main Body, it supports a scenario in which some Paleocene species persisted into earliest Eocene time (Wing, 1998). No diagnostically Eocene plant macrofossils, such as *Platycarya* (Wing, 1984), were found at the handful of Main Body localities. The Bighorn Basin, which has a richer megafossil record in the Paleocene–Eocene boundary interval, records the gradual extinctions of many Paleocene forms in the latest Clarkforkian and earliest Wasatchian, limited appearances of characteristic Eocene taxa in

the earliest Wasatchian, and a large number of new appearances in the Lostcabinian (Wing et al., 1995; Wing, 1998).

By Latham time a major turnover clearly had occurred in plant communities. Only a handful of species remain from the Clarkforkian (*Averrhoites affinis*, *Zingiberopsis isonervosa*, and palms). However, the most abundant form, "*Meliosma*" *longifolia*, ranges to the Tiffanian in northern Wyoming (Hickey, 1980). The rest of the assemblage consists of new appearances, including several characteristically Eocene taxa (see (D) in Table A4).

In the Sourdough assemblage, few Paleocene holdovers remain (see (E) in Table A4). These include several "returns," probably due to better preservation than in the preceding Latham assemblage (see (E) in Table A4). The percentage of Sourdough species not found in the Clarkforkian and the percentage of Clarkforkian species that do not survive to the Sourdough assemblage are 87% and 83%, respectively. The Sourdough assemblage shares many species, including several first appearances, with the megafloora of the early Lostcabinian 621 m level of the Elk Creek section in the Bighorn Basin (see (F) in Table A4; Wing et al., 1995; Wing, 1998; Davies-Vollum and Wing, 1998). This floristic similarity is strong evidence for the previously discussed possibility that the two horizons are temporally equivalent. Several species are also dominant or abundant in both samples (see (F) in Table A4). The Niland Tongue sample demonstrates no substantial turnover of species since Sourdough time (see (G) in Table A4). However, *Platycarya castaneopsis*, a Lostcabinian dominant in the Bighorn Basin, replaces *P. americana*, and *Alnus* (alder) is no longer dominant (Table 3).

The Sourdough and Niland Tongue samples preview later floras of western North America (see (H) in Table A4). Several species occur in the late early and middle Eocene Green River and Wind River floras of the Western Interior (MacGinitie, 1969, 1974), whereas others are similar or identical to elements of West Coast floras, particularly the late early–early middle Eocene Republic flora (Wolfe and Wehr, 1987), the middle Eocene Clarno flora (Manchester, 1994), and the early Oligocene Bridge Creek flora (Meyer and Manchester, 1997).

The Little Mountain assemblage documents a second significant species turnover in the area. Only a handful of survivors are found from lower in the section (See (I) in Table A4), and the most abundant species are unrelated to previous dominants (Table 3). Of the Little Mountain species, 86% are first appearances, and 88% of the Sourdough and Niland Tongue species are not found at Little Mountain. However, several Wasatchian species are known to have persisted

elsewhere (see (H) in Table A4). The floristic affinities of the assemblage are strongly with middle and late Eocene Rocky Mountain floras, such as the Green River (MacGinitie, 1969), Wind River (MacGinitie, 1974), and Florissant floras (MacGinitie, 1953).

Diversity

Decreasing latitude is generally associated with higher plant diversity, which includes such properties as local species richness (alpha diversity), regional species richness (gamma diversity), variation in species composition across a landscape (beta diversity), and evenness (Whittaker, 1972; Gentry, 1988; Crane and Lidgard, 1989; Schluter and Ricklefs, 1993; Latham and Ricklefs, 1993; Rosenzweig, 1995; Richards, 1996). The fossil record can address whether the same trends seen with decreasing latitude in extant forests hold with increasing temperature when latitude is held constant. Wing et al. (1995) found no strong relationship between diversity and paleotemperature in the Paleocene-Eocene of the Bighorn Basin, although revised estimates show much better corre-

lation (Wing, 1998).

To test temperature as a control on diversity using fossil floras, taphonomic factors, topography, and moisture should be held more or less constant. All of the samples with the exception of Little Mountain (mostly not discussed in this section) were primarily deposited in flooding events on flood plains and preserved in similar overbank lithologies. Surrounding uplifts are thought to have been higher in early Eocene than in late Paleocene time, but plant fossil formation only occurred in the lowest portions of basin centers. Therefore, local topography can be assumed to have been approximately uniform. Moisture was also generally abundant (Fig. 3).

Alpha diversity, approximated by species richness at individual quarries, shows little variation through time when only the mean is examined (Table 2). This result is not surprising because there appear to be general limits on the number of species that can be preserved, on average, in a single fluvial assemblage from a quarry of small spatial scale. Wing and DiMichele (1995) found a mean of about 10 species per quarry both for 116 Cenozoic and 35 Paleozoic fluvial compres-

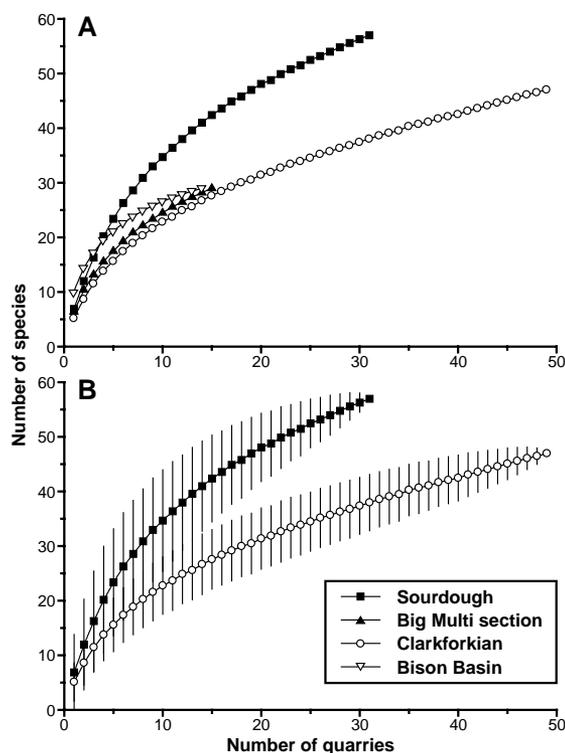


Figure 4. Bootstrapped richness curves for samples with more than 10 quarries. (A) Mean numbers of species drawn from 5000 random subsamples of k quarries, where k is the value of the horizontal axis. (B) The same means with error bars of $\pm 1\sigma$ for the two most intensively collected samples, Clarkforkian and Sourdough. One Clarkforkian and four Sourdough species are not included in this analysis because they were found at the same stratigraphic levels as designated quarries but not in them.

