

Plant and mammal diversity in the Paleocene to Early Eocene of the Bighorn Basin

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Abstract

Abundant plant and vertebrate fossils have been recovered from fluvial sediments deposited in the Bighorn Basin, Wyoming, during the first 13 m.y. of the Tertiary. Here we outline and discuss changes in the composition and diversity of floras and faunas during this period, which includes the recovery of terrestrial ecosystems from the K/T boundary extinctions, and later, during the Paleocene–Eocene transition, the greatest global warming of the Cenozoic.

Floral diversity has been studied at three levels of spatial resolution: sub-local (at individual collecting sites), local (along a single bed or stratigraphic horizon), and basin-wide (regional). Sub-local diversity shows a moderate increase from the early to late Paleocene, followed by a decrease across the Paleocene/Eocene boundary, then an increase into the later early Eocene. Local heterogeneity was lower in Paleocene backswamp floras, although distinct groups of species dominated in different local fluvial settings such as backswamps and alluvial ridges. Heterogeneity of backswamp forests increased by about 65% from the early to late Wasatchian (early Eocene). The number of plant species inferred from the Bighorn Basin dataset rose gradually from the Puercan to an early Clarkforkian peak of about 40 species, declined sharply to about 25 species by the Clarkforkian/Wasatchian boundary, then rose through the Wasatchian to about 50 species.

A regional analysis of mammalian genera shows high turnover and a rapidly increasing number of genera within a million years of the K/T boundary (10–50 genera), a slight decline to 40 genera by the early Clarkforkian, then an increase from 40 to 75 genera by the late Wasatchian.

Our analyses found no major extinctions in mammals during the Paleocene and early Eocene in the Bighorn Basin, but a one-third decrease in the number of plant species at about the Paleocene/Eocene boundary. Rates of taxonomic turnover were much higher for mammals than plants. The diversity trends for plants and mammals show little congruence, implying that the two groups responded in a very different manner to post K/T extinction opportunities. There is also little congruence between plant diversity levels and change in mean annual temperature (MAT) as inferred from foliar physiognomy.

1. Introduction

The early Cenozoic is marked by two major environmental changes. The first is the impact of the K/T bolide and its direct physical and biologi-

cal sequelae, which extend through an undetermined part of the Paleocene (Alvarez et al., 1980; Sharpton and Ward, 1990; Wolfe, 1987). The second is the late Paleocene–early Eocene warming of global climate, the most recent extreme “hot-

house" interval in earth history (Miller et al., 1987). The Paleocene and Eocene are also a period of floral and faunal modernization, and may be the time of origin for many extant plant–animal interactions (Wing and Sues et al., 1992).

Fossils from the Paleocene–early Eocene strata of the Bighorn Basin, Wyoming, offer an unusual opportunity to examine the response of terrestrial faunas and floras to these two major extrinsic changes, and also to assess the degree of congruence between floral and faunal diversity. Few other terrestrial sections span so much time (about 13 m.y.), preserve both plant and animal fossils in abundance, and maintain a broadly similar set of environments through the entire interval.

In this paper we describe changes in plant and mammal diversity through the Paleocene–early Eocene interval, and note their congruence with one another and with extrinsic events such as climatic change (we use "diversity" to refer to the number of species or genera, rather than the distribution of their relative abundances). Parallel trends in diversity could be attributed to a common evolutionary response to extrinsic factors (e.g., adaptive radiation following the extinction and disturbance at the end of the Cretaceous) or to a coevolutionary spiral of increasing diversity. Lack of congruence between the two groups in patterns of diversity change can be explained by different reactions to the same extrinsic forces, the absence of a strong effect of coevolution on diversification, and/or a fossil record that biases diversity trends for the two groups in different ways. Because multiple interpretations can account for any pattern, we identify and explore patterns rather than definitively test hypotheses. Our work here follows on an earlier effort by Lillegraven (1972),

who was one of the first to trace plant and animal diversity together and consider their relation to climate.

2. Data

2.1. Floral lists

Floral lists were derived from 133 sites distributed through the Fort Union and Willwood Formations in the central and northern Bighorn Basin (Appendix 1). Each of the sites represents a collection of plant fossils made from an area <5 m² and a stratigraphic interval <0.5 m thick. Localities do not include plants from more than one depositional environment, even if two or more stratigraphically or laterally adjacent units bear plant fossils. Depositional environment was inferred for each locality based on field observations of sedimentary features such as geometry of the deposit, grain size, primary bedding features, and contact with underlying units (Table 1).

Most of the central Bighorn Basin localities are in the composite stratigraphic section known as the Elk Creek section (Schankler, 1980), although we accept the adjustment recommended by Bown et al. (1994), who maintained that localities above 500 m were actually 79 m lower than originally measured. Most floral localities in the northern Bighorn Basin are in one of seven composite measured sections designated A–G (see Hickey, 1980 for a map showing the placement of these sections). The eastern sections, A–C, are close to sections that tie together vertebrate localities (Gingerich et al., 1980), and some floral localities can be directly correlated with vertebrate localities.

Table 1
Sedimentary criteria for assigning plant fossil localities to the four depositional environments recognized in this study

	Backswamp	Alluvial ridge	Channel	Pond
Grain size	clay, silt	silt, fine sand	fine to coarse sand	clay, silt
Plant distribution	dense leaf packs	plant frags. and leaves	leaves on mud drapes	leaf packs at top of FUS*
Bedding	fine, uneven lamination	ripple x-lamination	trough x-bedding	fining upward sequences
Bottom contact	conformable	conformable	erosional	erosional
Organics/color	very organic, dk. brown	moderately organic, brown	low organic, yellow-tan	moderately organic, gray

*FUS = fining upward sequence.

Several techniques were used to determine the age of floral localities, including mammalian fossils in the same stratigraphic sections, paleomagnetic reversals, radiometric dating, and interpolation based on stratigraphic thickness (Hickey, 1980; Wing, 1980; Wing et al., 1991; Bown et al., 1994).

Correlation of floral localities in the northern and central Bighorn Basin is difficult. There is no direct stratigraphic correlation between sections measured in the two areas, and biostratigraphic correlation of floras is also problematic. In the northern Bighorn Basin, there are few plant fossils in the upper Clarkforkian and Wasatchian part of the section, even though these time intervals produce copious mammalian fossils. There are four floral sites correlative with late Clarkforkian faunas in the northern Bighorn Basin. In the central Bighorn Basin, there are many floras but few mammalian fossils in the upper part of the Fort Union Formation. Because age-diagnostic mammalian fossils are uncommon in the Fort Union of the central Bighorn Basin, it is not clear if floras from this interval are late Clarkforkian. Eight sites in the upper Fort Union Fm. of the central Bighorn Basin are probably late Clarkforkian based on the absence of both *Platycarya* pollen and the typical Eocene megafloreal species that are known from very early Wasatchian floras. The exact stratigraphic relationship of the *Platycarya* FAD (first appearance datum) to the Clarkforkian/Wasatchian boundary is not known, but the events are approximately coeval. *Platycarya* pollen is absent from definite Paleocene beds (Nichols and Ott, 1978), but present stratigraphically below early Wasatchian mammalian fossils (Wing et al., 1991).

For 40 Eocene localities, we have numerical abundances of species recorded in the field. These field censuses were carried out by counting leaves and leaf fragments representing more than one half of a leaf. Between 200 and 400 leaves were counted for each census. Analogous censuses of leaf litter from the floor of extant forests have been shown to provide good estimates of the relative abundances of plant species in the area immediately surrounding the site (Burnham et al.,

1992). For 30 Paleocene localities we have “drawer” censuses; these were made by counting specimens in museum collections. Although these museum collections were derived from quarries of the same size range as the field censused samples, they were made with an emphasis on collecting specimens of all the species found. Therefore the museum collections tend to under-represent common taxa and over-represent rare ones. In most cases the dominant species at the locality will still be abundant in the museum collection because leaves of the dominant species will be found on blocks that were collected to demonstrate the occurrence of other species.

Many of the 295 species used in this analysis are not formally named, or the names are not valid. Informal taxonomy for the Paleocene and Eocene floras was standardized by consultation and joint examination of specimens by LJH and SLW (Appendix 2).

2.2. Mammalian lists

The Bighorn Basin preserves an excellent early Tertiary record of mammalian evolution. However, there are several very poorly represented intervals in the published sequence of faunas. The data set used here therefore supplements the Bighorn Basin faunal lists with lists from three surrounding basins. Several important early and middle Paleocene lists come from localities in the Crazy Mountains Basin, and several late Wasatchian lists come from localities in the Wind River Basin. A few early Eocene lists from the Powder River Basin were also included. The fossil localities from which the mammalian lists were derived include both surface lag and quarry sites. These sites vary greatly in areal extent, from quarry sites that are several meters on a side to surface lag sites that extend over several hectares of outcrop. Some surface lag sites include material derived from stratigraphic intervals up to 10 m thick (Schankler, 1980). All of the mammalian assemblages are probably substantially more time and space averaged than the plant assemblages, which will be discussed in more detail below. A total of 301 lists, each including at least two genera, were

compiled and revised in accordance with the most recent taxonomic literature (Appendix V).

3. Effect of local environment on floral composition and diversity

Depositional environments have a strong effect on floral composition and diversity, so depositional environment must be considered before temporal change in diversity or composition can be interpreted. Plant fossils in the Bighorn Basin Paleogene sequence are found in a range of depositional environments including channels, point bars, levees, crevasse splays, distal floodbasin backswamps, abandoned-channel ponds, and shallow lakes (Hickey, 1980; Wing, 1980, 1984; Yuretich et al., 1984). Plant assemblages preserved in some sandy channel sediments have been transported and winnowed, but the vast majority of assemblages are essentially autochthonous, meaning that remains were transported only short distances (meters) before deposition, and that there is essentially no mixing of plant debris from different vegetational types. The evidence for autochthonous plant assemblages includes the absence of hydrodynamic sorting of plant parts, the silt-to-clay grain size of the sediments that preserve the floras, and sharp shifts in species composition over distances of just a few meters.

The composition of floral assemblages varies with sedimentary environment because these environments fostered different edaphic conditions that favored the growth of different sets of species. Environmental heterogeneity on Paleogene floodplains presumably took the form of gradients, e.g., upper point bars grading into levees, levees into crevasse splays and backswamps. In order to examine the effect of local environment on floral composition we have simplified these gradients, using sedimentological criteria to place sites in one of four categories: channel, alluvial-ridge (including upper point bars, levees, and crevasse splays), backswamp, and abandoned-channel pond (Table 1, Appendix 1). Floristic and vegetational distinctions between these broadly defined environmental types are seen in fossil megaflores and palynoflores (Hickey, 1980; Wing, 1984; Farley,

1989, 1990; Wing and DiMichele et al., 1992). Channels contain the most highly sorted assemblages, usually dominated by woody plant remains and thick leaves of common riparian trees such as sycamores (Platanaceae). Alluvial-ridge sites are the most variable floristically, but usually contain a mixture of dicotyledonous trees (e.g. Platanaceae, Cercidiphyllaceae, Juglandaceae, Lauraceae, Hamamelidaceae, Betulaceae), ferns, monocots (including palms and Zingiberales), and some taxodiaceous conifers. Backswamps are most commonly dominated by the taxodiaceous conifers, *Metasequoia* and *Glyptostrobus*, but many of the dicot taxa found in alluvial-ridge sites also occur in backswamps. Floating aquatic ferns and angiosperms are also found at some backswamp sites. Sites from the pond environment typically have large quantities of floating and emergent aquatic plants (based on both form and taxonomic affinities), and a mixture of dicot taxa that are otherwise found most often in channel and alluvial-ridge settings.

The local environments also differ in floral richness (Fig. 1, Table 2). The most obvious differences are between the channel and abandoned-channel (pond) environments. Channel floras have few species because the highly disturbed channel-margin vegetation supports relatively few species (Bell, 1980), and because there is selective destruction of more fragile plant remains in channel

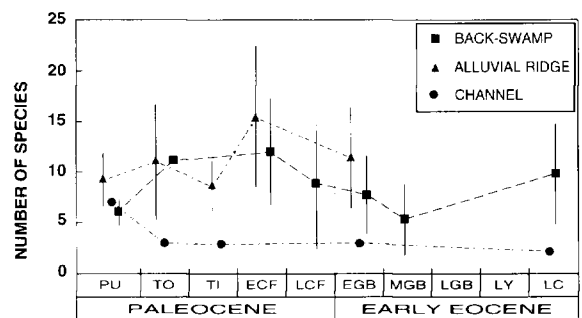


Fig. 1. Mean number of plant species per site by provincial age and sub-age in the Paleocene and early Eocene. Thin vertical lines are one standard deviation above and below the mean. Abbreviations for provincial ages: PU= Puercan, TO= Torrejonian, TI= Tiffanian, ECF= Early Clarkforkian, LCF= Late Clarkforkian, EGB= Early Graybullian, MGB= Middle Graybullian, LGB= Late Graybullian, LY= Lysitian, LC= Lostcabinian.

Table 2
Mean richness of plant localities by time and facies for localities with more than 4 species

NALMA	Facies types					
	Back-swamp	Alluvial ridge	Channel	Pond-fill	Other	All facies
PU	6.0	9.2	7.0			8.1
TO	11.0	11.0	3.0			11.0
TI		9.3	3.0			9.3
ECF	13.1	15.5				14.0
LCF	11.7			16.0		12.3
EGB	8.9	11.4	3.0			9.6
MGB	7.0			16.5		10.8
LGB				14.7		14.7
LY				38.0		38.0
LC	10.6		2.0		40.0	12.4
<i>Y</i>	10.2	11.1	3.6	18.7	40.0	
<i>S</i>	4.4	4.7	1.9	10.2	12.7	
<i>n</i>	71	23	5	7	2	

Time-unit abbreviations are as in Fig. 1. *Y* = mean richness of all localities assigned to an environment. *S* = standard deviation of same. *n* = number of localities assigned to an environment.

deposition. Leaves and other identifiable plant remains also occur in low density in many channel deposits, with the result that sample size may be small, an added factor that would reduce the number of species recovered.

Floras from abandoned-channel ponds typically have high diversity relative to other environments. This also reflects both taphonomic effects and the original vegetation. Diversity of pond assemblages is elevated in part because they sample a mixture of aquatic taxa that are rare or absent in other environments, as well as channel and alluvial-ridge species. Higher diversity in pond assemblages may also reflect a larger sampling area; the plant remains in even a small pond (tens of meters across and tens to hundreds of meters long) probably are derived from vegetation all around the perimeter, and from an even larger area if there are inflowing streams (Spicer, 1981). Autochthonous assemblages found in backswamp environments are more similar to forest floor litter samples in representing the vegetation in an area of just a few thousand m² (Burnham et al., 1992). Finally, plant remains from around the perimeter of the pond may be mixed before being preserved in bottom sediments, thus yielding a more homo-

geneous fossil assemblage in which there will be a better chance of recovering many species in a single small quarry site.

The difference in mean diversity between backswamp and alluvial-ridge sites is small and not statistically significant, only 0.9 species (Table 2). This small difference does not agree with the expectation that edaphically "challenging" substrates with low pH, low oxygen levels, or high water tables (the conditions probably represented by Paleogene backswamps) will support far fewer species than better drained substrates such as those represented by the alluvial-ridge sites (Bell, 1980). The diversity difference between backswamp and alluvial-ridge sites is 2.5 species, however, if we compare only sites that are from the same time interval. Even when this adjustment is made for the uneven stratigraphic distribution of environments, the original diversity difference between backswamp and alluvial-ridge vegetation is likely to be blurred by our lumping a range of alluvial-ridge environments under a single category. For example, some distal splay localities, here included in the alluvial-ridge category, may have been edaphically and vegetationally more similar to the backswamp than to other alluvial-ridge sites.