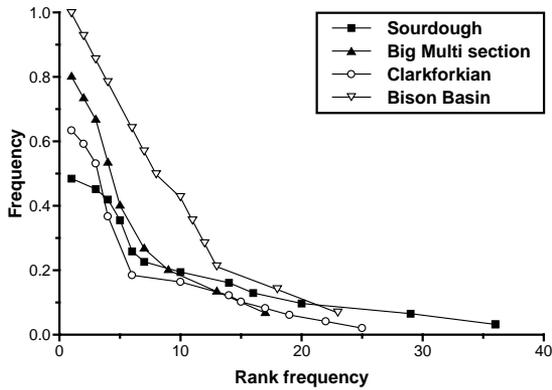


Figure 5. Frequency vs. rank frequency data for species in samples of more than 10 quarries. Vertical axis shows the proportion of quarries at which a species was found. Horizontal axis shows ranks for each species along the frequency axis using the standard ranking algorithm; most data points represent more than one species with the same rank value. One Clarkforkian and four Sourdough species are not included in this analysis because they were found at the same stratigraphic levels as designated quarries but not in them.

support the hypothesis that individual lacustrine deposits sample a larger window of space and time than do fluvial deposits and thus can bear richer and more evenly mixed paleofloras (e.g., Wing and DiMichele, 1995).

In summary, vegetational diversity and dominance structure did not change substantially from the Tiffanian to the Clarkforkian by most measures, despite climatic warming and some species turnover. However, nearly all measures of diversity increased by the time of the Wasatchian thermal maximum, and all dominant species were replaced. What caused the final breakdown of the homogenous forest structure of Paleocene time and the turnover of most plant species by the middle early Eocene? Early Wasatchian cooling near 54 Ma, as suggested by Wing et al. (1999; see also Fricke et al., 1998; Bao et al., 1999) from leaf-margin and oxygen isotope data, brought temperatures back to Tiffanian values (Fig. 3). This cooling should not have caused much turnover because many of the dominant Clarkforkian species had persisted from the Tiffanian and presumably were still tolerant of such temperatures. Changes in regional rainfall patterns from orogenic activity, in combination with the cooling, may have played a significant role. The Tiffanian and the Clarkforkian are inferred here to have been humid, whereas there is sedimentary evidence from the Bighorn Basin and leaf-area evidence discussed in this study that indicate relatively dry conditions in the early half of the early Eocene (Davies-Vollum and Wing, 1998; Fig. 3; Table 2).

CONCLUSIONS

The greater Green River Basin of southwestern Wyoming contains an excellent late Paleocene–early Eocene megafloreal record, which I have used to analyze changes in climate, floral composition, and diversity. Late Paleocene estimated mean annual temperature increased from about 12 °C in the Tiffanian to nearly 19 °C within the early Clarkforkian. Humid conditions prevailed, with annual rainfall of 130–150 cm. Mild climates continued in the Graybullian, although some relatively cool and dry intervals probably occurred. Temperatures increased again from the late Graybullian to the middle Wasatchian, and humid conditions returned. Middle Wasatchian mean annual temperatures were near 21 °C, and mean annual precipitation was near 140 cm. Warm temperatures persisted in the later Wasatchian. The latest Wasatchian and earliest Bridgerian were cyclically hot and arid to warm temperate. Following these arid events, early Bridgerian mean annual temperatures were still subtropical, but marginally cooler than the Wasatchian, about 20 °C, and the annual rainfall of ~80 cm was more seasonal. Generally

sion assemblages. In the present study, numerous low-diversity sites were encountered at most levels sampled, possibly reflecting a taphonomic overprint. The relatively high mean for Bison Basin, 9.9 species, is the exception.

Maximum site richness per sample (N_{max} in Table 2) is perhaps a more informative approximation of alpha diversity because species-poor sites are eliminated. This figure was distinctly higher for the Lostcabinian Sourdough and Niland Tongue assemblages than for the Paleocene samples. Three Sourdough quarries were richer than or as rich as (33, 23, and 17 species) the most speciose sites in the Bison Basin (15) and Clarkforkian samples (17), and the maximum site richness for the Sourdough sample approaches that of the lacustrine Little Mountain sample (Table 2).

One proxy for gamma diversity is the raw number of species recovered per sampling interval (Table 2). This measure does not account directly for sampling intensity. However, the Sourdough assemblage yielded 61 species from 31 quarries in a restricted stratigraphic range, whereas the more time-averaged Clarkforkian assemblage produced 48 species from 49 sites. By this basic measure, the Sourdough flora was far more species rich than the floras of the cooler Clarkforkian.

A bootstrapping procedure that randomly resamples quarries from the best-sampled levels allows a direct comparison of species richness at equivalent sampling intensities (Fig. 4). The Bison Basin curve saturates quickly, showing more richness than the Clarkforkian samples at low numbers of quarries and then leveling off. The Sourdough assemblage is clearly more rich than the Clarkforkian samples (Fig. 4A). The error bars for the Clarkforkian and Sourdough samples separate at 14 quarries (Fig. 4B): the probability is <3% that if a random 14 quarries were collected, the Sourdough assemblage would appear

less diverse than the Clarkforkian assemblage. The steeper bootstrap curve for the Sourdough sample also indicates greater beta diversity because it shows that adding sampling sites is more likely to add new species. Similarly, the 3295 census specimens from five quarries produced 32 dicot species for the Sourdough sample, whereas 4216 specimens from 10 quarries produced only 16 Clarkforkian species (Tables A1 and A2).

The Clarkforkian census data demonstrate homogeneity and monodominance (Tables A1 and A2), yielding diversity indices as low as for the Bison Basin sample, also dominated by *Corylites* sp. (Table 2). Census data from most of the Sourdough sites show greater evenness and species richness than the Tiffanian and Clarkforkian data (Table A2), resulting in markedly higher values for diversity indices at some sites and for the cumulative data (Table 2).