4. Floral diversity through time

4.1. Site diversity

The strong influence of local environment on floral composition and diversity makes it difficult to separate long-term change in the diversity and composition of the flora from the effect of shifting local environments and vegetation types. This is especially true since the stratigraphic distribution of environments is uneven (Table 3). To factor out the effect of local environment on diversity we have calculated the mean number of species per locality for each of ten time periods across the Paleocene and early Eocene (Fig. 1). Channel, alluvial-ridge, and backswamp environments have been treated separately.

This approach implicitly treats sites in the same time period and depositional environment as multiple measures of species richness for that time and local setting, but other factors, such as differences in sampling effort, also affect the number of species recorded. Such factors increase the range of diversity values in the sample. The subtle pattern of variation through time in Fig. 1 might be more pronounced, or more statistically significant, if sampling effort across all localities were equivalent.

Table 3
Distribution of paleocene and eocene floral localities by time unit and environment type

NALMA	Facies types					Total
	Back-swamp	Alluvial ridge	Channel	Pond-fill	Other	
PU	2	5	1			8
TO	1	2	1			4
TI		7	1			8
ECF	8	4			1	13
LCF	11			1		12
EGB	25	8	1			34
MGB	5			2		7
LGB				4		4
LY				1		1
LC	35	1	1		3	40
<i>Total</i>	87	27	5	8	4	131

Time-unit abbreviations are as in Fig. 1.

The backswamp environment has the most continuous stratigraphic distribution of any of the plant fossil bearing depositional environments. Even so, three of ten time intervals have no backswamp sites and another three have fewer than five sites each. Mean diversity of backswamp sites rises from the Puercan to a peak in the early Clarkforkian, falls into the early Wasatchian reaching a nadir in the middle Graybullian, then rises again in the Lostcabinian (Fig. 1).

The effect of making sampling effort equal is demonstrated by comparing 7 field censused backswamp sites from the early Graybullian with 19 field-censused sites from the early Lostcabinian. At each site roughly 400 leaves were identified. The mean richness for the early Graybullian is 7.9 spp./site (standard deviation, $S = 1.9$); for the Lostcabinian it is 12.2 spp./site ($S = 3.8$). This 54% increase in the number of species per site is statistically significant ($p < 0.01$ in a Kruskal-Wallis ANOVA).

Mean diversity of alluvial-ridge sites shows a similar trend to that of the backswamp sites in being lower in the Puercan, higher in the early Clarkforkian, then declining into the Wasatchian. Lack of alluvial-ridge sites younger than the early Graybullian prevents us from determining if diversity on alluvial-ridge sites increased in the later Wasatchian.

There are only four channel sites for the whole Paleocene–early Eocene sequence, so little can be said about temporal change in diversity. It is clear, however, that with the exception of one Puercan locality, channel site diversity is always substantially lower than that of sites from the other environments.

4.2. Local diversity within a single horizon

The increase in the number of plant species from the early Graybullian to the early Lostcabinian is more pronounced if we compare total diversity at two stratigraphic levels rather than mean number of species per locality. Summing floras by level creates a small amount of spatial and temporal mixing, so that each aggregate flora will better represent the original local floodplain vegetation. Samples aggregated by level can be thought of as

simulating a roughly linear transect of extant vegetation one to several km long. At the 112–114 m level of the Elk Creek section (early Graybullian) is a laterally extensive, plant-bearing layer that has been sampled at 15 sites distributed across 3 km of nearly continuous outcrop. The 621–624 m level of the Elk Creek section (early Lostcabinian) has been sampled at 26 sites distributed across 5 km of nearly continuous outcrop. Inter-site distances at both levels are on the order of tens to hundreds of meters. The Graybullian level has seven backswamp sites, seven alluvial-ridge sites, and one channel site. The Lostcabinian level has one channel and one alluvial-ridge site; the rest are all in the backswamp environment. Even though the 112-m level shows a greater variety of facies, indicating greater original environmental variety, this level contains an aggregate of 31 species compared with an aggregate of 68 species from the 621-m level.

The larger number of species recovered from the 621-m level might result from the greater number of samples at that level. To adjust for the different number of sites at the two levels, we have used a sub-sampling (boot-strapping) procedure to estimate how many species would have been recovered from the 621-m level with fewer sampling sites (Fig. 2). The bootstrap data show clearly that the greater richness of the 621-m level is not a result of greater sample number: the mean number of species recovered from sub-samples of 15 sites from the 621-m level was 51 (Fig. 2b), 65% more than the 31 species present in the 15 sites from the 112-m level (Fig. 2a). Comparing the bootstrap curves for the early Graybullian and early Lostcabinian levels shows that the number of species rises much more quickly with increasing sample number at the 621-m level than at the 112-m level. Furthermore, at the 621-m level, there is no clear flattening of the curve of species plotted against increasing number of sites, whereas at the 112-m level the increase in species number with increasing sample number becomes nearly asymptotic at sample numbers greater than eight (Fig. 2c).

These results suggest that there was a substantial increase in the heterogeneity of the floodplain vegetation from the early Graybullian to the early

Lostcabinian. The increase in floral richness at the larger spatial scale is more pronounced than it is at the scale of individual localities. This increase in backswamp floral heterogeneity may have been caused by drying regional climate and local flood-plain topography. The generally drab, organic-rich character of the older sediments is consistent with perennially high water-tables. Under wet climatic conditions, topographic lows such as flood-plain backswamps would have been almost uniformly wet, even though slight topographic variations typically exist even within flood-plain backswamps (Smith and Smith, 1980). Paleosol characteristics in the Willwood Formation indicate that seasonal fluctuations in water tables became more marked during the middle and later Wasatchian (Bown and Kraus, 1981a). This is consistent with a regional trend toward drier climates, also suggested by sedimentological features and paleobotanical evidence from the Green River Basin (MacGinitie, 1969; Smoot, 1983). Seasonally dry climates would be expected to generate more heterogeneous edaphic conditions in backswamp areas because even slightly elevated areas would have experienced periods of soil dryness. Such differences of only a few centimeters or decimeters in elevation are important in creating edaphic and floral mosaics in seasonally dry, wetland areas of the southern U.S. today (e.g., Connor et al., 1981; Christensen, 1988), but are difficult to detect in the fossil record (e.g., Bown and Beard, 1990).

5. Biochronology

In order to describe changes in species richness through time over a broad region the relative ages of the samples must be established. As mentioned above, the floral and faunal samples used in this study are derived from many local areas, some of which cannot be correlated by physical stratigraphy. For instance, the northern and central Bighorn Basin have not been correlated stratigraphically because of the lack of continuous outcrop between the two areas.

Traditionally the different parts of the Bighorn Basin, and the adjacent Rocky Mountain intermontane basins, have been correlated using a set

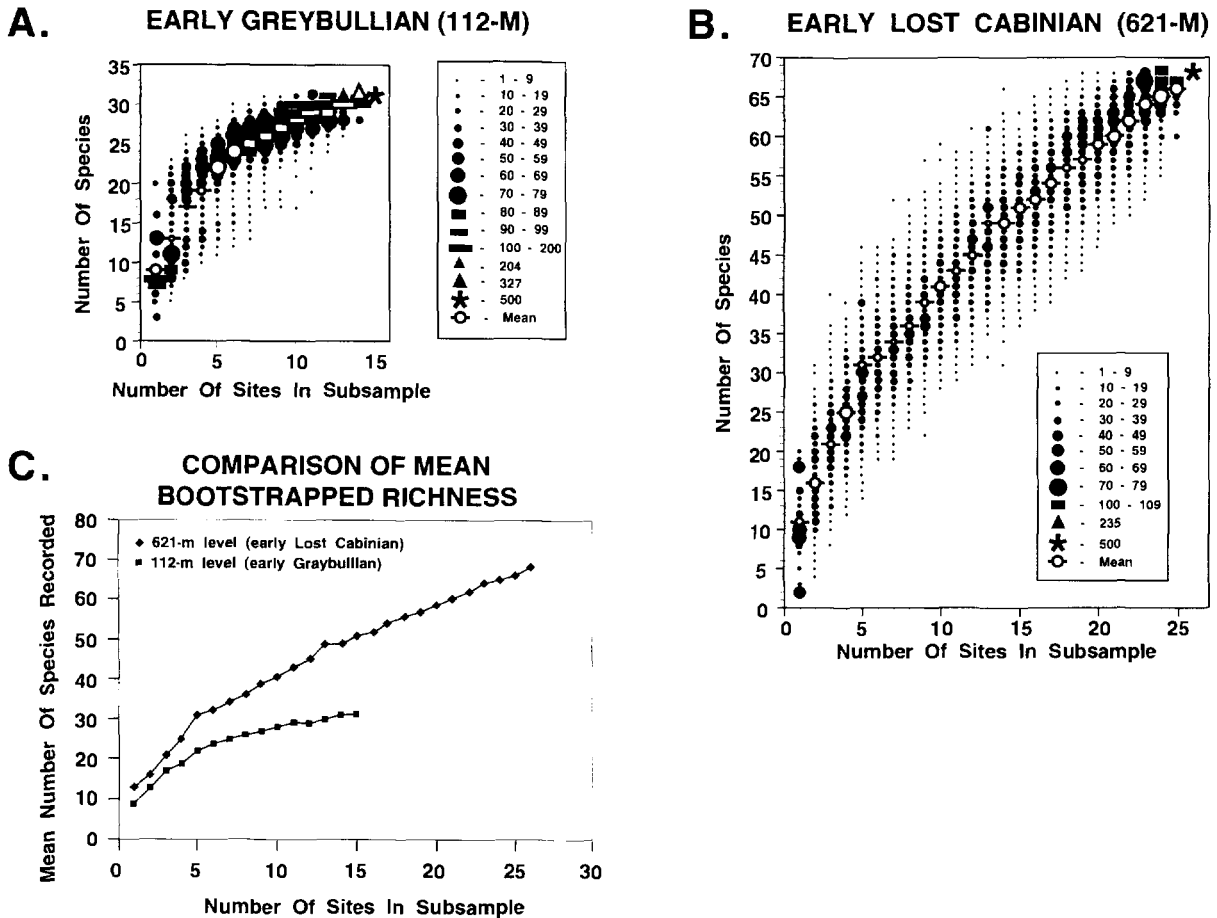


Fig. 2. Bootstrap results for plant fossil sites from (A) the 112-m level, and (B) the 621-m level of the Willwood Fm. One of us (JA) wrote a BASIC program to carry out the bootstrap procedure. The program uses the presence/absence species lists for all of the sites at a single level. In the first round, the list for one site is selected at random, and the number of species at that site is calculated. This procedure is repeated 500 times, yielding a distribution of species richness numbers found in a subsample composed of one site. In the second round, the species lists for two sites are selected at random and without replacement from the full set of lists, then the total number of species occurring in those two lists is calculated. Again the procedure is repeated 500 times, yielding a distribution of richness figures for a subsample composed of two sites. The whole routine is repeated, increasing the number of sites in the subsample by one in each round, until the subsample contains all of the lists known for that level. (C) Comparison of mean bootstrapped richness curves for the 112-m and 621-m level floras from the Willwood Fm. The curves give the mean number of the species obtained using the procedure described above. The curve for the 112-m flora shows a strong tendency to flatten at about 8 sites, whereas the curve for the 621-m flora has a much steeper slope and little flattening, indicating that the 621-m flora is much more heterogeneous over a spatial scale of several kilometers.

of mammalian biochrons referred to as North American Land Mammal Ages, or NALMAs (Wood et al., 1941). Four NALMAs are recognized in the Paleocene, and one, the Wasatchian, is recognized in the early Eocene (Fig. 1; Archibald et al., 1987). The Wasatchian, which is about 5 m.y. long, has been further subdivided into four

sub-NALMAs: the Sandcouleean, Graybullian, Lysitian, and Lostcabinian (for discussions see Schankler, 1980; Gingerich, 1989). The Sandcouleean has been recognized chiefly in the northern Bighorn, or Clarks Fork, Basin (Gingerich, 1989), rather than in the central or southern Bighorn Basin.

Although the NALMA system provides a robust framework for determining the relative ages of faunas in the Rocky Mountain region, it has two major flaws for application in this study. First, the NALMA system cannot be used to date floras except when they are intercalated in local sections with mammalian faunas. Second, lumping faunas into biochrons creates artificially diverse assemblages that never really existed; this exaggerates the apparent extinction and diversification events between the biochrons, potentially creating the appearance of mass extinctions or radiations at those boundaries.

Instead of using a zone system, the floral and faunal samples in this study were ordered in time by applying multivariate ordination techniques specifically developed for this purpose. The method used here is Appearance Event Ordination (AEO; Alroy, 1994). A time scale created using AEO relies on the stratigraphic distributions of all taxa, instead of basing biochrons on occurrences of one or two common species, as in traditional zone systems.

5.1. Appearance Event Ordination

Appearance Event Ordination is related to correspondence analysis (Digby and Kempton, 1987) but makes use of both conjunction and stratigraphic data instead of raw presence–absence data. This is accomplished by translating the conjunction and stratigraphic data into statements about first and last appearance events. The use of conjunction data, which are observations that pairs of taxa have been found at least once in the same sample, is important because continued sampling leads to an improved knowledge of conjunctive relationships, reducing taphonomic bias, small sample size effects, and small-scale ecological factors. Thus, conjunction data sets have a property of convergence that presence–absence data sets lack: generating more and more raw species lists does nothing to free the lists themselves of these effects, but it does cause the conjunction data set to converge on the real set of conjunctions.

AEO translates all conjunction statements into statements about appearance events. For example, if taxa i and j are conjunct, then it must be that

the first appearance event of i (FAE i) comes before the last appearance event of j (LAE j), and conversely, the first appearance event of j comes before the last appearance event of i . This can be stated as FAE i < LAE j , and FAE j < LAE i . These sorts of statements, called F/L data, have the same convergence property that conjunction data do. However, F/L data are unlike conjunctions in that F/L statements can be demonstrated by biostratigraphic relationships even in the absence of a species list for each horizon. For example, if an isolated fossil of species i is found at the 10-m level and a second fossil of species j is found at the 20-m level, then FAE i < LAE j . The use of F/L statements makes it possible to merge stratigraphically isolated species lists and biostratigraphic relationships into a single data set. Other kinds of relationships among events, such as LAE i < FAE j or FAE i < FAE j , do not have the advantageous properties of converging on a real set of conjunctions, and of being inferrable from both faunal or flora lists and occurrence in stratigraphic sections.

In AEO, F/L statements are subjected to an eigenanalysis procedure modeled on the reciprocal averaging routine used by ecologists to perform correspondence analysis (Digby and Kempton, 1987). The algorithm requires modifying a matrix of F/L statements where rows stand for FAEs, columns stand for LAEs, zeroes stand for apparent LAE j < FAE i statements, and ones stand for known F/L statements. The algorithm produces separate scores for the rows and columns that indicate the order in which events occurred. The matrix is modified during the computation by taking advantage of the fact that if the LAE scores would imply LAE i < LAE j , it must be true that FAE i < LAE j because FAE i < LAE i by definition and the temporal order of events is transitive. Similarly, if the score of FAE i is less than the score of FAE j , one can infer that FAE i < LAE i . Back and forth multiplying of scores across the matrix continues until the FAE scores consistently generate LAE scores that give back the original FAE scores, and vice versa. The scores are then used to infer a sequence of first and last appearance events for all of the taxa in the data set. These first and last appearance events are the equivalent of age ranges, and can be summed to obtain a

diversity curve. A more detailed description of AEO is given by Alroy (1994).

5.2. Plant analysis

The AEO analysis of the plant data set was carried out at the species level. The total data set consisted of floral lists from 131 localities; in aggregate these lists contained 244 species. One hundred and thirty-three (133) of the 244 plant species (54.5%) occurred at only a single site and provided no biochronological information. Furthermore, 22 of the lists (17%) were subsets of longer lists, and provided no additional information on conjunctions or F/L data; these uninformative lists were therefore removed from the AEO analysis. The remaining 109 unique lists contained 970 records of species occurrences and demonstrated 1760 conjunctions of taxa. Eighty-four (84) of the sites that provided lists (77.1%) were part of measured stratigraphic sections.