Another way to examine vegetational heterogeneity is to compare frequency data. Like bootstrapping, this approach allows the use of a presence-absence matrix of all sites and species, rather than only dicot leaves at census sites. A frequency vs. rank frequency plot (Fig. 5) shows that in the Sourdough assemblage, no species occurs at more than about half of all sites, whereas several taxa each occur at a majority of sites in the late Paleocene. In this analysis, the Bison Basin sample possesses the largest number of ubiquitous taxa (Fig. 5). The combination of relatively higher species frequency and local richness (Fig. 5; Table 2), quick saturation of the bootstrap curve (Fig. 4), and a more pond-like setting for Bison Basin vs. the Clarkforkian assemblage (Gemmill and Johnson, 1997) favors the scenario of more spatial mixing of vegetation prior to deposition at Bison Basin.

The high richness values and diversity indices of the Little Mountain sample from only three quarries (Table 2), in a cooler and more seasonal climate than indicated by the Sourdough sample,

frost-free conditions were present throughout the study interval, with the exception of the Tiffanian and possibly parts of the Graybullian. The Green River lake system was not a primary cause of mild Eocene winters in southern Wyoming because the lakes were not present or not well developed during several warm intervals.

Floristic response to these climate changes was pronounced. There were two turnover events that each involved the first and last appearances of more than 80% of species and the replacement of dominants. The first accompanied the Clarkforkian-Wasatchian warming trend, and the second coincided with Wasatchian-Bridgerian drying. New appearances of families with modern tropical affinities occurred with Clarkforkian as well as Wasatchian warming, although most families of plants already present in the Clarkforkian persisted throughout the study interval. In similar depositional settings, Wasatchian plant assemblages show markedly greater diversity than the Tiffanian and Clarkforkian assemblages, as predicted by analogy to modern latitudinal gradients.

These results complement and generally agree with the Bighorn Basin record at current levels of resolution. Similar climatic and biotic events have now been observed in both northern and southern Wyoming, showing that they are regional and not local in extent and increasing their value for understanding terrestrial events during the Paleocene-Eocene interval. New data from continental areas elsewhere in the world will help to construct a more global picture of Paleocene-Eocene events.

APPENDIX

The following supplemental tables (A1–A4) contain dicot leaf census data for the Clarkforkian and Sourdough samples, a preliminary floral list with sampling intervals of occurrence for each taxon, and annotation of species turnover.

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TABLE A1. DICOT LEAF CENSUS DATA: CLARKFORKIAN (SAMPLE 2)

Leaf type	USNM locality no. 41-										Cum.	f
	263	265	270	272	281	287	293	295	300	301		
<i>Corylites</i> sp.	180	274	498	327	281	0	137	2	698	262	63%	9
<i>Persites argutus</i>	2	0	31	3	0	411	0	17	29	37	13%	7
" <i>Ampelopsis</i> " <i>acerifolia</i>	0	6	349	11	0	5	0	0	3	0	8.9%	5
<i>Averrhoites affinis</i>	0	0	0	0	0	0	0	188	1	4	4.6%	3
aff. <i>Ocotea</i>	0	0	27	22	0	16	3	1	113	0	4.3%	6
" <i>Cinnamomum</i> " <i>sezannense</i>	109	0	0	0	0	0	0	0	0	0	2.6%	1
Magnoliaceae sp.	0	0	32	0	0	0	0	0	28	0	1.4%	2
<i>Cornus hyperborea</i>	0	0	29	0	0	17	0	0	0	0	1.1%	2
" <i>Carya</i> " <i>antiquorum</i>	0	0	1	0	14	0	0	6	10	0	<1%	4
<i>Ternstroemites aureavallis</i>	0	0	1	0	0	0	0	14	0	0	<1%	2
Cercidiphyllaceae sp.	7	0	1	0	0	0	0	0	1	0	<1%	3
aff. " <i>Viburnum</i> " <i>antiquum</i>	0	0	3	0	0	0	0	0	0	0	<1%	1
cf. <i>Vinea pugetensis</i>	0	0	0	0	0	0	0	0	2	0	<1%	1
FW18	0	0	0	1	0	0	0	0	0	0	<1%	1
FW25	0	1	0	0	0	0	0	0	0	0	<1%	1
FW27	0	0	0	0	0	0	0	0	1	0	<1%	1
#Leaf types	4	3	10	5	2	4	2	6	10	3	16	
#Leaves	298	281	972	364	295	449	140	228	886	303	4216	
Simpson's Index	0.50	0.049	0.61	0.19	0.091	0.16	0.042	0.31	0.36	0.24	0.57	
Shannon-Wiener Index	0.79	0.13	1.2	0.43	0.19	0.37	0.10	0.69	0.78	0.44	1.3	

Notes: Cum.—cumulative data; f—frequency. Fewer leaves were censused at quarries with very low diversity (fewer than five leaf types) or if yield was very low. Quarries with relatively high diversity were censused in more than one field season (270, 300), resulting in high leaf counts but nearly unchanged diversity indices (Wilf, 1998; Wilf et al., 1998a).

TABLE A2. DICOT LEAF CENSUS DATA: SOURDOUGH (SAMPLE 5)

Leaf type	USNM locality 41-					Cum.	f
	332	336	341	342	352		
<i>Platycarya americana</i>	967	9	131	19	0	34%	4
<i>Alnus</i> sp.	3	374	0	368	156	27%	4
Apocynaceae sp.	0	0	0	37	400	13%	2
Lauraceae sp. 2	0	0	129	0	3	4.0%	2
aff. <i>Sloanea</i>	0	0	1	123	1	3.8%	3
<i>Hovenia</i> cf. <i>oregonensis</i>	0	0	0	20	92	3.4%	2
" <i>Dombeya</i> " <i>novi-mundi</i>	0	0	0	98	8	3.2%	2
RR48	0	0	60	0	6	2.0%	2
<i>Populus wyomingiana</i>	1	0	2	0	48	1.5%	3
<i>Allophylus flexifolia</i>	0	0	0	4	39	1.3%	2
<i>Cinnamomophyllum</i> sp.	0	0	3	13	19	1.1%	3
RR40	0	4	18	0	0	<1%	2
RR37	0	0	0	15	5	<1%	2
<i>Chaetoptelea microphylla</i>	0	0	17	0	0	<1%	1
RR20	0	0	0	17	0	<1%	1
<i>Averrhoites affinis</i>	0	16	0	0	0	<1%	1
<i>Stillingia casca</i>	0	0	13	0	1	<1%	2
RR57	0	0	0	13	0	<1%	1
cf. Magnoliales	0	0	0	11	0	<1%	1
RR31	0	0	0	2	6	<1%	2
cf. Magnoliaceae	0	0	0	0	5	<1%	1
<i>Syzygioides americana</i>	0	0	0	0	3	<1%	1
RR88	0	0	0	0	3	<1%	1
RR38	0	0	0	2	0	<1%	1
RR63	0	0	0	0	2	<1%	1
RR95	0	0	0	0	2	<1%	1
cf. <i>Schoepfia republicensis</i>	0	0	0	1	0	<1%	1
aff. <i>Sinomenium</i>	1	0	0	0	0	<1%	1
RR65	0	0	0	0	1	<1%	1
RR66	0	0	0	0	1	<1%	1
RR67	0	0	1	0	0	<1%	1
RR94	0	0	0	0	1	<1%	1
#Leaf types	4	4	10	15	21	32	
#Leaves	972	403	375	743	802	3295	
Simpson's Index	0.010	0.14	0.73	0.71	0.69	0.79	
Shannon-Wiener Index	0.037	0.33	1.5	1.7	1.6	2.0	

Notes: Cum.—cumulative data; f—frequency. Quarries with highest diversity (342, 352) or outstanding preservation (332) were censused in more than one field season, resulting in high leaf counts but nearly unchanged diversity indices (Wilf, 1998).

TABLE A3. PRELIMINARY FLORAL LIST, WITH SAMPLING INTERVAL(S)
OF OCCURRENCE (+) AND RANGE IN THE BIGHORN BASIN (GRAY)

Taxon or morphotaxon (organ; morphotype no.; reference specimen no.)	(1) BB	(2) Cf	(3) WM	(4) La	(5) Sd	(6) NT	(7) LM	Taxon or morphotaxon (organ; morphotype no.; reference specimen no.)	(1) BB	(2) Cf	(3) WM	(4) La	(5) Sd	(6) NT	(7) LM
SPHENOPSISIDA								Bignoniaceae							
Equisetaceae								Bignoniaceae sp. (Fr;GR559; UF15882-8200')	-	-	-	-	-	-	+
<i>Equisetum</i> sp. (A;FW21;7978)	+	+	-	-	+	+	+	?Caprifoliaceae							
POLYPODIOPSISIDA								<i>Calycites ardtunensis</i> Crane (Fr;GR581;8136)	-	-	-	-	-	-	+
Blechnaceae								" <i>Viburnum</i> " <i>antiquum</i> (Newberry) Hollick (F;FW43;8014)	+	+	-	-	-	-	-
<i>Woodwardia gravida</i> Hickey (F;So;FW19-47;7979)	-	+	-	-	+	-	-	" <i>Viburnum</i> " <i>asperum</i> Newberry (F;BB08;DMNH7088)	+	+	-	-	-	-	-
Cyatheaceae								Ceratophyllaceae							
<i>Cnemidaria magna</i> Hickey (F;RR22;7980)	-	-	-	+	+	-	-	<i>Ceratophyllum muricatum</i> Cham. subsp. <i>incertum</i> (Berry)	-	-	-	-	-	-	+
?Dryopteridaceae								Herendeen, Les, and Dilcher (Fr;GR516;UF15882-7455')	-	-	-	-	-	-	-
"Tatman fern" of Wing, 1998 (F;So;RR21;7988)	-	-	-	-	+	-	-	Cercidiphyllaceae							
Osmundaceae								<i>Cercidiphyllum genatrix</i> (Newberry) Hickey (F;FW51;8015)	-	+	-	-	-	-	-
<i>Osmunda macrophylla</i> Penhallow (F;FW33;UF18203-28826)	+	-	-	-	-	-	-	<i>Cercidiphyllum</i> sp. (F; BB34-52; DMNH18841)	+	-	-	-	-	-	-
?Polypodiaceae								aff. <i>Cercidiphyllum</i> (Fr;BB21;DMNH7101)	-	-	-	-	-	-	-
<i>Allantodiopsis erosa</i> Lesquereux (F;RR32;7981)	-	+	+	-	+	-	+	<i>Joffrea</i> sp. 1 (Fr; BB20; DMNH7100)	+	-	-	-	-	-	-
" <i>Allantodiopsis</i> sp. 2" of Wing, 1998 (F;RR35;7982)	-	-	-	-	+	-	-	<i>Joffrea</i> sp. 2 (Fr;FW50;8016)	-	+	-	-	-	-	-
Pteridaceae								Cercidiphyllaceae sp. (?Trochodendraceae) (F;FW09;8017)	-	+	-	-	-	-	-
<i>Acrostichum hesperium</i> Newberry (F;RR80;7983)	-	-	-	-	-	+	+	Cornaceae							
aff. " <i>Pteris</i> " <i>silvicola</i> Hall (F;So;RR51;7989)	-	-	-	-	-	-	+	<i>Cornus hyperborea</i> Heer (F;FW34;8018)	+	+	-	-	-	-	-
Salviniaceae								<i>Beringiaphyllum cupanioides</i> (Newberry) Manchester, Crane, and Golovneva (F;FW44;8019)	+	+	-	-	-	-	-
<i>Salvinia preauriculata</i> Berry (F;RR06;7984)	-	-	-	+	+	+	-	Elaeocarpaceae							
Schizaeaceae								aff. <i>Sloanea</i> ("Dicot XXV" of Wing, 1998) (F;RR18;8148)	-	-	-	-	+	-	+
<i>Lygodium kaulfussii</i> Heer (F;So;RR07,RR07a;8143,7986)	-	-	-	+	+	+	-	Euphorbiaceae							
Thelypteridaceae								aff. <i>Alchornea</i> (F;GR546;UCMP153135)	-	-	-	-	-	-	+
<i>Thelypteris iddingsi</i> (Knowlton) MacGinitie (F;RR69;7987)	-	-	-	-	+	+	-	<i>Stillingia casca</i> Hickey (F;RR47;8021)	-	-	-	-	+	+	-
Incertae sedis								Fagaceae							
(F;GR553;UF15882-7376)	-	-	-	-	-	-	+	cf. <i>Quercus</i> (F;GR522; UF15882-7405)	-	-	-	-	-	-	+
CYCADOPSISIDA								? ? <i>Quercus</i> cupules (Fr;GR575;UF15882-7450)	-	-	-	-	-	-	+
Cycadaceae								? aff. <i>Fagaceae</i> (F;RR94;8131)	-	-	-	-	-	-	+
<i>Eostangeria pseudopteris</i> Kvaček and Manchester (F;FW26;7992)	-	+	-	-	-	-	-	Hamamelidaceae							
<i>Cycad</i> sp. (F;FW52;7991)	-	+	-	-	-	-	-	" <i>Acer</i> " (<i>Liquidambar</i>) <i>lesquereuxii</i> Knowlton (F;GR545;UCMP153007)	-	-	-	-	-	-	-
<i>Cycad</i> sp. 2 (F;RR68;7990)	-	-	-	-	-	+	-	Hippocastanaceae							
PINOPSISIDA								<i>Aesculus</i> sp. (F;FW63;DMNH15273)	-	+	-	-	-	-	-
Pinaceae								Hydrangeaceae							
<i>Pinus</i> sp. (5-needled) (F;GR542;7993)	-	-	-	-	-	-	+	<i>Hydrangea</i> sp. sepal (I;GR537;UF15882-20757)	-	-	-	-	-	-	+
<i>Pinus florissantii</i> Lesquereux (Fr;GR543;UF15882-20762)	-	-	-	-	-	-	+	Juglandaceae							
Pinaceae sp. (Fr;GR578;UF15882-20756)	-	-	-	-	-	-	+	" <i>Carya</i> " <i>antiquorum</i> Newberry (F;BB03;DMNH7105)	+	+	+	-	-	-	-
Taxodiaceae								<i>Palaeocarya clarnensis</i> Manchester (Fr;GR531;UF15882-7359)	-	-	-	-	-	-	+