The AEO appearance event sequence implies 3202 conjunctions, and the conjunction index (CI = number of known conjunctions/number of conjunctions, or range overlaps, implied by the event sequence) for the floral data set is 0.55. The relatively low CI indicates that at least 45% of the true conjunctions of taxa are not demonstrated in the data set, either because taxa are strongly separated along ecological and/or biogeographic gradients, because the floras are undersampled, or both. Results of the AEO can be compared with those from a Disjunct Distribution Ordination (DDO: Alroy, 1992), which uses floral conjunction data without reference to stratigraphic relationships. The relationship between first appearance events (FAE) and analogous left edges (LE) from the DDO is fairly high ($r^2 = 0.854$; $n = 111$; significance statistics not applicable), and there is a similar degree of correspondence between last appearance events (LAE) and right edges (RE) from the DDO ($r^2 = 0.873$; $n = 92$). The similarity of results from the DDO and AEO analyses shows that even in the floral data set, where ecological and/or sampling effects are strong, the conjunction information alone still gives much of the information about temporal ordering of events.

Only three tie points are available for calibrating

the floral AEO scores against time: the K/T boundary (Cande and Kent, 1992), the Paleocene/Eocene boundary (Cande and Kent, 1992), and the 630-m level of the Elk Creek section (Wing et al., 1991). Given the small number of points available, it is not advisable to calculate a regression of floral AEO scores against time. Generally speaking, the AEO analysis demonstrates a moderately strong temporal signal in the flora, but confirms the idea that floral composition is much influenced by factors other than time.

5.3. Mammalian analysis

The mammalian fossil record has a very conservative and reliable genus-level taxonomy, and the AEO analysis was performed on generic lists. Species names were recorded, however, in order to guarantee that reshuffling of species among genera did not invalidate the genus-level information. There are 234 genera present in the data set, and with 3423 records, the average list included 11.4 genera. Eighty-six (86) “redundant” lists whose contents were entirely duplicated by longer lists were eliminated. Lists were eliminated from the analysis only if they were stratigraphically isolated or duplicated by a longer list in the same horizon or an adjacent horizon. The remaining 215 lists included 3098 records and the full set of 234 genera. Of the lists used in the analysis, 162 (75.3%) were part of measured stratigraphic sections. There were eight local or composite stratigraphic sections (Table 4). As with the floral data, a high proportion of the lists were in measured

Table 4
Stratigraphic sections used in AEO analysis of mammals

Section name	Basin	No. lists	No. levels
Bear/Lebo/Melville	Crazy Mountains	10	10
Buck Spring	Wind River	2	2
Cedar Mountain	Bighorn	15	13
Clark's Fork	Bighorn	69	25
Deadman Butte	Wind River	3	3
Elk Creek	Bighorn	56	55
Red Creek	Wind River	3	3
Shoshone River	Bighorn	4	4

sections, indicating the relatively high quality of stratigraphic control on distributional data.

A total of 7471 conjunctions and 22,725 F/L statements were demonstrated by the lists and sections; 18,272 of the F/L statements (80.4%) could be demonstrated by stratigraphic relationships alone. The AEO appearance event sequence implies 10,616 conjunctions (conjunction index = 0.704). Because no post-Wasatchian lists were used in the analysis, standing generic diversity artifactually decreases in the late Wasatchian. To avoid this problem, which is analogous to the Signor-Lipps effect, the AEO algorithm was modified to account for the fact that 66 of the mammalian genera in the Paleocene–Wasatchian data set are also known from the succeeding Bridgerian age. This was accomplished by constraining the LAE scores for these “surviving” genera to equal 1.0 at each iteration of the algorithm (see Alroy, 1994). The event-sequence computation was also modified to exclude last appearances for the genera known to survive to the Bridgerian.

The strong time signal in the mammalian data set is indicated by the congruence of the stratigraphy-constrained AEO results with DDO results that used only faunal data. DDO left edges and analogous AEO first appearances correlate very strongly ($r^2 = 0.980$), as do the right edges and last appearances ($r^2 = 0.976$). The strength of the temporal signal also is indicated by the fact that virtually all of the major mammalian localities fell in exactly the order predicted by Archibald et al. (1987). Perhaps the only controversial result derived from the AEO analysis involves the correlation of the earliest Wasatchian WaO fauna (Gingerich, 1989) with supposedly younger but still early Wasatchian faunas from the lower Elk Creek section (Bown, 1979; Schankler, 1980) and the Powder River Basin (Delson, 1971), a disagreement that involves at most a few hundred thousand years. These remarkably conservative results are not just an artifact of AEO's use of stratigraphic relationships, because the alignment of several coeval stratigraphic sections could have departed significantly from the traditional scheme. The stronger relationship between time and turnover in the mammalian results than in the floral analyses is a result of shorter stratigraphic ranges,

that is higher turnover rates, for the mammals. This difference in turnover rates does not appear to be the result of sampling differences. Undersampling should not only cause short-ranging species to be under-represented, but should result in under-estimates of the temporal ranges of all taxa. Although the flora is less densely sampled than the mammalian fauna, there are many plant species with long stratigraphic ranges.

Only seven paleomagnetic and radioisotopic dates are available to calibrate the event sequence (Table 5, Fig. 3). Unfortunately, some of the paleomagnetic correlations are ambiguous, were decided upon in the first place using mammalian biochronologic relationships, and like all paleomagnetic age determinations rely on a time scale that is calibrated with only a handful of dates (in this case, Cande and Kent, 1992). In particular, the Lancian/Puercan boundary is assumed to equate with the Cretaceous/Tertiary in order to constrain the position of the Mantua Lentil within Chron 29R. A second date is based on age estimates for the Paleocene/Eocene boundary made in marine sections (Cande and Kent, 1992), and therefore relies on the validity of equating the Paleocene/Eocene boundary with the Clarkforkian/Wasatchian boundary as defined in the study area. Thus, the calibration used here (Fig. 3) should not be construed as an independent test of the event sequence, unlike the calibrations

Table 5
Calibration of AEO results with time

Ma	Locality	AEO#	Event*	Reference
64.86	Mantua Lentil	13–14	Chron 29R	1
61.94	Rock Bench Q.	106–107	Chron 27R	1
57.16	Princeton Q.	212–213	Chron 25N	2
54.62	SC-136	243–244	Chron 24R/25N	2
55.00	SC-67	297–298	Pal/Eoc boundary	3
52.80	Elk Creek 633 m	357–358	$^{40}\text{Ar}/^{39}\text{Ar}$ date	4
50.30	Halfway Draw	380–381	K/Ar date	5

*Paleomagnetic time scale based on Cande and Kent (1992). 1 = Butler et al. (1987). 2 = Butler et al. (1981). 3 = Gingerich (1989). 4 = Wing et al. (1991). 5 = Evernden et al. (1964); Korth and Evander (1982).

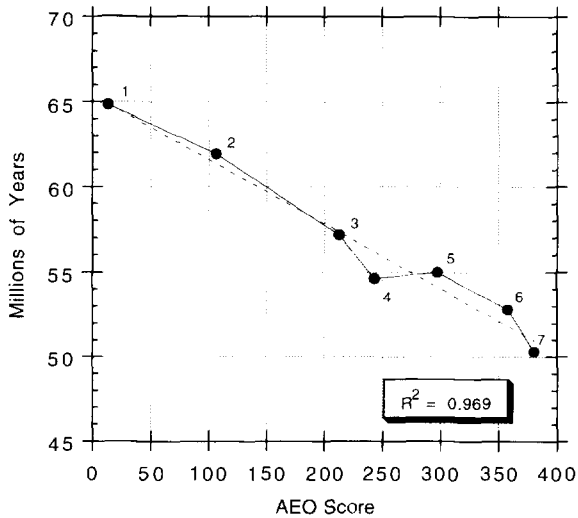


Fig. 3. Time vs. scores from the Appearance Event Ordination (AEO) of mammalian generic lists. See text for explanation of AEO, and Appendix V for lists used in this analysis. Sources and methods for inferring ages of points 1–7 are given in Table 5. Points: 1 = Mantua Lentil, 2 = Rock Bench Q., 3 = Princeton Quarry, 4 = University of Michigan loc. SC-136, 5 = University of Michigan loc. SC-67, 6 = 633-m level of the Elk Creek section, 7 = Halfway Draw locality.

shown in Alroy (1994). Nonetheless, a monotonic relationship between time and faunal turnover (as represented by AEO scores) is apparent ($r^2 = 0.969$). This relationship can be used to calculate the ages of the North American provincial age/stage boundaries (Table 6).

6. Regional diversity

6.1. Mammals

The most striking feature of the generic diversity curve based on the results of the mammalian AEO analysis is the absence of major declines (Fig. 4). It is important to note that this curve, like the one presented in Alroy (1992), is calculated in a way that yields the highest and lowest possible diversity levels that the appearance event sequence allows. In other words, any major extinction event should be represented by a steep drop corresponding to many last appearances closely spaced in time. The only drops in the curve are relatively minor (<12 genera). Furthermore, the inferred diversity levels

Table 6

Interpolated ages of North American stage/age boundaries based on calibration of AEO results

AEO no.	Ma at base	Age
13	64.9	Puercan
40.5	63.9	Torrejonian
109.5	61.2	Tiffanian
221.5	56.8	Clarkforkian
274.5	54.8 (54.9–54.2)	Wasatchian
402	49.8	Bridgerian

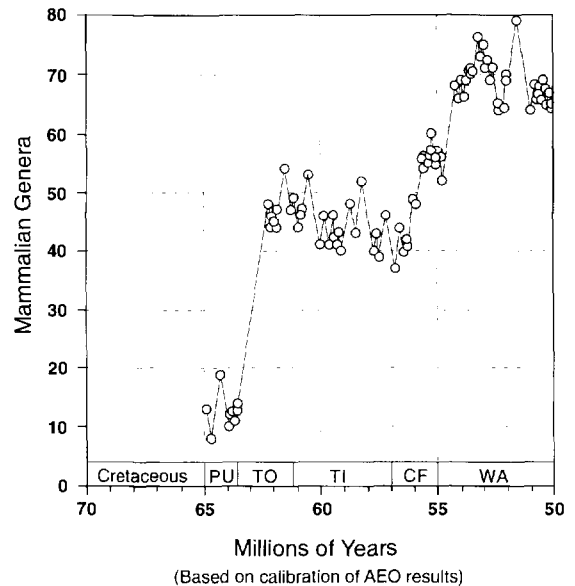


Fig. 4. Regional diversity of mammalian genera through the Paleocene and early Eocene. The x-axis is based on the calibration of AEO results with time shown in Fig. 3 and Table 5. The number of genera at any given time is the number of generic ranges that overlap at that time according to the AEO. Provincial age abbreviations as in Fig. 1, except CF = Clarkforkian, and WA = Wasatchian.

do not vary outside the range of 37–54 genera in the Torrejonian and Tiffanian, or outside the range of 64–76 genera in the Wasatchian. The Clarkforkian serves as a bridge between these intervals of stability, exhibiting a largely monotonic increase in diversity. This climb appears to have been punctuated with a minor extinction event prior to a very rapid diversity increase in the basal Wasatchian, fueled by the arrival of several Eurasian migrants (e.g., basal perissodactyls, artio-

dactyls, and adapid primates: Gingerich, 1989; Maas et al., 1995). The long middle Paleocene and early Eocene plateaus have not been recognized by earlier studies such as Lillegraven (1972), Rose (1981), Savage and Russell (1983), and Archibald (1993) because of the relatively coarse resolution of the traditional time scale.

One expected result of the analysis is the pattern of very rapid diversification of mammals in the early Paleocene, which has been recognized for decades (e.g., Simpson, 1949, Chapter 6; Lillegraven, 1972). A similar pattern was also illustrated by Archibald (1993). Our data appear to show a lag phase in the diversification event that spanned the entire Puercan, a period of about a million years (Archibald et al., 1987). This lag probably reflects, at least in part, a sampling deficiency; there are at most two recently described, well-sampled faunas from the Puercan in the four basins under discussion here. Better Puercan faunas are widely scattered through other parts of the Rocky Mountains. If those samples were added to the data set, the early Paleocene diversification probably would appear to be more confined to the Puercan than this analysis indicates.

The general features of our mammalian diversity analysis are concordant with those of Maas et al. (1995, Fig. 4a), in spite of the differences in analytical techniques and data sets. Both curves show substantially higher diversity in the early Wasatchian than in the Tiffanian–Clarkforkian interval. Three features of the Maas et al. curve differ from the one presented here: generally lower levels of generic diversity (30–40 for the Tiffanian–Clarkforkian interval, 60–70 for the early Wasatchian), a diversity decline in the late Wasatchian, and no sign of increasing generic diversity in the late Clarkforkian. The first two discrepancies are probably due to differences in the data sets. Our data set includes samples from the Wind River, and Powder River Basins (and central Bighorn Basin?) not used by Maas et al., this increases the number of genera detected. Maas et al. (1995) comment that the diversity decline they record in the mid-late Wasatchian is probably a consequence of reduced sampling density; this is the problem we have tried to correct for by including late-Wasatchian samples from the Wind River

Basin and by discounting the last appearances of genera known to occur in the Bridgerian.

This leaves the late Clarkforkian as the only period for which the diversity curves are substantially different. Here our curve shows a 50% increase in number of genera during the later Clarkforkian (40–60 genera), whereas the Maas et al. curve indicates between 40 and 45 genera for the middle Clarkforkian through earliest Wasatchian (Cf2–Wa0), before increasing to about 60 genera in the Wa1 zone. We do not know what causes this discrepancy in the timing of the increase in number of genera.

6.2. Plants

Several unexpected patterns emerge when standing diversity in the regional flora is plotted against time using the results of the AEO (Fig. 5a). Although both floral and mammalian diversity increased during the first half of the Paleocene, the increase in plant species diversity was gradual, at least compared to the rate at which the number of mammalian genera increased. The number of plant species increased by a factor of three during the first 5–7 m.y. of the Paleocene and then reached a plateau of about 35 species through most of the late Paleocene, whereas mammalian genera increased by a factor of five to six during a much shorter period. The sharpest diversity decline in the plant record occurred just at the Paleocene/Eocene boundary, when the number of species drops by about 30% from 37 to 26 species. This extinction coincides with a major, though interrupted, rise in mammalian diversity and with local and global indicators of increasing mean annual temperatures (Hickey, 1980; Miller et al., 1987; Wing et al., 1991). The Eocene began with a sharp increase in plant diversity, which reaches its highest levels at 49 species in the early Wasatchian, from which it declines back to the mid-30's in the Lysititan and Lostcabinian. The earliest Eocene increase in plant diversity parallels the mammalian trend for the same time period. The sharp decline in floral diversity at the last point in the graph (Fig. 5a) reflects the small number of sample sites in the upper part of the Elk Creek section.