<i>Glyptostrobus europaeus</i> (Brogniart) Heer (F;C;FW20;7994)	-	+	-	-	+	-	-	<i>Platycarya</i> ? <i>americana</i> (F)	-	-	-	-	+	-	-
<i>Metasequoia occidentalis</i> Newberry- (F;C;Fr;FW04,BB19,BB51;7995,DMNH7099,DMNH18855)	+	+	+	-	-	-	-	<i>Platycarya americana</i> Hickey (F;Fr,I [pistillate];RR01,RR70, RR02;8023,8024,8147)	-	-	-	-	-	-	-
Taxodiaceae sp. (F;GR541;UF15882-20766)	-	-	-	-	-	-	+	? ? <i>Platycarya americana</i> Hickey, staminate (I;RR75;8026)	-	-	-	-	-	-	+
LILIOPSIDA								<i>Platycarya castaneopsis</i> (Lesquereux) Wing and Hickey (F;Fr,I [pistillate];RR09,RR16,RR93;8027,8146,8110)	-	-	-	-	-	-	+
Araceae								aff. <i>Platycarya</i> (F;BB09;DMNH7089)	+	-	-	-	-	-	-
aff. <i>Philodendron</i> (F;RR61;8134)	-	-	-	-	+	-	-	<i>Pterocarya macginitii</i> Manchester and Dilcher (Fr;GR532;UF15882-7457')	-	-	-	-	-	-	+
Arecaceae								cf. <i>Vinea pugetensis</i> Wolfe (F;FW10;8140)	-	+	-	-	-	-	-
<i>Sabalites/Amesoneuron</i> (F;RR34;7998)	-	+	-	+	+	+	+	Juglandaceae sp. (F;GR519;UF15882-28829)	-	-	-	-	-	-	+
Smilacaceae								Lauraceae							
aff. <i>Smilax</i> (F;GR550;UF15882-20791)	-	-	-	-	-	-	+	" <i>Cinnamomum</i> " <i>sezannense</i> Watelet (F;FW02;8031)	-	+	-	-	-	-	-
Zingiberaceae								<i>Cinnamomophyllum</i> sp. (F;RR19;8030)	-	-	-	-	-	-	+
<i>Zingiberopsis isonervosa</i> Hickey (F;RR03;8001)	-	+	+	+	+	+	+	<i>Lindera varifolia</i> MacGinitie (F;GR521;UCMP20651)	-	-	-	-	-	-	+
? Monocot B- aff. Zingiberales (F;GR513;UF15882-20793)	-	-	-	-	-	-	+	aff. <i>Ocotea</i> (F;FW03;8032)	-	-	-	-	-	-	+
Incertae sedis								<i>Persites argutus</i> Hickey (F;FW08,WM10;8036)	-	+	+	-	-	-	-
" <i>Sparganium</i> " <i>stygium</i> Heer ("Alismataceae sp." of Wing, 1998) (Fr;RR91;8000)	-	-	-	-	+	-	-	<i>Lauraceae</i> sp. (F;FW28;8035)	-	+	-	-	-	-	-
Leaf with spiny margin (?bromeliad) (F;RR28;8133)	-	-	-	-	+	-	-	<i>Lauraceae</i> sp. 2 (F;RR46;8034)	-	-	-	-	-	-	+
sedge-like fruits (Fr;RR53;7999)	-	-	-	+	-	-	-	? " <i>Ficus</i> " <i>planicostata</i> Lesquereux (F;FW54;8037)	-	+	-	-	-	-	-
Monocot A (F;RR86;7997)	-	-	-	-	-	+	-	? aff. Lauraceae (F;BB11;DMNH18838)	+	-	-	-	-	-	-
Monocot C (F;RR81;8135)	-	-	-	-	+	-	-	Leguminosae							
Monocot D (F;GR560;UF15882-7489)	-	-	-	-	-	-	+	<i>Caesalpinia flumen-viridensis</i> Herendeen and Dilcher (Fr;GR534;UF15882-7388)	-	-	-	-	-	-	+
MAGNOLIOPSISIDA								" <i>Caesalpinia</i> " <i>pecorae</i> Brown (F;GR583;UF15882-7371)	-	-	-	-	-	-	+
Aceraceae								<i>Cladrastis</i> sp. 1 (Fr;GR579;UF15882-20223)	-	-	-	-	-	-	+
<i>Acer</i> sp. 1 (Fr;GR557;UF15882-7447)	-	-	-	-	-	-	+	<i>Cladrastis</i> sp. 2 (Fr;GR580;UF15882-14790)	-	-	-	-	-	-	+
<i>Acer</i> sp. 2 (Fr;GR558;UF15882-20761)	-	-	-	-	-	-	+	aff. <i>Gleditsia</i> (F;RR29;8039)	-	-	-	-	-	-	+
<i>Dipteronia</i> sp. (Fr;GR551;UF15882-7383')	-	-	-	-	-	-	+	" <i>Gymnocladus</i> " <i>hesperia</i> (Brown) MacGinitie (F;GR515;8152)	-	-	-	-	-	-	+
Anacardiaceae								<i>Leguminosites lesquereuxiana</i> (Knowlton) Brown (F;GR517;UCMP153134)	-	-	-	-	-	-	+
<i>Rhus nigricans</i> (Lesquereux) Knowlton (F;GR529;8004)	-	-	-	-	-	-	+	<i>Parvilleguminophyllum coloradensis</i> (Knowlton) Call and Dilcher (F;GR520;8040)	-	-	-	-	-	-	+
Apocynaceae								<i>Leguminosae</i> sp. (F;GR501;UF15882-7367)	-	-	-	-	-	-	+
"Apocynaceae sp." of Wing, 1998 (F;RR17;8145)	-	-	-	-	+	-	-	<i>Leguminosae</i> sp. 2 (F;GR554;UF15882-7411)	-	-	-	-	-	-	+
Araliaceae								<i>Leguminosae</i> sp. 3 (F;GR567;UF15882-21178)	-	-	-	-	-	-	+
<i>Dendropanax latens</i> MacGinitie (F;RR60;8149)	-	-	-	-	+	+	-	Magnoliaceae							
Betulaceae								" <i>Bauhinia</i> " (<i>Liriodendrites</i>) <i>wyomingiana</i> Brown (F; BB37; DMNH18843)	+	-	-	-	-	-	-
" <i>Alnus</i> sp." of Wing, 1998 (F;Fr;RR14,RR14a;8007,8008)	-	-	-	+	+	+	-	<i>Magnoliaceae</i> sp. (F;FW07-22-46;8041)	-	+	-	-	-	-	-
? <i>Alnus</i> catkins (I;RR90;8009)	-	-	-	-	+	-	-								
cf. <i>Alnus</i> (F;GR548;UF15882-7389)	-	-	-	-	-	-	+								
<i>Corylites</i> sp. ("Betulaceae sp. 1" of Wing, 1998) (F;FW01;8010)	+	+	+	-	-	-	-								
<i>Palaeocarpinus aspinosa</i> Manchester and Chen (Fr;BB23;DMNH7102)	+	+	-	-	-	-	-								
<i>Betulaceae</i> sp. catkin (I;FW67;8012)	-	+	-	-	-	-	-								

TABLE A3. (Continued.)

Taxon or morphotaxon (organ; morphotype no.; reference specimen no.)	(1) BB	(2) Cf	(3) WM	(4) La	(5) Sd	(6) NT	(7) LM	Taxon or morphotaxon (organ; morphotype no.; reference specimen no.)	(1) BB	(2) Cf	(3) WM	(4) La	(5) Sd	(6) NT	(7) LM
cf. Magnoliaceae (F;RR36;8042)	-	-	-	-	-	-	-	" <i>Eucommia</i> " <i>serrata</i> (Newberry) Brown (F;FW45;8070)	-	+	-	-	-	-	-
? cf. Magnoliales (F;RR12;8038)	-	-	-	-	-	-	-	<i>Fortuna</i> cf. <i>marsilioides</i> (Bell) McIver and Basinger (F;BB01;DMNH7081)	+	-	-	-	-	-	-
Malvales (Bombacaceae-Malvaceae-Sterculiaceae-Tiliaceae)								" <i>Meliosma</i> " <i>longifolia</i> (Heer) Hickey (F;RR52;8003)	-	-	-	+	-	-	-
" <i>Dombeya</i> " <i>novi-mundi</i> Hickey (F;RR05;8044)	-	-	+	+	+	-	-	<i>Porosia verrucosa</i> (Lesquereux) Hickey (?Fr;FW17;UF18202-28825)	-	+	-	-	-	-	-
<i>Triumfetta ovata</i> MacGinitie (Tiliaceae) (F;GR503;UCMP20648)	-	-	-	-	-	-	-	<i>Fraxinus</i> -like fruit (Fr;GR535;UF15882-20575)	-	-	-	-	-	-	+
Malvales aff. <i>Kydia</i> (F;FW61;DMNH15279)	+	-	-	-	-	-	-	aff. ??Rhamnaceae (F;GR505;UF15882-26201)	-	-	-	-	-	-	+
Malvales sp. (F;BB38;DMNH18844)	+	-	-	-	-	-	-	aff. " <i>Viburnum</i> " <i>antiquum</i> (Newberry) Hollick (F;FW40;8069)	-	+	-	-	-	-	+
Menispermaceae								"Dicot XXXVI" of Wing, 1998 (F;RR48;8096)	-	-	-	-	+	-	-
aff. <i>Abuta</i> (F;GR507;UF15882-20788)	-	-	-	-	-	-	+	"Dicot XXXVII" of Wing, 1998 (F;RR27;8088)	-	-	-	-	+	-	-
cf. <i>Anamirta milleri</i> Wolfe ("Dicot II" of Bown et al., 1994) (F;RR92;8043)	-	-	-	-	-	-	-	Unknown dicot sp. (F;RR73;8105);	+	-	-	-	-	-	-
cf. <i>Atriacarpum clarnense</i> Manchester (Fr;RR56;8045)	-	-	-	-	-	-	-	?Aquatic herb (F;FW31;8068)	-	+	-	-	-	-	-
cf. <i>Palaeosinomenium venablesii</i> Chandler (Fr;RR77;8142)	-	-	-	-	-	-	-	Fertilized catkin (Fr;FW65;8055)	-	-	-	-	-	-	-
aff. <i>Sinomenium</i> (F;RR08;8089)	-	-	-	-	-	-	-	Fruit w/ two wings (Fr;GR539;UCMP153003)	-	-	-	-	-	-	+
aff. <i>Trichlisia</i> (F;RR72;8047)	-	-	-	-	-	-	-	Fruit w/ two wings, sp. 2 (Fr;GR584;8137)	-	-	-	-	-	-	+
Menispermaceae sp. (F;GR569;UF15882-20792)	-	-	-	-	-	-	-	Unknown samara (Fr;GR587;8138)	-	-	-	-	-	-	+
Myrtaceae								Winged fruit (Fr;GR523;UF15882-7481)	-	-	-	-	-	-	+
<i>Paleomyrtinaea</i> sp. Pigg, Stockey, and Maxwell (Fr;FW66;8049)	+	-	-	-	-	-	-	11 unknown leaf types, sample 1 (F;BB15;DMNH7095);	+	-	-	-	-	-	-
<i>Syzygioides americana</i> (Lesquereux) Manchester, Dilcher and Wing (F;RR23;8048)	-	-	-	-	-	-	-	(F;BB40;DMNH18847); (F;BB41;DMNH18848);	-	-	-	-	-	-	-
Nymphaeaceae								(F;BB42;DMNH18849); (F;BB45;DMNH18850);	-	-	-	-	-	-	-
Nymphaeaceae sp. (F;RR43;8051)	-	-	-	-	-	-	-	(F;BB47;DMNH18852); (F;BB49;DMNH18853);	-	-	-	-	-	-	-
Olivaceae								(F;BB50;DMNH18854); (F;BB53;DMNH18861);	-	-	-	-	-	-	-
cf. <i>Schoepfia republicensis</i> (LaMotte) Wolfe and Wehr (F;RR44;8052)	-	-	-	-	-	-	-	(F;BB55;DMNH18862); (F;BB57;DMNH18859)	-	-	-	-	-	-	-
Platanaceae								4 unknown reproductive types, sample 1 (Fr;BB24;DMNH7104);	+	-	-	-	-	-	-
<i>Macginitiea gracilis</i> (Lesquereux) Wolfe and Wehr (F;FW48;8054)	+	+	-	-	-	-	-	(Fr;BB25;DMNH7120); (Fr;BB28;DMNH8270);	-	-	-	-	-	-	-
<i>Macginitiea wyomingensis</i> (Knowlton and Cockerell) Manchester (F;GR518; UF15882-20803)	-	-	-	-	-	-	-	(Fr;BB58;DMNH18860)	-	-	-	-	-	-	-
<i>Platanus raynoldsi</i> Newberry (F;BB39;DMNH18846)	+	-	-	-	-	-	-	9 unknown leaf types, sample 2 (F;FW05;8072); (F;FW18;8073);	-	+	-	-	-	-	-
<i>Platanus</i> sp. achene (Fr;GR552;UF15882-7362)	-	-	-	-	-	-	-	(F;FW23;8074); (F;FW24;8075); (F;FW25;8076);	-	-	-	-	-	-	-
Platanaceae sp. (Fr;BB27;DMNH7121)	+	-	-	-	-	-	-	(F;FW27;8077); (F;FW32;8078); (F;FW62;DMNH15282);	-	-	-	-	-	-	-
? " <i>Ficus postartocarpoides</i> " (F;FW06;8056)	+	-	-	-	-	-	-	(F;FW68;8079)	-	-	-	-	-	-	-