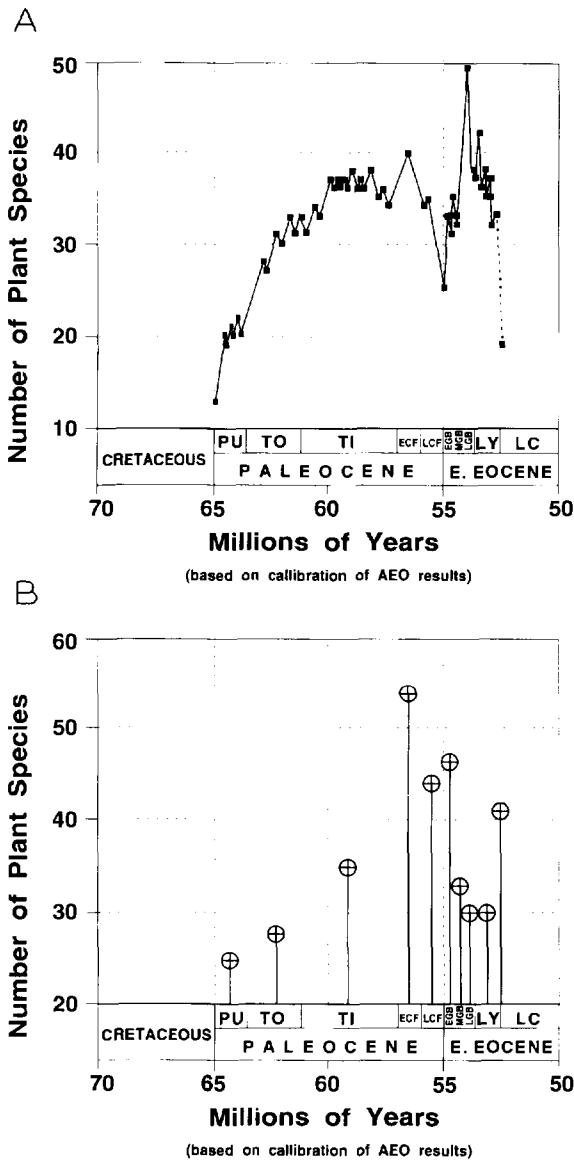


Fig. 5.A. Regional diversity of plant species through the Paleocene and early Eocene based on AEO results. The number of plant species at any given time is the number of species ranges that overlap at that time according to the AEO. B. Number of plant species per provincial age or sub-age calculated by the range-through method (see text for explanation). Provincial age abbreviations as in Figs. 1 and 4. Ages for the subdivisions of the Graybullian were estimated by evenly subdividing the time between the Clarkforkian/Wasatchian boundary (54.8 Ma) and the base of the Lostcabinian (52.8 Ma).

Given the low rate of turnover in floral species and the moderate level of correlation between the AEO scores and time, there is substantial uncertainty about the details of the timing and magnitude of changes in floral diversity. The major characteristics of the curve, however, are less likely to change with additional data: these include the slow increase of diversity in the first half of the Paleocene, the sharp diversity decrease in the latest Paleocene and the increase in the early Wasatchian.

To provide perspective on the diversity curve based on AEO results, we have also calculated standing floral diversity in a more traditional way (Fig. 5b). The number of plant species in each age (Puercan–Wasatchian) was tabulated using a range-through method in which species known from preceding and following ages were counted as present during an interval that produced no specimens of that species. As with the AEO analysis, species recorded from only a single stratigraphic level were excluded. The diversity curve created in this way shows the same early to mid-Paleocene increase in species richness seen in the AEO results. However, the extinction event at the Paleocene/Eocene boundary indicated by the AEO method is not as pronounced in the zonally-averaged data, although there are 20% fewer species in the late Clarkforkian than the early Clarkforkian (Fig. 5b). It is to be expected that relatively short-term events, such as the Paleocene/Eocene boundary extinction, would be difficult to detect with data averaged over zones that are generally 1–2 m.y. in duration.

The zonally-averaged diversity data differ most strongly from the AEO results in the early Wasatchian; the AEO curve rises sharply during this time interval, whereas the zonally-averaged curve shows declining diversity from the early Graybullian to the Lysitican. The difference between the results from the two analyses for the early Wasatchian may be caused in part by shorter durations for the subdivisions of the Graybullian than for the other zones used in this analysis. The Wasatchian is approximately 5 m.y. long, and the Lostcabinian about 2.5 m.y. long (Table 6; Wing et al., 1991); this leaves about 2.5 m.y. for the Graybullian and Lysitican together. If the

Graybullian and Lysitian are roughly equal in duration, then each would be about 1.25 m.y., and the three recognized subdivisions of the Graybullian might well have durations of less than 0.5 m.y each. This is less than half as long as the other intervals used in this analysis, so fewer species should be expected in the subdivisions of the Graybullian.

7. The different fossil records of plants and mammals

Comparing the diversity and turnover rate of plants and mammals is complicated because the fossil records of the two groups are arrayed differently in time and space. Although plant and mammalian fossil assemblages are intercalated throughout the Fort Union and Willwood Formations in the Bighorn Basin, those assemblages are different kinds of samples of the biotas from which they were derived. This is because, in general, greater spatial mixing and time-averaging takes place within each mammalian assemblage than within each plant fossil assemblage (Behrensmeyer and Chapman, 1993; Burnham, 1993; Johnson, 1993), and because the stratigraphic distribution of the two types of fossils is different in the Bighorn Basin.

Spatial mixing of mammalian remains occurs because mammals are mobile, and because mammalian bones are durable enough to be transported by surface processes, reworked from older sediments, and concentrated or dispersed by scavengers and predators (Badgley et al., this issue). Although spatial heterogeneity in mammalian assemblages has been documented in the Willwood Fm. (Bown and Beard, 1990), it is much more pronounced in plants. Plants are sessile and the most abundant of the parts they shed, leaves, are fragile and unlikely to be deposited and redeposited. Forest floor leaf litter is derived almost entirely from trees within 20–30 m, a circle of less than 10^4 m² (Burnham et al., 1992). Although transported leaf assemblages are common in some depositional settings such as lakes and deltas, most floodplain assemblages like those from the Fort Union and Willwood Formations are essentially

autochthonous (Hickey, 1980; Wing, 1984; Gastaldo et al., 1989; Behrensmeyer and Hook et al., 1992).

Mammalian and plant assemblages also differ greatly in the amount of temporal mixing, or time averaging, within a single assemblage. Leaves decay within a few months to years when they are exposed at the soil surface (Ferguson, 1985), and floodplain leaf accumulations like those in the Fort Union and Willwood Formations probably represent a few years at most. Some analytical time-averaging (*sensu* Behrensmeyer and Hook et al., 1992) could occur if collections from a laterally extensive bed are considered together, because the thin fossiliferous unit within the thicker bed may have been deposited at different times in different places (e.g., Greenwood and Basinger, 1993). Even in this situation, the total duration represented by the fossils is likely to be only decades to hundreds of years, roughly on the order of the lifespan of the organisms being sampled (Burnham, 1993).

In contrast, most mammalian assemblages in the Bighorn Basin are taphonomically time-averaged paleosol accumulations or bone concentrations in channel or near-channel deposits (Rose, 1981b; Bown and Kraus, 1981b; Gingerich et al., 1980; Badgley et al., this volume). Paleosol assemblages may contain remains of individuals that accumulated over periods of hundreds to thousands, perhaps even ten-thousand, years (Bown and Kraus, 1993), and bone assemblages in channel deposits may contain elements removed from older floodplain soils during bank cutting (Behrensmeyer, 1988). In addition to taphonomic time averaging within assemblages, most mammalian remains in the Bighorn Basin sequence are collected by prospecting modern surface lag deposits. Thus many collections, especially those made prior to the last 20 years, may have been analytically time-averaged over thousands to tens of thousands of years (Schankler, 1980; Winkler, 1983; Bown et al., 1994).

Mammalian assemblages in the Bighorn Basin sequence also have a denser and more continuous stratigraphic distribution than do plant assemblages. This is due in part to more intense collecting of mammals, but also reflects the near absence of plant-preserving lithologies during the latest

Clarkforkian and earliest Wasatchian part of the northern Bighorn Basin section (Hickey, 1980), and the Lysititan part of the central Bighorn Basin section (Wing, 1980). In contrast, the Willwood Formation in the central Bighorn Basin has at least one mammalian assemblage from most 10-m intervals between 50 and 600 m, spanning much of the Wasatchian (Schankler, 1980; Bown et al., 1994), and there is a similar stratigraphic density of mammalian localities in the Clarkforkian and early Wasatchian part of the Willwood Formation in the northern Bighorn Basin (= Clarks Fork Basin) (Gingerich, 1982).

As a result of spatial mixing, and both taphonomic and analytical time-averaging, well-collected mammalian assemblages are probably moderate to good representations of species composition and diversity in the local region over a time period of thousands of years. The number of mammalian species found at the richest levels compares favorably with diverse extant mammalian communities (Rose, 1981a; Bown et al., 1994). The absence of spatial mixing and taphonomic time averaging in floral assemblages results in a sample of the original vegetation that is probably an excellent reflection of the relative abundances of the common species in the immediately surrounding (sub-local) area, but which gives almost no information about the vegetation more than 20–30 m away. Species richness at Fort Union and Willwood Formation plant localities is comparable to that seen in autochthonous litter samples from extant deciduous forests (7–15 species; Burnham et al., 1992), which only contain a small proportion of the woody species that live in the surrounding region.

As a consequence of these differences in sampling regime, long-term change in diversity and composition should be better recorded by mammals than plants. Changes in floral composition and diversity will be more affected by sampling effort, and by the depositional environments that are sampled at each stratigraphic level. We have compensated for these differences by analyzing floras from each type of depositional environment separately, by exploring the effect of sampling effort on floral composition and diversity, and by applying the same analytical technique, Appearance Event Ordination, to both the fauna

and flora in an examination of regional diversity over the entire Paleocene–early Eocene period. Still, the differences in the diversity patterns of plants and mammals may in part arise from the taphonomic and sampling differences that we have not been able to remove.

8. Discussion

The regional diversity curves for plants and mammals (Fig. 6) are each supported by independent sources of information. In plants, the general shape of the regional curve is also seen in diversity analyses carried out at smaller spatial scales; furthermore, the relatively slow increase in plant diversity through the Paleocene is consistent with the long-held view that Paleocene floras of the Northern Rocky Mountains are fairly homogeneous and depauperate (e.g., Brown, 1962). Palynofloras from the Atlantic and Gulf coastal plain also show the same pattern of slow diversity increase through the early and mid-Paleocene, and

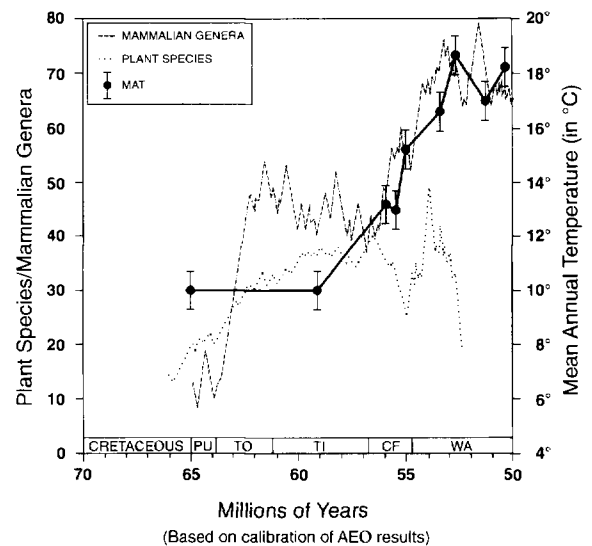


Fig. 6. Plant and mammalian regional diversity (from Figs. 4 and 5A) and inferred mean annual temperature (MAT) in the Bighorn Basin. Temperature estimates are from physiognomic analyses of dicot leaves by Hickey (1980) and Wing et al. (1991); the standard error of the estimate is indicated by the height of the vertical bar ($\pm 0.98^{\circ}\text{C}$). X-axis is calculated in the same manner as for Figs. 5 and 6.

a sharp extinction at the Paleocene/Eocene boundary followed by a rapid rebound in the earliest Eocene (Frederiksen, 1994).

The shape of the mammalian diversity curve generally is consistent with those determined by other workers (e.g., Rose, 1981; Archibald, 1993; Maas et al., this issue). Although the pattern of diversity change for each group individually is familiar, the very loose congruence between the two groups is unexpected, as is the relatively poor correspondence between plant species diversity and temperature as determined from leaf physiognomy (Hickey, 1980; Wing et al., 1991).

There are several reasons to expect plant and mammal diversity to change in a congruent fashion during the Paleocene–early Eocene interval. Both vertebrates and plants suffered major extinctions at or near the K/T boundary (Johnson et al., 1989; Johnson, 1992), so diversification into depauperate adaptive zones might be expected to characterize both groups during the Paleocene. The global warming during the late Paleocene and early Eocene (e.g., Kennett and Stott, 1991; Koch et al., 1992), would also be expected to increase diversity in both groups, because there is a positive correlation in extant ecosystems between warm climate and plant and mammal diversity (e.g., Gentry, 1988; Eisenberg, 1981), as long as rainfall is not very low. Finally, one might expect a synergistic effect, in which increasing diversity in one group would lead to higher diversity in the other.

Mammals and plants, particularly flowering plants, are linked by an array of ecological interactions: plants are a food resource and substrate for mammals, mammals are consumers of plants, but also disperse seeds and pollinate flowers. Diversification in flowering plants should increase the range of resources for herbivorous mammals. A greater variety of mammalian dispersers and pollinators should enhance speciation in plants by increasing the chances of reproductive isolation of plant populations. Even an increased range of herbivory might permit a higher number of plant species to coexist by preventing the fastest growing species from out-competing slower growing but more heavily defended species (e.g., Crawley, 1983). There is little to support this scenario in the data we have assembled here. A recent study

of ordinal diversity in insects also has failed to detect congruent diversity changes in animals and plants over tens of millions of years (Labandeira and Sepkoski, 1993).

8.1. *The Paleocene radiation*

The main difference in the diversity curves of mammals and plants during the Paleocene is the much slower rate of diversity increase in plants, especially considering the plant analysis used species and the mammalian analysis used genera. The plants do not approach a Paleocene “plateau” of diversity until 5–6 m.y. after the K/T boundary, while the mammals reach a plateau in less (perhaps substantially less) than 3 m.y. Several explanations for this difference can be offered: rates of speciation may be intrinsically higher in mammals than in plants, the Paleocene may have presented more unexploited resources for mammals than plants, or there may have been some extrinsic factor that continued to depress plant diversity even while mammals were speciating rapidly.

It has previously been suggested that evolutionary rates in plants are slower than in animals (e.g., Traverse, 1988). This would seem to be supported by the relatively common occurrence of extant genera of plants in the Late Cretaceous or early Tertiary; mammals of the same antiquity do not generally belong even in extant orders. The presence of extant genera of plants in the early Tertiary, however, is an indication of taxon longevity, and does not necessarily imply low rates of taxonomic origination. The slower rate of addition of new species of plants compared to mammals in the early to mid-Paleocene is consistent with lower origination rates in plants, but obviously does not establish this as a general rule. However, the similarly slow rate of increase in diversity in both Bighorn Basin megaflores and in palynoflores from the southeastern U.S. (Frederiksen, 1994) does suggest the slow rate of diversity increase is not caused by environmental factors operating only in the northern Rocky Mountain region.

A second hypothesis for explaining the relatively slow rate of increase in diversity among plants in the early to mid-Paleocene is that K/T extinctions were more severe among vertebrates than among

plants. This would have left more unoccupied resources for surviving mammals, leading them to have a higher rate of diversification during the Paleocene “recovery.” The severity of the K/T extinctions in North America is a contentious issue. Both plants and terrestrial vertebrates were strongly affected (terrestrial vertebrates: Archibald and Bryant, 1990; Sheehan and Fastovsky, 1992; plants: Sweet and Braman, 1992; Nichols and Fleming, 1990; Wolfe and Upchurch, 1987; Johnson and Hickey, 1990; Johnson, 1992), and even if estimates of the percent of species eliminated are accurate, they may not predict the “opportunity” available in the early Paleocene, since that would depend on the ecological roles as well as the number of species eliminated. In spite of the difficulty of evaluating this hypothesis, it may be significant that some of the numerically important elements of Maastrichtian backswamp vegetation, especially taxodiaceous conifers and some lineages of ferns, survived and prospered in the early Paleocene. The most apparent vertebrate group of the Maastrichtian, the dinosaurs, did not fare so well. Even if plants and vertebrates lost similar percentages of species at the K/T boundary, the vertebrate fauna probably retained fewer of its former ecological dominants.

A third hypothesis for the slow increase in plant species during the Paleocene would invoke some sort of environmental factor that limited plant diversity without having a strong effect on mammals. This last hypothesis seems the least likely because most large-scale environmental factors that would limit diversity in one group would have the same effect on the other (e.g., harsh climate).

None of the suggested hypotheses are mutually exclusive, but we currently favor some combination of the first two, that the rate of plant diversification in the early Paleocene was slower than that of mammals both because of intrinsically slower rates of speciation, and because the K/T extinctions created more unused resources for mammals than for plants. This interpretation is in general agreement with the idea that plants are more resistant to mass extinction than animals, and that the pattern of their evolution is less influenced by boom-and-bust cycles generated by such extinctions (Knoll, 1984; Traverse, 1988).

8.2. *Effect of global warming*

A discrepancy between the plant and mammal diversity records occurs at the Paleocene/Eocene boundary. Here plant diversity declines sharply just as mammalian diversity is increasing. Although the plant extinction is not catastrophic (roughly 30% at the species level), it is interesting that the sharpest extinction event seen in this record is in plants, not animals, even though plants have been supposed to be more extinction resistant (Knoll, 1984).

The Paleocene/Eocene boundary interval increasingly is being recognized as an interval of rapid change in global ocean circulation and global climatic conditions (Rea et al., 1990; Kennett and Stott, 1991; Koch et al., 1992; Pak and Miller, 1992; Gibson et al., 1993). Oxygen isotope records from planktonic and benthic foraminifera at many DSDP sites indicate a strong warming trend beginning in the latest Paleocene and continuing into the latter part of the early Eocene (Shackleton et al., 1984; Miller et al., 1987). Similar evidence for warming is seen in studies of leaf physiognomy in the Bighorn Basin (Hickey, 1980; Wing et al., 1991; Fig. 6). In addition to this long-term trend, carbon isotope data from foraminifera, and from soil carbonates in the Bighorn Basin, show a very large excursion lasting for no more than a few tens of thousands of years during the last 0.5 m.y. of the Paleocene (Kennett and Stott, 1991; Koch et al., 1992; Koch et al., this issue). This isotopic shift has been taken as evidence for a change in deep-ocean circulation from a system driven by cold bottom water to one driven by warm, saline bottom water (Kennett and Stott, 1991). If such a shift occurred over a short period of time, it could have resulted in major changes in atmospheric circulation and continental climate regimes.

Given that warmer climates are usually associated with greater plant diversity (in the absence of severe water-stress) the response of plant diversity to the Paleocene–Eocene warming is surprising. There was a sharp drop in diversity approximately at the Paleocene/Eocene boundary and close in time to the short-term carbon-isotope excursion. Diversity rebounded quickly in the early

Wasatchian. The similarity of this pattern to that shown by palynofloras in the southeastern U.S. (Frederiksen, 1994) implies that the Paleocene/Eocene plant extinction and earliest Eocene recovery is not an artifact of local preservational effects or even regional environmental change.

It is intriguing that the sharp reduction in plant diversity coincides with a minor dip in mammal diversity as well as the major immigration event that marks the Clarkforkian/Wasatchian boundary. It has been proposed that the warming at the Paleocene/Eocene boundary was responsible for the opening of high-latitude migration routes and the exchange of mammalian faunas among Europe, North America, and Asia (Rose, 1981b; Maas et al., this issue). Plants are also capable of geologically rapid range change in the face of climatic shifts (e.g., Overpeck et al., 1992). However, if the sharp carbon isotope excursion near the end of the Paleocene was associated with a very rapid climate change ($<10^3$ yr ?) it might have exceeded the capacity for plant ranges to adjust, resulting in local extinction, at least at mid-latitudes where the warming is thought to have been most pronounced. As yet the carbon isotope and floral events cannot be precisely correlated, but because the floral changes near the Paleocene/Eocene boundary are at least continent-wide in scope, it may well be that the pattern of plant diversity change was entrained by the same global environmental events that were affecting marine and other terrestrial organisms.

9. Conclusions

There are both methodological and paleontological conclusions from this work. Plant diversity has not often been studied at the relatively fine temporal and taxonomic scale attempted here. Such studies are inherently difficult because of the confounding effects of facies and sampling intensity on floral diversity. In order to interpret changes in floral diversity through time it is clearly necessary to account for these factors, which operate so much more powerfully on plant than on vertebrate assemblages. The inherent "localness" of plant fossil assemblages does permit, however,

an easier parsing of diversity into alpha, beta, and gamma spatial scales. With enormous sampling effort it may be possible to understand the spatial texture of diversity change through time in plants—a goal that is probably unattainable in the better-mixed vertebrate fossil record.

The relatively slow increase in plant diversity during the first half of the Paleocene provides new evidence for the long held notion that rates of evolution are slower in plants than in mammals. The weaker correspondence between floral turnover and time than between mammalian turnover and time is also consistent with lower rates of origination and extinction for the flora.

Although in the present day there is a strong association of warmer climates with higher floral diversity, the correlation through time in the Bighorn Basin record is not strong. This is most obvious at the Paleocene/Eocene boundary itself. At present we are not able to resolve time in the Bighorn Basin sections at the level of thousands or tens-of-thousands of years, which makes it difficult to determine rates of environmental and floral change at ecological time scales. It is possible that the lack of correlation between plant diversity with temperature is because rates of change are also important. Rapid climatic shifts may initially decrease plant diversity regardless of the direction of change. In this light it is intriguing that the temperature curve is more closely paralleled by changes in the diversity of the motile mammals.

There is little congruence between changes in plant and mammal diversity during the Paleocene–early Eocene interval. This cannot be considered strong evidence against the theory that diffuse coevolution played a major role in the Tertiary diversification of plants and mammals, but should continued work of this sort fail to demonstrate congruence, the notion will eventually have to be abandoned.

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Appendix A1

Plant localities, depositional environment, NALMA equivalent, meter level, richness

Locality	Env	NALMA	Meter	Richness	Locality	Env	NALMA	Meter	Richness
15M	BS	LC	621	2	Ginkgo Site	BS	PU		7
15ME	BS	LC	621	7	H	PO	LGB	420	22
A	BS	LC	601	5	Horse Valley #2	AR	TI		11
AL	AR	LC	621	2	(LJH72122)				
B	BS	LC	706	5	Horse Valley #1	AR	TI		8
BCT	BS	LC	719	11	(LJH72121)				
BCT2	BS	LC	719	6	HsI Unit 8	AR	EGB	112	8
BCT3	BS	LC	719	2	HsI Unit 9	BS	EGB	112	11
BCT4	BS	LC	719	5	HsII	AR	EGB	112	5
Bell Road Cut (LJH7654)	AR	TI		8	Hunters Creek #1	AR	PU		10
(LJH7654)					(LJH7675)				
Bird Track Sand (KJ83102)	CH	TO		3	Hunt Creek #2	AR	TO		7
(KJ83102)					(KJ84a)				
Black Widow Gulch (LJH72127)	AR	TI		10	Kirk Valley #1	AR	PU		13
(LJH72127)					(KJ83101, KJ8415)				
Bobcat Pass #2	AR	PU		6	Kisinger Lakes	OT	LC		49
Bobcat Pass #3 (LJH7652)	BS	PU		5	LB	PO	MGB	311	22
(LJH7652)					LHE	BS	EGB	30	3
BR	AR	EGB	112	20	LJH6721a	BS	ECF		16
Br1.5	AR	EGB	112	13	LJH6721b	BS	ECF		14
BR11	AR	EGB	112	16	LJH6723	BS	ECF		18
Brosh	CH	LC	621	2	LJH6854	BS	ECF		3
Bs	BS	EGB	112	7	LJH7143	BS	ECF		10
Bugger to get to (Cedar Mtn.)	AR	PU		8	LJH7627	BS	ECF		16
(Cedar Mtn.)					LJH7634	PO	LCF		16
Chance Loc (LJH7132)	AR	TI		11	LJH7635	BS	LCF		5
(LJH7132)					LJH7834	BS	LCF		20
Cn1	BS	EGB	112	9	LJH7871 (SLWM216)	BS	ECF		12
CnII	BS	EGB	112	8	LJH7873	ECF		4	
CQ1	BS	LC	621	19	LJH72116	AR	ECF		16
CQ2	BS	LC	621	9	LJH72123	AR	TI		4
CQ3	BS	LC	621	9	LJH72126	BS	ECF		6
CQA	BS	LC	621	8	LJH72141	BS	LCF		12
Damn Boulder Site (LJH72103)	AR	ECF		12	LW	BS	EGB	10	4
(LJH72103)					M	BS	LC	601	3
DCF	BS	MGB	353	11	Mantua Lentil (LJH7868)	CH	PU		7
DCI	PO	MGB	312	11	(LJH7868)				
Debeya Site	BS	TO		11	MBR	PO			8
Double Kill Hill (LJH7134)	AR	ECF		25	P	CH	EGB	112	3
(LJH7134)					PN(SLW8610)	PO	LY	468	38
FL	BS	LC	621	11	RC	AR	EGB	112	13
Foster Gulch #2 (LJH7153)	AR	ECF		9	RR1(SLW8630)	BS	EGB	150	21
(LJH7153)					RR2(SLW8412)	BS	EGB	7	10
FUCS1	BS	CF		3	RR4	BS	EGB	87	3
GER	BS	LGB		4	RR5	BS	MGB	235	5

Appendix A1 (continued)

Locality	Env	NALMA	Meter	Richness	Locality	Env	NALMA	Meter	Richness
S	BS	EGB	100	9	SLW8925	BS	LC	621	18
Scorpion Hollow (LJH7650,KJ83100)	AR	FU		9	SLW9140 (WCS7)	BS	EGB	112	3
Serendipity Summit (LJH72128)	AR	TO		15	SLW9141 (WCS7)	BS	EGB	112	8
Silver Tip (LJH7866)	AR	TI		8	SLW9142 (WCS7)	BS	EGB	112	6
SL	BS	LC	621	3	SLW9143 (same bed as YPM98)	BS	EGB	180	10
SLW826	BS	CF	-35	20	SLW9144 (same bed as YPM98)	BS	EGB	180	6
(SLW8631,SLW873,SLW824,SLW825)					SLW9145 (same bed as YPM98)	BS	EGB	180	10
SLW841	BS	EGB	145	5	South of Airport (LJH7835)	CH	TI		3
SLW847 (low-in-Tw)	AR	EGB	50	9	T	BS	LC	740	10
SLW867	BS	LCF		5	T2	BS	LC	740	5
SLW868	BS	LCF		11	TAT79	BS	LC	740	13
SLW869	BS	LCF		3	Tatman Fm Squaw Buttes Princeton	OT	LC		4
SLW882	PO	LGB	420	16	TL	BS	LC	621	15
SLW893	BS	LC	621	10	Tuffaceous Lake Beds Princeton	OT	LC		31
SLW894	BS	LC	621	9	USGS6177	BS	EGB		4
SLW898	BS	LC	621	14	UU	AR	EGB	112	7
SLW8410	BS	EGB	7	5	VS1 (SLW822)	BS	EGB	20	12
SLW8611	BS	LCF		4	WCS6	BS	EGB	96	9
SLW8612	BS	LCF		4	WCS8-1	BS	EGB	124	9
SLW8614	BS	LCF		4	WCS8-2	BS	EGB	124	6
SLW8822F	BS	LC	621	12	WHBG	BS	LC	706	10
SLW8822L	BS	LC	621	20	WhBgL	BS	LC	706	5
SLW8828	BS	LC	621	5	YPM67	PO	LGB	420	3
SLW8830	BS	EGB	112	7	YPM98	BS	EGB	180	9
(WCS7level)					YPM281	BS	MGB	353	5
SLW8910	BS	LC	621	11	YPM281-1	BS	MGB	353	3
SLW8911	BS	LC	621	14	YPM281-3	BS	MGB	353	2
SLW8912	BS	LC	621	15	YPM320	PO	LGB	429	6
SLW8914	BS	LC	621	18					
SLW8915	BS	LC	621	12					
SLW8917	BS	LC	621	10					
SLW8919	BS	LC	621	8					

Appendix A2

Alphabetical index of 244 Bighorn Basin plant taxa. Taxa with informal names such as those beginning with "unid" or "dicot" are undescribed and presumed to be new species

1	<i>Acer silberlingii</i>	11	<i>Betula stevensonii</i>	21	<i>Cissus marginata</i>
2	<i>Aleurites glandulosa</i>	12	Betulaceae sp. 1	22	<i>Cnemidaria magna</i>
3	Alismataceae sp. 1	13	Betulaceous leaf	23	<i>Cocculus flabella</i>
4	<i>Allantoidiopsis erosa</i>	14	Bryophyte sp. 1	24	<i>Cornus hyperborea</i>
5	<i>Alnus</i> sp. 1	15	<i>Calycites polysepala</i>	25	<i>Cornus nebrascensis</i>
6	<i>Ampelopsis acerifolia</i>	16	<i>Canavalia diuturna</i>	26	<i>Corylus insignis</i>
7	Apocynaceae sp. 1	17	<i>Carya antiquorum</i>	27	<i>Crataegus</i> sp. 1
8	<i>Asplenium coligniticum</i>	18	<i>Cercidiphyllum genatrix</i>	28	<i>Dalbergia</i> sp. 1
9	<i>Averrhoites affinis</i>	19	<i>Cinnamomum sezannense</i>	29	<i>Debeysa</i> sp. 1
10	<i>Azolla</i> sp. 1	20	<i>Cissites rocklandensis</i>	30	<i>Dennstaedia americana</i>

Appendix A2 (continued)