?Proteaceae								Unknown flower (F;FW55;8081)	-	+	-	-	-	-	-
<i>Proteaphyllum minutum</i> MacGinitie (F;RR84;8057)	-	-	-	-	-	-	-	Unknown reproductive structure (?Fr;FW58;8080)	-	-	-	-	-	-	-
Rhamnaceae								3 unknown leaf types, sample 3 (F;WM04;8116);	-	-	+	-	-	-	-
<i>Hovenia</i> cf. <i>oregonensis</i> Meyer and Manchester (F;RR15;8084)	-	-	-	-	-	-	-	(F;WM16;8118); (F;WM21;8029)	-	-	-	-	-	-	-
Salicaceae								4 unknown leaf types, sample 4 (F;RR04;8082); (F;RR54;8098);	-	-	-	+	-	-	-
<i>Populus cinnamomoides</i> (Lesquereux) MacGinitie (F;GR528;8058)	-	-	-	-	-	-	-	(F;RR78;8108); (F;RR79;8109)	-	-	-	-	-	-	-
<i>Populus wyomingiana</i> (Berry) MacGinitie (F;RR62;8059)	-	-	-	-	-	-	-	Unknown fruit (Fr;RR11;8127)	-	-	-	-	-	-	-
cf. <i>Populus</i> (F;FW60;UF18126-13262)	+	-	-	-	-	-	-	19 unknown leaf types, sample 5 (F;RR10;8065);	-	-	-	-	+	-	-
Sapindaceae								(F;RR13;8083); (F;RR20;8085); (F;RR24;8086);	-	-	-	-	-	-	-
<i>Allophylus flexifolia</i> (Lesquereux) MacGinitie (F;RR59;8144)	-	-	-	-	-	-	-	(F;RR26;8087); (F;RR31;8090); (F;RR37;8091);	-	-	-	-	-	-	-
("Dicot XXXI" of Wing, 1998)	-	-	-	-	-	-	-	(F;RR38;8092); (F;RR40;8093); (F;RR42;8094);	-	-	-	-	-	-	-
<i>Cardiospermum coloradensis</i> (Knowlton) MacGinitie (F;GR511;UCMP153075)	-	-	-	-	-	-	-	(F;RR45;8095); (F;RR57;8100); (F;RR63;8046);	-	-	-	-	-	-	-
<i>Koeleruteria viridifluminis</i> (Hollick) Brown (Fr;GR530;UCMP153080)	-	-	-	-	-	-	-	(F;RR65;8102); (F;RR66;8103); (F;RR67;8104);	-	-	-	-	-	-	-
? Sapindales sp. (F;GR525;8062)	-	-	-	-	-	-	-	(F;RR74;8106); (F;RR88;8130); (F;RR95;8132)	-	-	-	-	-	-	-
? aff. Sapindales (F;GR585;8128)	-	-	-	-	-	-	-	3 unknown reproductive types, sample 5 (F;RR76;8141);	-	-	-	-	+	-	-
Simaroubaceae								(Fr;RR87;8114); (Fr;RR89;8115)	-	-	-	-	-	-	-
<i>Ailanthus lesquereuxi</i> Cockerell (Fr;GR533;UF15882-7382)	-	-	-	-	-	-	-	4 unknown leaf types, sample 6 (F;RR49;8097); (F;RR55;8099);	-	-	-	-	-	-	+
? aff. Simaroubaceae (F;GR566;UF15882-7368)	-	-	-	-	-	-	-	(F;RR83;8112); (F;RR85;8113)	-	-	-	-	-	-	-
Theaceae								18 unknown leaf types, sample 7 (F;GR504;UF15882-7443);	-	-	-	-	-	-	+
<i>Ternstroemites aureavallis</i> Hickey (F;FW29;8064)	-	+	-	-	-	-	-	(F;GR508;UF15882-7430); (F;GR509;UF15882-7408);	-	-	-	-	-	-	-
? aff. Theaceae (F;FW49;UF18126-13239)	-	+	-	-	-	-	-	(F;GR524;8151); (F;GR526;8122); (F;GR549;UF15882-7415);	-	-	-	-	-	-	-
? aff. Theaceae sp. 2 (F;FW57;DMNH15277)	-	+	-	-	-	-	-	(F;GR555;8123); (F;GR561;UF15882-7422);	-	-	-	-	-	-	-
Ulmaceae								(F;GR562;UF15882-28840); (F;GR563;UF15882-28839);	-	-	-	-	-	-	-
<i>Cedrelospermum nervosum</i> (Newberry) Manchester (F;Fr;GR512;GR512a;UCMP153099;UF15882-20240)	-	-	-	-	-	-	-	(F;GR564;UF15882-20799); (F;GR565;UF15882-20801);	-	-	-	-	-	-	-
<i>Celtis</i> sp. (Fr; collected by H. Roehler, not catalogued)	-	-	-	-	-	-	-	(F;GR568;UF15882-28844); (F;GR570;UF15882-7426);	-	-	-	-	-	-	-
<i>Chaetoptelea microphylla</i> (Newberry) Hickey (F;RR50;8066)	-	-	-	-	-	-	-	(F;GR571;UF15882-7435); (F;GR572;UF15882-20790);	-	-	-	-	-	-	-
? " <i>Celtis</i> " <i>peracuminata</i> Brown (F;FW59;DMNH15271)	-	+	-	-	-	-	-	(F;GR573;UF15882-7433); (F;GR588;8129)	-	-	-	-	-	-	-
?Vitaceae								3 unknown reproductive types, sample 7 (Fr;GR536;8124);	-	-	-	-	-	-	+
" <i>Ampelopsis</i> " <i>acerifolia</i> Newberry (F;FW14;8067)	+	+	-	-	-	-	-	(Fr;GR574;UF15882-20224); (Fr;GR589;8139)	-	-	-	-	-	-	-
Incertae sedis															
" <i>Astronium</i> " <i>truncatum</i> (Lesquereux) MacGinitie (F;GR556;8150)	-	-	-	-	-	-	-								
<i>Averrhoites affinis</i> (Newberry) Hickey (F;RR41;8053)	-	+	+	+	+	+	+								
<i>Calycites</i> sp. (5 sepals) (F;RR58;8071)	-	-	-	-	-	-	-								
<i>Calycites</i> sp. (6 sepals) (F;RR71;8002)	+	-	-	-	-	-	-								

Notes: Notation of samples as in Table 2. Shading indicates range in Bighorn Basin (Bown et al., 1994; Wing et al., 1995; Wing, 1998), correlated as follows: Tiffanian of Bighorn Basin to (1); Clarkforkian to (2); Graybullian to (3); Lysitean to (4); Lostcabinian to (5) and (6). Organs: A, axis; F, foliage; C, cone; Fr, fruit/seed; I, part of inflorescence; So—sori; ?—tentative assignment to indicated family; aff.—morphological affinity to indicated taxon; cf.—no characters contradictory to indicated taxon but identification incomplete (i.e., more confidence than aff.). Quotation marks around a published genus name indicate assignment thought to be incorrect. Specimen numbers: for National Museum of Natural History (USNM), last four digits of six are shown—first two are "49"; for other institutions, complete numbers are given. See Wilf et al. (1998a) for a list of taxa in the Big Multi section, with the addition here of *Ternstroemites aureavallis*.

TABLE A4. SPECIES TURNOVER ANNOTATION

(A) Tiffanian/Clarkforkian survivors: "Ampelopsis" acerifolia; Beringiaphyllum cupanioides; "Carya" antiquorum; Cornus hyperborea; Corylites sp.; Equisetum sp.; Macginitiea gracilis; Metasequoia occidentalis; Palaeocarpinus aspinosa; "Viburnum" antiquum; "Viburnum" asperum
(B) Clarkforkian first appearance datum in study area and Bighorn Basin: "Cinnamomum" sezannense; Sabalites/Amesoneuron; Ternstroemites aureavallis; Zingiberopsis isonervosa
(C) Tiffanian first appearance datum in study area, Clarkforkian first appearance datum in Bighorn Basin: Allantodiopsis erosa; Averrhoites affinis; Cornus hyperborea; Corylites sp.; Palaeocarpinus aspinosa; Persites argutus
(D) Latham assemblage, new appearances: Alnus sp.; Apocynaceae sp.; Cnemidaria magna; "Dombeya" novi-mundi; Lygodium kaulfussii; Platycarya sp.; Salvinia preauriculata; Stillingia casca
(E) Tiffanian and/or Clarkforkian survivors in Latham and/or Sourdough samples: Averrhoites affinis; Equisetum sp.; Glyptostrobus europaeus; Macginitiea gracilis; Sabalites/Amesoneuron; Woodwardia gravida; Zingiberopsis isonervosa; RR73
(F) Sourdough assemblage and 621 m level of Bighorn Basin Elk Creek section, first appearance datum in both (*) or abundant in both (†): Allophylus flexifolia*; Alnus sp.†; Cnemidaria magna†; "Dombeya" novi-mundi†; Lygodium kaulfussii†; cf. Schoepfia republicensis*; aff. Sloanea†; Syzygioides americana*; "Tatman fern"††; RR27*; RR48*
(G) Sourdough and Niland Tongue samples: Alnus sp.; Averrhoites affinis; cf. Schoepfia republicensis; Dendropanax latens; "Dombeya" novi-mundi; Equisetum sp.; Lygodium kaulfussii; Populus wyomingiana; Sabalites/Amesoneuron; Salvinia preauriculata; Thelypteris iddingsii; Zingiberopsis isonervosa
(H) Sourdough or Niland Tongue sample and same or similar species found in younger strata of the Western Interior (*) or West Coast (†): Acrostichum hesperium*; Allantodiopsis erosa*, cf. Anamirta millerit†, cf. Atriaecarpum clarnense†; Dendropanax latens*; Hovenia cf. oregonensis†; Macginitiea gracilis†; cf. Palaeosinomenium venablesii†, Populus wyomingiana†; Proteaciphyllum minutum*; aff. "Pteris" silvicola†; cf. Schoepfia republicensis†; Syzygioides americana*; Thelypteris iddingsii†
(I) Lostcabinian/Bridgerian survivors (* = from Paleocene): Acrostichum hesperium; Allantodiopsis erosa*; Allophylus flexifolia; Averrhoites affinis*; Equisetum sp.*; Platanus raynoldsi*; Proteaciphyllum minutum; Sabalites/Amesoneuron*; aff. Sloanea; Syzygioides americana

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