31	<i>Dicotylophyllum anomalum</i>	86	<i>Paleonelumbo macroloba</i>	141	dicot XV
32	<i>Dicotylophyllum mercerensis</i>	87	<i>Paranymphaea crassifolia</i>	142	dicot XVI
33	<i>Dombeya novi-mundi</i>	88	<i>Paraternstroemia hypophenosa</i>	143	dicot XVII
34	<i>Drimys</i> sp. 1	89	<i>Penosphyllum cordatum</i>	144	dicot XX
35	<i>Equisetum</i> sp. 1	90	<i>Persites argutus</i>	145	dicot XXI
36	<i>Eucommia serrata</i>	91	<i>Phoebe</i> sp. 1	146	dicot XXII
37	<i>Eugenia americana</i>	92	<i>Platanus brownii</i>	147	dicot XXIII
38	<i>Ficus artocarpoides</i>	93	<i>Platanus gracilis</i>	148	dicot XXIV
39	<i>Ficus planicostata</i>	94	<i>Platanus guillelmae</i>	149	dicot XXV
40	Flacourtiaceae sp. 1	95	<i>Platanus raynoldsii</i>	150	dicot XXVI
41	Flacourtiaceae sp. 3	96	<i>Platanus wyomingensis</i>	151	dicot XXVII
42	<i>Foekenia catenulata</i>	97	<i>Platycarya castaneopsis</i>	152	dicot XXVIII
43	<i>Fraxinus eocenica</i>	98	<i>Populus meigsii</i>	153	dicot XXX
44	<i>Ginkgo adiantoides</i>	99	<i>Populus nebraskana</i>	154	dicot XXXI
45	<i>Glyptostrobus europaeus</i>	100	<i>Populus wyomingiana</i>	155	dicot XXXII
46	Hamamelidaceae sp. 1	101	<i>Potosia verrucosa</i>	156	dicot XXXIV
47	Hymenophyllaceae sp. 1	102	<i>Potamogeton</i> sp. 1	157	dicot XXXIX
48	<i>Isoetes horridus</i>	103	<i>Potamogeton</i> sp. 2	158	dicot XXXV
49	Juglandaceae sp. 2	104	<i>Proteaciphyllum minutum</i>	159	dicot XXXVI
50	LJH n.sp. IIIa	105	<i>Pterocarya glabra</i>	160	dicot XXXVII
51	LJH n.sp. IV	106	<i>Quercus greenlandica</i>	161	dicot XXXVIII
52	LJH n.sp. IVa	107	<i>Quereuxia angulata</i>	162	okra sp. 1
53	LJH n.sp. VII	108	<i>Rhamnus cleburni</i>	163	palm sp. 1
54	LJH n.sp. X	109	<i>Salvinia preauriculata</i>	164	rhamnophyll sp. 1
55	LJH n.sp. XIV	110	<i>Sassafras thermale</i>	165	sapindaceous samara
56	LJH n.sp. XIX	111	<i>Schloepfia republicensis</i>	166	sapindaceous samara-sp. 2
57	LJH n.sp. XV	112	<i>Spirodela magna</i>	167	tatman fern
58	LJH n.sp. XVII	113	<i>Stillingia casca</i>	168	tiny winged seeds cf. <i>Cercidiphyllum</i>
59	LJH n.sp. XVIII	114	<i>Taxodium obrikii</i>		
60	LJH n.sp. XX	115	<i>Ternstroemites aureavallis</i>	169	unid sp6723-1
61	LJH n.sp. XXI	116	<i>Ternstroemites</i> n.sp. 1	170	unid sp6723-2
62	LJH n.sp. XXIX	117	<i>Thelypteris iddingsii</i>	171	unid sp6723-3
63	LJH n.sp. XXX	118	<i>Thuites interruptus</i>	172	unid sp7871-1
64	LJH n.sp. XXXI	119	<i>Typha</i> sp. 1	173	unid sp822-2
65	LJH magnolia sp. 1	120	<i>Ulmus microphylla</i>	174	unid sp822-3
66	LJH magnolia sp. 2	121	<i>Viburnum antiquum</i>	175	unid sp822-4
67	Legume phyllode?	122	<i>Viburnum asperum</i>	176	unid sp826-1
68	Leguminosae sp. 1	123	<i>Viburnum cupanioides</i>	177	unid sp826-2
69	Leguminosae sp. 2	124	<i>Vitis stantoni</i>	178	unid sp826-3
70	Leguminosae sp. 3	125	<i>Woodwardia gravida</i>	179	unid sp826-4
71	<i>Lygodium kaulfussii</i>	126	<i>Zamia coloradensis</i>	180	unid sp826-5
72	<i>Magnolia borealis</i>	127	<i>Zingiberopsis isonervosa</i>	181	unid sp8412-1
73	<i>Magnolia magnifica</i>	128	dicot I	182	unid sp847-1
74	Magnoliales sp. 1	129	dicot III	183	unid sp847-2
75	<i>Meliosma flexuosa</i>	130	dicot IV	184	unid sp8610-1
76	<i>Meliosma longifolia</i>	131	dicot V	185	unid sp8610-2
77	Menispermaceae sp. 1	132	dicot VI	186	unid sp8610-3
78	<i>Menispermites parvareolatus</i>	133	dicot VII	187	unid sp8610-4
79	<i>Metasequoia occidentalis</i>	134	dicot VIII	188	unid sp8614-1
80	Monocot III	135	dicot X	189	unid sp8614-2
81	Monocot leaf 2	136	dicot XI	190	unid sp8614-3
82	<i>Musophyllum complicatum</i>	137	dicot XII	191	unid sp8630-1
83	<i>Nelumbo</i> sp. 1	138	dicot XIII	192	unid sp8630-2
84	<i>Nyssa alata</i>	139	dicot XIV	193	unid sp8630-3
85	<i>Onoclea hesperia</i>	140	dicot XIX	194	unid sp8630-4

Appendix A2 (continued)

195	unid sp867-1	212	unid sp882-5	229	unid sp8915-4
196	unid sp868-1	213	unid sp882-6	230	unid sp8915-5
197	unid sp868-2	214	unid sp882-7	231	unid sp8925-1
198	unid sp868-3	215	unid sp882-8	232	unid sp8925-3
199	unid sp868-4	216	unid sp882-9	233	unid sp8925-4
200	unid sp869-1	217	unid sp8822-3	234	unid sp893-2
201	unid sp873-1	218	unid sp8822-8	235	unid sp893-3
202	unid sp873-2	219	unid sp8822-9	236	unid sp894-1
203	unid sp879-1	220	unid sp8910-1	237	unid sp898-3
204	unid sp879-2	221	unid sp8910-2	238	unid sp905-10
205	unid sp879-3	222	unid sp8910-3	239	unid sp905-2
206	unid sp879-4	223	unid sp8911-1	240	unid sp905-5
207	unid sp882-1	224	unid sp8911-4	241	unid sp905-8
208	unid sp882-10	225	unid sp8912-2	242	unid sp905-9
209	unid sp882-2	226	unid sp8914-8	243	unid sp906-1
210	unid sp882-3	227	unid sp8914-9	244	unid sp907-1
211	unid sp882-4	228	unid sp8915-3		

Appendix A3

Complete set of 131 Bighorn Basin floral lists, with species names replaced by index numbers taken from Appendix 2

Bs	5 9 35 45 78 127 163
Cn1	4 5 9 35 45 46 71 90 127
Hs1 Unit 9	4 5 9 22 35 45 71 78 91 127 163
Br1.5	5 6 9 35 45 46 49 76 78 95 98 127 144
Hs1 Unit 8	5 9 15 35 45 46 109 127
DCF	5 18 33 46 49 78 79 91 120 147 165
H	3 10 12 18 41 44 49 68 78 92 93 94 95 98 109 112 127 133 140 142 143 163
FL	4 5 7 22 33 35 45 97 117 129 149
TL	4 5 7 9 18 33 35 71 93 97 127 129 138 159 163
CQ1	5 16 22 28 33 45 71 97 111 127 128 129 135 136 137 146 152 159 167
CQ2	5 22 33 45 71 97 129 136 137
CQ3	5 33 45 71 97 117 129 136 149
CQA	5 16 33 45 71 97 129 136
BCT	4 5 9 22 33 71 97 117 128 129 167
WHBG	4 5 7 9 22 33 71 97 117 135
TAT79	3 5 22 33 35 97 98 109 119 127 128 163 228
FUCSI	5 46 79
LW	22 79 90 144
RR2 (SLW8412)	15 17 18 45 79 163 178 180 181 201
LHE	9 89 106
USGS6177	35 76 79 90
RR4	46 78 163
GER	76 78 79 127
WCS6	4 5 9 22 45 46 120 127 163
S	3 5 45 46 78 79 109 120 165
P	93 95 98
ChII	4 5 9 35 45 119 127 163
BR	4 5 6 9 12 18 35 45 46 49 76 78 93 95 98 119 127 132 144 163
BRII	4 5 6 9 45 46 49 76 78 93 95 98 109 127 132 144
UU	5 9 45 49 91 125 127
HsII	5 9 35 45 49
RC	9 12 45 46 78 93 95 98 130 132 145 150

Appendix A3 (continued)

WCS8-1	4 5 18 45 46 49 93 95 98
WCS8-2	5 18 45 46 78 127
RR1 (SLW8630)	4 5 6 18 40 45 46 49 77 78 79 91 120 131 148 165 191 192 193 194 200
YPM98	5 9 17 45 46 78 79 98 163
RR5	49 79 109 119 127
LB	3 9 12 18 33 35 44 45 46 49 76 78 91 93 95 98 109 127 132 141 144 165
DCI	5 9 18 33 35 45 78 109 119 127 163
YPM281	4 5 33 79 143
YPM281-1	4 5 79
YPM281-3	4 79
YPM320	9 18 78 94 109 127
YPM67	44 68 94
MBR	4 28 41 97 109 119 127 163
A	28 93 94 129 163
M	4 22 28
SL	35 97 163
15ME	4 16 71 97 127 129 136
15M	5 97
T	4 5 18 33 35 71 97 127 129 163
Brosh	18 93
AL	93 95
B	3 22 71 97 117
WhBgL	5 97 128 129 135
BCT2	4 5 22 97 117 129
BCT3	149 167
BCT4	5 71 119 129 167
T2	3 33 71 97 127
SLW893	4 5 33 129 149 152 153 159 234 235
SLW894	4 5 33 71 97 129 149 234 236
SLW898	5 16 33 45 71 97 129 135 137 152 158 159 237
SLW8910	5 22 33 45 71 97 129 135 220 221 222
SLW8911	5 16 22 33 45 71 97 129 135 149 156 167 223 224
SLW8912	5 33 45 71 97 109 111 129 135 136 149 152 153 159 167
SLW8914	5 22 33 45 47 71 97 129 135 136 149 152 154 155 167 225 226 227
SLW8915	5 16 33 71 97 109 125 149 152 228 229 230
SLW8917	5 33 45 71 97 117 129 135 136 154
SLW8919	4 33 45 71 117 129 154 159
SLW8822F	4 5 33 45 71 97 129 135 136 151 159 217
SLW8822L	2 5 8 16 33 45 97 100 109 117 129 135 136 149 151 157 160 161 218 219
SLW8925	5 22 28 33 45 71 97 104 129 135 136 137 149 154 159 231 232 233
SLW8828	33 37 97 129 152
SLW882	12 28 41 49 68 94 207 208 209 210 211 212 213 214 215 216
SLW8830 (WCS7level)	5 9 35 45 119 125 127
SLW841	9 18 44 119 127
SLW847 (low-in-Tw)	20 39 78 93 95 106 118 182 183
SLW8410	5 35 79 109 120
SLW867	6 45 78 163 195
SLW868	4 9 18 45 90 98 101 196 197 198 199
SLW869	4 13 200
SLW8611	4 9 13 200
SLW8612	17 44 46 79
SLW8614	4 6 13 45 90 188 189 190 200
SLW826 (SLW8631, SLW873, lateral-to- SLW824, SLW825)	5 17 18 45 46 49 78 79 91 98 125 149 163 176 177 179 180 200 201 202

Appendix A3 (continued)

SLW9140 (WCS7)	9 35 45
SLW9141 (WCS7)	4 5 9 17 35 45 119 127
SLW9142 (WCS7)	4 9 22 35 45 127
SLW9143 (same bed as YPM98)	4 5 9 17 45 46 79 119 125 163
SLW9144 (same bed as YPM98)	4 18 45 46 78 98
SLW9145 (same bed as YPM98)	5 17 18 45 46 78 79 98 125 176
Tatman Fm Squaw Buttes Princeton	37 71 96 117
LJH6721a	6 9 15 18 35 36 45 56 79 82 86 90 101 123 127 163
LJH6723	1 6 11 17 18 26 30 35 43 49 79 93 98 121 122 169 170 171
LJH6854	1 30 43
LJH72141	17 18 35 43 44 45 48 76 79 84 101 127
LJH7627	1 6 18 19 32 45 65 73 79 90 93 95 110 121 127 164
LJH7634	4 17 18 35 38 45 54 62 65 66 76 86 93 95 123 162
LJH7635	1 11 18 45 79
LJH7834	6 17 18 25 26 32 36 50 52 57 64 65 73 79 84 90 95 110 120 121
LJH7871 (SLWM216)	6 17 18 32 45 46 79 90 110 120 172 200
LJH7873	19 52 54 90
Hunt Creek 2 (KJ84a)	6 18 36 79 95 114 124
Bobcat Pass 2	18 39 44 79 95 124
Kirk Valley 1 (KJ83101, KJ8415)	6 18 23 36 38 44 45 79 85 87 95 99 122
Bobcat Pass 3 (LJH7652)	17 39 79 83 114
Debeya Site	18 29 38 44 45 63 64 79 87 95 114
Ginkgo Site	3 18 29 44 61 79 95
Mantua Lentil (LJH7868)	6 18 38 58 59 95 124
Hunters Creek 1 (LJH7675)	18 35 36 38 42 45 95 108 114 124
Bird Track Sand (KJ83102)	18 35 108
Bugger to get to (Cedar Mtn.)	3 17 18 36 45 95 99 163
Scorpion Hollow (LJH7650, KJ83100)	6 17 18 21 30 31 36 79 114
LJH72123	18 95 110 121
Chance Loc (LJH7132)	6 18 44 45 55 73 75 79 95 101 122
Horse Valley 1 (LJH72121)	18 27 36 45 101 121 122 123
Horse Valley 2 (LJH72122)	18 36 45 72 75 79 81 84 95 101 122
Black Widow Gulch (LJH72127)	6 17 18 27 44 45 79 121 122 123
South of Airport (LJH7835)	6 18 26
Silver Tip (LJH7866)	6 17 18 45 51 75 84 101
Belfry Road Cut (LJH7654)	6 18 43 95 105 120 121 122
LJH6721b	6 9 15 17 18 35 36 45 56 79 90 110 122 126
LJH72116	4 9 15 17 24 35 38 45 90 107 115 120 122 123 127 163
Foster Gulch 2 (LJH7153)	9 45 79 81 90 115 122 123 163
LJH7143	1 9 11 17 18 73 79 81 84 122
Damn Boulder Site (LJH72103)	1 4 6 17 18 38 45 79 90 101 115 122
Double Kill Hill (LJH7134)	4 6 9 17 18 24 25 45 49 60 79 87 88 89 90 101 105 107 113 115 116 120 122 123 163
LJH72126	11 18 35 45 79 95
Serendipity Summit (LJH72128)	6 17 18 19 25 34 36 53 55 59 72 74 101 123
PN(SLW8610)	10 14 28 41 67 69 70 80 93 94 96 98 100 103 109 112 117 127 134 139 163 166 168 184 185 186 187 203 204 205 206 238 239 240 241 242 243 244
VS1(SLW822)	4 5 24 45 46 79 91 102 148 173 174 175

Appendix A4

Alphabetical index of 234 Northern Rocky Mountains mammalian genera

1	<i>Absarokius</i>	4	<i>Acritoparamys</i>	7	<i>Aletodon</i>	10	<i>Ambloctonus</i>
2	<i>Acarictis</i>	5	<i>Adunator</i>	8	<i>Alveojunctus</i>	11	<i>Anacodon</i>
3	<i>Acmeodon</i>	6	<i>Ageina</i>	9	<i>Amarammus</i>	12	<i>Anconodon</i>

Appendix A4 (continued)

13	<i>Anemorhysis</i>	69	<i>Ectoganus</i>	125	<i>Microsyops</i>	181	<i>Procerberus</i>
14	<i>Anisonchus</i>	70	<i>Ectypodus</i>	126	<i>Mimatuta</i>	182	<i>Prochetodon</i>
15	<i>Antiacodon</i>	71	<i>Elphidotarsius</i>	127	<i>Mimetodon</i>	183	<i>Prodiacodon</i>
16	<i>Apatemys</i>	72	<i>Elpidophorus</i>	128	<i>Mimoperadectes</i>	184	<i>Prolimmocyon</i>
17	<i>Apheliscus</i>	73	<i>Eoconodon</i>	129	<i>Mimotricentes</i>	185	<i>Promioclaenus</i>
18	<i>Aphronorus</i>	74	<i>Eolestes</i>	130	<i>Mixodectes</i>	186	<i>Prorothodectes</i>
19	<i>Arctocyon</i>	75	<i>Eoryctes</i>	131	<i>Myrmecoboides</i>	187	<i>Propalaeomodon</i>
20	<i>Arctodontomys</i>	76	<i>Eotitanops</i>	132	<i>Mytonomys</i>	188	<i>Propalaeosinopa</i>
21	<i>Arctostylops</i>	77	<i>Esthonyx</i>	133	<i>Nannodectes</i>	189	<i>Protentomodon</i>
22	<i>Arfia</i>	78	<i>Eucosmodon</i>	134	<i>Navajovius</i>	190	<i>Prothryptacodon</i>
23	<i>Armintodelphys</i>	79	<i>Eudaemonema</i>	135	<i>Neoliotomus</i>	191	<i>Protictis</i>
24	<i>Armintomys</i>	80	<i>Franimys</i>	136	<i>Neoplagiaulax</i>	192	<i>Protoselele</i>
25	<i>Asiabradypus</i>	81	<i>Galecyon</i>	137	<i>Niptomomys</i>	193	<i>Prototomus</i>
26	<i>Avunculus</i>	82	<i>Gelastops</i>	138	<i>Notharctus</i>	194	<i>Protungulatum</i>
27	<i>Azygonyx</i>	83	<i>Goniacodon</i>	139	<i>Nyctitherium</i>	195	<i>Psittacotherium</i>
28	<i>Baiocoonodon</i>	84	<i>Hapalodectes</i>	140	<i>Oodectes</i>	196	<i>Ptilodus</i>
29	<i>Baiotomeus</i>	85	<i>Haplaletes</i>	141	<i>Orohippus</i>	197	<i>Purgatorius</i>
30	<i>Bathyopsis</i>	86	<i>Haplomylys</i>	142	<i>Oxyacodon</i>	198	<i>Raphictis</i>
31	<i>Bisonalveus</i>	87	<i>Helaletes</i>	143	<i>Oxyaena</i>	199	<i>Reithroparamys</i>
32	<i>Bryanictis</i>	88	<i>Heptodon</i>	144	<i>Oxycloenus</i>	200	<i>Rigby pantolestid</i>
33	<i>Bunophorus</i>	89	<i>Hexacodus</i>	145	<i>Oxyprimus</i>	201	<i>Scenopagus</i>
34	<i>Caenolambda</i>	90	<i>Homogalax</i>	146	<i>Pachyaena</i>	202	<i>Shoshonius</i>
35	<i>Cantius</i>	91	<i>Huerfanodon</i>	147	<i>Pagonomus</i>	203	<i>Simpsonictis</i>
36	<i>Carcinodon</i>	92	<i>Hyopsodus</i>	148	<i>Palaeamodon</i>	204	<i>Spanoxyodon</i>
37	<i>Cardiolphus</i>	93	<i>Hyracotherium</i>	149	<i>Palaechthon</i>	205	<i>Steimius</i>
38	<i>Carpodaptus</i>	94	<i>Icaronycteris</i>	150	<i>Palaeictops</i>	206	<i>Stelocyon</i>
39	<i>Carpolestes</i>	95	<i>Ictidopappus</i>	151	<i>Palaeonictis</i>	207	<i>Stilpnodon</i>
40	<i>Catopsalis</i>	96	<i>Ignacius</i>	152	<i>Palaeoryctes</i>	208	<i>Stygimys</i>
41	<i>Cedrocherus</i>	97	<i>Jepsenella</i>	153	<i>Palaeosinopa</i>	209	<i>Stylinodon</i>
42	<i>Centetodon</i>	98	<i>Knightomys</i>	154	<i>Palenochtha</i>	210	<i>Talpavoides</i>
43	<i>Ceutholestes</i>	99	<i>Labidolemur</i>	155	<i>Paleotomus</i>	211	<i>Talpavus</i>
44	<i>Chalicomomys</i>	100	<i>Lambdotherium</i>	156	<i>Pantolambda</i>	212	<i>Teilhardina</i>
45	<i>Chiromyoides</i>	101	<i>Lampadophorus</i>	157	<i>Paramys</i>	213	<i>Tetonius</i>
46	<i>Chriacus</i>	102	<i>Leipsanolestes</i>	158	<i>Pararyctes</i>	214	<i>Tetraclaenodon</i>
47	<i>Cimexomys</i>	103	<i>Leptacodon</i>	159	<i>Parectypodus</i>	215	<i>Thusbemys</i>
48	<i>Cimolestes</i>	104	<i>Leptonysson</i>	160	<i>Paromomys</i>	216	<i>Thryptacodon</i>
49	<i>Colpoclaenus</i>	105	<i>Leptotomus</i>	161	<i>Pauromys</i>	217	<i>Thylacodon</i>
50	<i>Conoryctes</i>	106	<i>Limaconyssus</i>	162	<i>Pentacodon</i>	218	<i>Tinimomys</i>
51	<i>Copecion</i>	107	<i>Litales</i>	163	<i>Pentacosmodon</i>	219	<i>Titanoides</i>
52	<i>Copelemur</i>	108	<i>Litocherus</i>	164	<i>Peradectes</i>	220	<i>Torrejonia</i>
53	<i>Coriphagus</i>	109	<i>Litolestes</i>	165	<i>Peratherium</i>	221	<i>Tritemnodon</i>
54	<i>Coryphodon</i>	110	<i>Litomylys</i>	166	<i>Periptychus</i>	222	<i>Tubulodon</i>
55	<i>Cyriacotherium</i>	111	<i>Lophiparamys</i>	167	<i>Phenacodaptus</i>	223	<i>Tytthaena</i>
56	<i>Deuteronogonodon</i>	112	<i>Loveina</i>	168	<i>Phenacodus</i>	224	<i>Uintacyon</i>
57	<i>Diacocherus</i>	113	<i>Loxolophus</i>	169	<i>Phenacolemur</i>	225	<i>Uintasorex</i>
58	<i>Diacodexis</i>	114	<i>Macrocranium</i>	170	<i>Picrodus</i>	226	<i>Unuchinia</i>
59	<i>Diacodon</i>	115	<i>Maiorana</i>	171	<i>Plagiocitenodon</i>	227	<i>Vassacyon</i>
60	<i>Didelphodus</i>	116	<i>Mattimys</i>	172	<i>Plagiocitenoides</i>	228	<i>Viverravus</i>
61	<i>Didymictis</i>	117	<i>Megadelphys</i>	173	<i>Plagiomene</i>	229	<i>Vulpavus</i>
62	<i>Dipassalus</i>	118	<i>Megalesthonyx</i>	174	<i>Planetetherium</i>	230	<i>Washakius</i>
63	<i>Dipsalidictis</i>	119	<i>Meutsotherium</i>	175	<i>Plesiadapis</i>	231	<i>Worlandia</i>
64	<i>Dipsalodon</i>	120	<i>Mesodna</i>	176	<i>Plesiolestes</i>	232	<i>Wyonycteris</i>
65	<i>Dissacus</i>	121	<i>Miacis</i>	177	<i>Pontifactor</i>	233	<i>Xenicolhippus</i>
66	<i>Dorraletes</i>	122	<i>Microcosmodon</i>	178	<i>Premuoides</i>	234	<i>Zanycteris</i>
67	<i>Earendil</i>	123	<i>Micromomys</i>	179	<i>Princetonia</i>		
68	<i>Ectocion</i>	124	<i>Microparamys</i>	180	<i>Probathyopsis</i>		

Appendix A5

Complete set of 301 northern Rocky Mountains mammalian faunal lists, with genus names replaced by index numbers taken from Appendix 4. Lists are grouped by Land-Mammal Age and alphabetized, except for Wasatchian lists from the Schankler-Wing section, which are grouped separately and arranged stratigraphically

Puercan

Mantua [Russell, 1967]	28 40 47 67 73 115 120 126 142 145 181 208 217
Simpson Quarry [Hartman et al., 1989]	14 28 36 40 47 48 70 110 113 120 136 142 144 145 159 181 194 197 208
UW V-82007 [Hartman, 1986]	29 145
UW V-82010 [Hartman, 1986]	120 164

Torrejonian

Gidley Quarry [Rose, 1981]	5 12 14 18 19 26 29 32 46 50 53 65 70 71 79 82 85 95 97 103 104 107 110 120 127 129 131 136 149 154 156 159 160 170 183 185 186 188 190 191 196 203 204 207 208 214
Lower Lebo Loc. 73 [Simpson, 1937]	19 129 214
Rock Bench Quarry [Rose, 1981]	5 12 14 18 19 29 32 40 46 53 59 65 70 71 79 82 83 85 91 96 97 103 107 110 120 127 129 131 150 154 156 160 170 176 178 185 186 191 196 203 208 214 226
Silberling Quarry [Simpson, 1937]	12 18 29 32 46 50 53 65 72 79 82 129 149 159 160 170 185 188 190 191 195 196 208 214

Upper Lebo Loc. 5 and 6 [Simpson, 1937]

Upper Lebo Loc. 24 [Simpson, 1937]	14 32 46
Upper Lebo Loc. 25 [Simpson, 1937]	14 46 56 208 214
Upper Lebo Loc. 50 [Simpson, 1937]	12 14 46 196
Upper Lebo Loc. 51 [Simpson, 1937]	14 46 107 129 185 191 196 208 214
Upper Lebo Loc. 81 [Simpson, 1937]	18 46 129 190 191
UW V-81056 [Hartman, 1986]	3 12 18 32 85 107 120 136 149 185 186 191 196
UW V-81061 [Hartman, 1986]	14 18 32 46 110 129 183 185 191 196 200 214
UW V-82004 [Hartman, 1986]	3 5 12 14 18 19 32 46 53 70 82 85 97 107 108 110 127 129 136 149 154 170 183 185 186 188 190 191 196 214

UW V-82005 [Hartman, 1986]	3 18 32 185 196
UW V-82006 [Hartman, 1986]	32 107 129 136 183 188 190
UW V-82008 [Hartman, 1986]	12 18 32 196
UW V-82022 [Hartman, 1986]	14 18 185
UW V-82039 [Hartman, 1986]	26 107 110 136 160 196
UW V-82040 [Hartman, 1986]	32 46 53 79 85 149 160 183 188 196
UW V-82045 [Hartman, 1986]	3 14 18 32 46 79 82 107 136 149 160 183 185 186 196

Tiffanian

Bangtail [Gingerich et al., 1983]	18 70 103 131 133 149 170 176
Cedar Point Quarry [Rose, 1981]	7 19 31 34 38 41 46 57 65 68 70 72 96 99 103 108 129 131 136 152 164 168 170 175 188 191 196 198 216 219 223
Cub Creek/Hunt Creek PU Section 29 [Butler et al., 1987]	18 206
Cub Creek 3 [Butler et al., 1987]	18 46
Douglass Quarry [Krause and Maas, 1990]	3 12 19 31 46 49 65 68 71 72 96 103 110 120 122 127 129 131 133 136 155 164 168 170 175 183 188 191 196 203 216 219 168 175
Eagle Quarry [Butler et al., 1987]	39 57 103 109 150 163 164 175 187 191 216
Jepsen Valley Quarry [Schaff, 1985]	5 38 51 61 68 70 72 96 103 108 110 129 130 136 160 168 175 183 185 188 192 216 234
Love Quarry [McKenna, 1980]	18 39 46 68 70 96 99 110 120 122 129 164 167 168 175 182 196 201 211
Malcolm's Locality [Krishtalka et al., 1975]	19 68 72 160 175 214 216
Melville Locality [Simpson, 1937]	3 12 14 18 31 46 68 85 110 133 136 149 164 170 188 196
Newell's Nook (USGS D-2003) [Robinson and Honey, 1987]	11 16 32 38 61 66 70 72 96 103 108 127 133 134 136 139 147 153 164 169 170 175 188 189 191 196 197 201 211 216 219
Olive Locality [Wolberg, 1979]	19 39 57 65 68 70 103 109 122 123 127 135 136 150 152 159 163 164 165 167 168 169 175 179 182 183 187 191 216 226
Princeton Quarry [Rose, 1981]	

Appendix A5 (continued)

Princeton Locs. (Miscellaneous) [Simpson, 1937]	14 68
Scarritt Quarry [Krause and Maas, 1990]	19 38 46 65 70 72 96 103 108 120 133 136 153 155 158 175 188 191 196 216 219 226
Shotgun [Gunnell, 1989]	11 12 14 18 19 38 40 46 49 59 68 70 71 72 78 82 96 110 120 127 133 136 149 154 156 159 160 162 164 166 170 175 176 185 220
UW V-81047 [Hartman, 1986]	3 18 82 185 196
UW V-81054 [Hartman, 1986]	3 12 18 107 175 185 190 196
UW V-82015 [Hartman, 1986]	3 12 18 32 85 133 136 175 185 188
UW V-82021 [Hartman, 1986]	3 18 110 133 175 185
UW V-82026 [Hartman, 1986]	3 18 85 110 196
Clarkforkian	
Bear Creek [Rose, 1981]	4 18 39 45 65 86 99 101 102 153 164 167 168 169 174 175 189 216 228
Cleopatra Reservoir [Rose, 1981]	39 54 61 68 153 168 175
Discovery Site [Gingerich, 1987]	39 70 94 103 106 164 171 218 228 231 232
Foster Gulch Oil Well No. 1 [Rose, 1981]	54 68 101 157 168 216
Holly's Microsite [Krause, 1986]	4 21 39 54 57 61 63 68 70 86 96 99 102 103 122 124 137 152 164 168 169 171 175 183 199 216 218 224 228 231
Paint Creek [Krause, 1986]	7 17 20 39 45 57 61 65 68 70 99 122 148 159 168 169 171 175 177 179 180 216
Ries [Rose, 1981]	54 68 101 180
SC-8 [Rose, 1981]	27 54 61 68 168 180
SC-9 [Rose, 1981]	68 168
SC-10 [Rose, 1981]	17 20 27 68 86 125 168 228
SC-11 [Rose, 1981]	54 61 68 168
SC-19 [Rose, 1981]	21 27 39 46 54 61 63 65 68 86 164 168 169 175 180 228
SC-20 [Rose, 1981]	27 54 63 68 169 175 180
SC-21 [Rose, 1981]	7 54 61 68 168
SC-22 [Rose, 1981]	27 54 65 68 86 168 180 224
SC-23 [Rose, 1981]	61 63 68 86 137 168 228 231
SC-24 [Rose, 1981]	17 27 61 65 68 86 168 169 216 228
SC-25 [Rose, 1981]	27 61 68 168
SC-28 [Rose, 1981]	68 168 224
SC-48 [Rose, 1981]	17 61 68 151 168 169 173 180 183 224
SC-49 [Rose, 1981]	54 68 168
SC-50 [Rose, 1981]	4 57 61 63 68 153 168 169 175 180 228
SC-52 [Rose, 1981]	61 68 86 168 169 179 216 228
SC-53 [Rose, 1981]	39 54 61 63 68 86 168 175
SC-55 [Rose, 1981]	7 27 54 68 151 168 173 180
SC-57 [Rose, 1981]	54 61 68 92 168 180 224 228
SC-58 [Rose, 1981]	54 61 68 168 175 180
SC-59 [Rose, 1981]	61 68 168
SC-61 [Rose, 1981]	175 216
SC-62 [Rose, 1981]	27 43 54 55 61 63 64 68 103 168 169 175
SC-65 [Rose, 1981]	68 86 168 169 175
SC-66 [Rose, 1981]	45 54 61 65 68 168 180
SC-70 [Rose, 1981]	7 17 63 65 68 86 180 228
SC-71 [Rose, 1981]	20 68 168
SC-72 [Rose, 1981]	7 17 27 61 63 68 86 168 175
SC-74 [Rose, 1981]	4 7 17 20 27 61 63 64 65 68 168 169 175 179 180 223
SC-75 [Rose, 1981]	61 68 168
SC-76 [Rose, 1981]	7 68
SC-77 [Rose, 1981]	65 68 86 137
SC-78 [Rose, 1981]	68 180
SC-80 [Rose, 1981]	27 61 65 68 168
SC-81 [Rose, 1981]	27 54 61 65 68 86 103 128 168 169 175 216 228

Appendix A5 (continued)

SC-82 [Rose, 1981]	57 68 168
SC-83 [Rose, 1981]	27 54 61 68 135
SC-84 [Rose, 1981]	54 61 68 168 216
SC-90 Granger Mountain [Rose, 1981]	7 17 27 61 63 68 86 168 169 173 216 224
SC-91 [Rose, 1981]	27 61 68
SC-92 [Rose, 1981]	17 68 168 175 180
SC-93 [Rose, 1981]	68 168
SC-99 [Rose, 1981]	54 68 86 148 168 169
SC-100 [Rose, 1981]	61 168 180 231
SC-101 [Rose, 1981]	68 168
SC-102 [Rose, 1981]	27 68 86 101 168 175
SC-105 [Rose, 1981]	4 54 65 68 168
SC-107 [Rose, 1981]	68 168 228
SC-108 [Rose, 1981]	4 7 17 54 68 86 153 168
SC-109 [Rose, 1981]	27 54 61 65 68 99 101 168 169 216
SC-110 [Rose, 1981]	68 168
SC-115 [Rose, 1981]	54 61 63 68 70 168 175
SC-116 [Rose, 1981]	21 54 61 68 70 122 168 175
SC-117 [Rose, 1981]	27 54 57 61 63 68 102 122 164 168 175 216
SC-118 [Rose, 1981]	61 68
SC-119 Franimys Hill [Rose, 1981]	4 54 68 80 137 168 175 180
SC-120 [Rose, 1981]	54 61 63 68 70 96 168 175 180
SC-127 [Rose, 1981]	27 39 54 61 68 86 96 153 164 168 169 175 223 224
SC-134 [Rose, 1981]	65 68
SC-135 [Rose, 1981]	4 27 180
SC-136 [Rose, 1981]	7 17 27 45 46 54 61 63 68 86 101 152 153 168 169 175 179 183
SC-137 [Rose, 1981]	17 20 68 86 168
SC-138 [Rose, 1981]	27 68 168 169
SC-149 [Rose, 1981]	7 27 54 61 68 168
SC-150 [Rose, 1981]	27 54 65 68 168 224
SC-152 [Rose, 1981]	68 168
SC-153 [Rose, 1981]	4 7 27 54 61 68 86 92 151 168
SC-154 [Rose, 1981]	27 61 68 180 216
SC-155 [Rose, 1981]	7 17 27 46 61 68 86 180 228
SC-156 [Rose, 1981]	61 68 153 175 216
SC-157 [Rose, 1981]	68 168 180
SC-158 [Rose, 1981]	61 68 86
SC-159 [Rose, 1981]	4 20 27 55 61 68 86 125 168 169 180 216
SC-162 [Rose, 1981]	4 68 86 168
SC-163 [Rose, 1981]	27 61 68 153 168
SC-164 [Rose, 1981]	27 54 61 68 86 168 180
SC-166 [Rose, 1981]	54 68 175
SC-171 [Rose, 1981]	39 63 68 168 175 180
SC-173 [Rose, 1981]	61 68 86 168 175
SC-174 [Rose, 1981]	68 169 180
SC-175 [Rose, 1981]	54 61 68 168
SC-176 [Rose, 1981]	7 17 27 54 61 68 86 153 168 169 180
SC-177 [Rose, 1981]	68 168
SC-179 [Rose, 1981]	4 17 68 135 168 175 216 228
SC-183 [Rose, 1981]	27 68 86 168 216
SC-184 [Rose, 1981]	4 27 54 61 65 68 86 168 216
SC-189 [Rose, 1981]	27 54 63 65 68 168 175 224
SC-190 [Rose, 1981]	63 68 168
SC-195 Krause Quarry [Rose, 1981]	61 63 65 68 70 86 168 175 216 228
SC-196 Rough Gulch [Rose, 1981]	39 61 65 68 157 168 175 180
SC-197 [Rose, 1981]	4 27 54 61 68 86 168 169 228

Appendix A5 (continued)

SC-200 [Rose, 1981]	68 122 168 173
SC-201 [Rose, 1981]	4 27 61 68 168 169 175 224 228
SC-202 [Rose, 1981]	17 54 55 61 68 153 168 173
SC-203 [Rose, 1981]	7 17 21 54 61 68 86 168 169
SC-205 [Rose, 1981]	54 61 63
SC-208 [Rose, 1981]	68 168 180
SC-209 Phil's Hill [Rose, 1981]	4 168
SC-214 [Rose, 1981]	4 27 54 61 63 68 86 96 168 224 228
SC-215 [Rose, 1981]	68 168 180 228
SC-216 [Rose, 1981]	68 168
SC-217 [Rose, 1981]	68 168
SC-220 [Rose, 1981]	54 57 68 86 96 101 175
SC-222 [Rose, 1981]	68 168
SC-226 [Rose, 1981]	27 39 54 61 68 122 153 168 169 175 182
SC-230 [Rose, 1981]	27 61 68 168
SC-231 [Rose, 1981]	7 17 68 168
SC-233 [Rose, 1981]	61 64 68 148 168 180 224
SC-234 Rainbow Valley [Rose, 1981]	27 54 55 61 63 68 86 168 173 179 180 216
SC-235 [Rose, 1981]	61 68
SC-238 [Rose, 1981]	54 61 68 169
SC-248 [Rose, 1981]	61 168 175
SC-249 [Rose, 1981]	168 180
SC-250 [Rose, 1981]	61 68 101 168 175 223
SC-251 [Rose, 1981]	68 168 175
Unionid Coquina Site [Gingerich, 1987]	61 68 168
West Side of Shotgun Butte [Gazin, 1971]	68 168 175
Wasatchian	
Arminto [Stucky, 1984b]	54 77 92 93 100 125 141 157
Big Sand Draw/Carter Draw [Korth and Evander, 1982]	76 88 90 92 93 100 125 138 141 150 202
Bird Quarry Site [Gingerich, 1987]	17 20 58 157 164
Blue Croc Bed [Stucky, 1984b]	30 54 88 92 93 100
Boysen Reservoir (48FR65) [White, 1952]	54 60 76 77 88 92 93 117 184
Boysen Reservoir (48FR75) [White, 1952]	61 88 92 100
Boysen Reservoir (48FR76) [White, 1952]	33 61 76 77 88 93 100 112 125 157 184 209 229
Boysen Reservoir (48FR77) [White, 1952]	138 221
Boysen Reservoir (48FR78) [White, 1952]	58 77 92 93 100
Boysen Reservoir (48FR80) [White, 1952]	16 58 60 61 77 88 92 111 119 121 125 157
Bozeman [Delson, 1971]	17 20 35 54 58 68 81 86 92 93 114 135 157 168 169 184 193 213
Buck Spring Dark Red Stratum [Stucky, 1984b]	1 23 30 33 54 58 60 61 77 88 92 93 100 121 125 138 150 153 157 168 171 184 193 202 216 224 227 228 229
Buck Spring Quarries [Stucky et al., 1990]	1 9 16 23 33 42 54 58 60 61 62 84 88 92 93 98 100 114 116 121 124 125 138 139 148 150 157 161 164 165 168 169 184 201 202 211 215 225 228
Calcirudite Site [Gingerich, 1987]	20 86 92
CM Locality 1548 [Dawson et al., 1990]	24 52 58 60 76 92 93 121 125 150 157 169 201 228 230
Deadman Butte [Stucky, 1984b]	1 4 8 13 16 33 42 52 54 58 60 70 77 88 92 93 96 98 100 114 116 121 124 125 138 139 150 153 157 161 164 165 168 201 202 224 225 228 229
Dome Butte [Soister, 1968]	54 88 93 100
Dry Well [Delson, 1971]	17 20 22 35 51 58 68 77 86 92 93 153 157 159 168 169 183 184
East of Beaver Creek [Korth and Evander, 1982]	54 61 88 92 93 100
Farther East of Badwater Creek [Korth, 1982]	54 92 93
FG-61 [Gingerich, 1987]	54 93
Fross Quarry and White Trash Quarry [Korth, 1982]	1 33 88 93 98 114 125 157 228
Guthrie Locality 4 [Stucky, 1984a]	1 4 33 58 60 61 77 87 88 92 93 98 100 111 112 116 121 125 138 141 153 157 165 168 201 202 225 228

Appendix A5 (continued)

HG-3 [Gingerich, 1989]	68 69
Jane's Locality [Stucky, 1984b]	88 93 100 138 141 169
Lysite [Guthrie, 1967]	1 11 13 16 17 33 35 51 54 58 60 61 69 77 80 84 88 92 93 98 105 111 112 114 121 124 125 132 143 150 157 168 169 180 184 193 199 215 216 221 222 224 228 229
Monument [Delson, 1971]	4 13 60 86 90 92 93
MP-3 [Zhou and Gingerich, 1989]	35 54 58 68 77 84 92 93 96 121 152 168
North Fork of the Shoshone River NF 9 [Torres, 1985]	33 93
North Fork of the Shoshone River PU [Torres, 1985]	93 100 157 211
North Fork of the Shoshone River NF 2/3/10/17 [Torres, 1985]	54 76 92 93 100
North Fork of the Shoshone River NF 1 [Torres, 1985]	77 93 100 112
Powder River 38-41/41-33 [Delson, 1971]	46 58 68 125
Powder River 51-3/31/32 [Delson, 1971]	22 35 54 93
Powder River 51-11/12/13 [Delson, 1971]	22 35 54 58 93 125
Powder River 51-18/44/45 [Delson, 1971]	35 60 86 125
Powder River 51-19 [Delson, 1971]	22 92
Powder River 51-20/21/22/23/24 [Delson, 1971]	17 54 58 68 77 86 92 93 125
Powder River 51-25/51-30/61-1 [Delson, 1971]	35 60 86 92 125 152 183 184
Powder River 51-33 [Delson, 1971]	17 224
Powder River 51-34 [Delson, 1971]	93 168
Powder River 51-35 [Delson, 1971]	35 58 86 92
Powder River 51-49/50/51/52 [Delson, 1971]	54 86
Powder River 51-62 [Delson, 1971]	17 35 58 86 92 125 157
Powder River 52-12/13/14/15 [Delson, 1971]	46 54 86 92 93 157
Powder River 52-20/21 [Delson, 1971]	35 86 92 213
Powder River 52-31 [Delson, 1971]	54 86
Powder River 52-36 [Delson, 1971]	16 35 58 86 92
Powder River 52-37 [Delson, 1971]	58 86 213
Reclusa [Delson, 1971]	17 20 22 35 51 54 58 60 61 68 77 86 90 92 93 102 114 128 153 157 168 169 183 184 213
SC-4 [Rose, 1981]	17 20 22 27 37 44 51 54 58 61 65 68 77 84 86 92 93 124 135 148 157 168 169 173 183, 193 212 216 218 224 228
SC-54 [Rose, 1981]	17 20 22 37 54 58 60 61 63 68 77 86 92 93 96 121 135 146 151 157 168 169 184, 193 212 216 224 228
SC-67 [Gingerich, 1989]	2 4 20 22 25 27 35 46 51 54 58 61 63 65 68 69 70 77 92 93 121 128 137 148 151 157 168 169 179 184, 193 228
SC-69 [Gingerich, 1989]	22 35 51 68 92 93 128
SC-79 [Gingerich, 1989]	22 46 51 63 92 93
SC-121 [Gingerich, 1989]	22 46 68 92 93 148 216
SC-139 [Gingerich, 1989]	51 54 68 93 157
SC-210 [Winkler, 1983]	17 20 22 35 37 54 58 68 69 70 75 77 86 92 93 121 143 146 148 157 169 183 184 193 211 212 216 221 224 228
SC-308 [Gingerich, 1989]	4 22 51 58 68 92
SC-348 [Gingerich, 1989]	22 51 121 146 169
SC-349 [Gingerich, 1989]	51 193
SC-350 [Gingerich, 1989]	121 157
SC-351 [Gingerich, 1989]	4 27 51 68
Turtle Blues/Oakie Trail Quarry [Korth, 1982]	54 92 93 100 224
UCM 80089 [Stucky, 1984b]	77 92 93 100 157
UCM 81009 [Stucky, 1984b]	77 93 100 112
Viverravus Locality [Stucky, 1984b]	6 33 54 58 70 92 93 98 100 112 114 125 137 138 157 165 168 225 228 229
West Red Creek [Stucky, 1984b]	1 54 93 98 125 138 216
Wolton [Stucky, 1984a]	16 30 33 54 58 61 77 88 92 93 100 125 153 157 168 184 202 216 224 227 228 229

Appendix A5 (continued)

Wasatchian (Schankler-Wing section)

No Water (110') [Bown, 1979]	4 17 20 22 27 35 44 51 54 58 60 61 63 68 77 86 92 93 96 114 121 137 146 151 152 153 157 159 164 165 168 169 171 172 183 193 201 212 216 218 224 228
No Water (150') [Rose, 1981]	4 17 20 22 35 54 58 60 61 68 77 80 86 92 93 96 124 135 137 153 157 159 164 165 168 169 171 172 177 183 184 193 201 210 212 216 218 224 228
Elk Creek (50 m) [Schankler, 1980]	17 35 54 58 61 77 86 92 93 140 157, 193 228
Elk Creek (80 m) [Schankler, 1980]	27 35 58 61 68 86 92 93 151 157 193 212 218
No Water (288') [Rose, 1981]	17 20 22 35 54 58 60 61 63 68 77 86 92 93 102 124 137 157 164 168 169 171 183 193 224 228
Elk Creek (90 m) [Schankler, 1980]	22 35 54 58 61 68 77 86 92 93 98 140 143 146 157 168 169 183 193 228
Elk Creek (100 m) [Schankler, 1980]	17 22 27 35 46 51 54 58 60 61 68 77 86 92 93 96 98 125 135 143 146 153 157 168 169 183 184 193 212 216 224 228
Elk Creek (130 m) [Schankler, 1980]	35 58 61 69 77 86 92 93 125 143 153 157 168 169 212
Elk Creek (140 m) [Schankler, 1980]	17 22 27 35 42 51 54 58 60 61 68 77 80 86 92 93 96 98 99 114 125 128 137 143 146 148 151 153 157 164 165 168 169 171 173 183 184 193 210 212 213 216 218 224 228
Elk Creek (150 m) [Schankler, 1980]	35 51 54 58 61 77 92 93 168 213 221
Elk Creek (160 m) [Schankler, 1980]	17 22 35 54 58 61 68 70 77 86 92 93 98 114 125 137 143 153 157 168 169 183 193 212 213 216 224
Elk Creek (170 m) [Schankler, 1980]	22 35 54 58 61 77 86 92 93 121 143 148 157 193 213
Elk Creek (180 m) [Schankler, 1980]	17 22 35 54 58 61 68 77 86 92 93 98 114 125 146 157 168 183 210 212 213 216 221 224 228
No Water (590') [Rose, 1981]	4 22 35 54 58 68 74 77 86 92 93 128 137 157 168 169 183 193 210 218 224 228
Elk Creek (190 m) [Schankler, 1980]	17 22 35 51 54 58 61 68 77 86 92 93 98 99 121 125 143 152 157 158 165 168 169 183 184 193 212 213 221 227 228
Elk Creek (210 m) [Schankler, 1980]	35 54 58 68 77 86 92 93 157 168 173 201 213 227 228
Elk Creek (220 m) [Schankler, 1980]	11 17 22 35 54 58 61 68 77 86 92 93 98 99 143 146 151 157 173 183 193 213 228 229
Elk Creek (230 m) [Schankler, 1980]	58 61 86 92 153 168 184
Elk Creek (240 m) [Schankler, 1980]	17 22 33 35 54 58 61 68 77 86 92 93 96 98 114 121 143 157 168 169 173 183 184 193 212 213 216 221 224 228
Elk Creek (250 m) [Schankler, 1980]	17 35 77 86 157 193
Elk Creek (270 m) [Schankler, 1980]	17 33 35 54 58 60 61 68 77 86 92 93 98 137 143 146 148 153 157 168 169 173 183 193 213 216 221 224 228 229
Elk Creek (280 m) [Schankler, 1980]	17 22 33 35 54 58 68 77 86 92 93 98 125 128 137 143 153 157 168 169 173 193 213 228
Elk Creek (290 m) [Schankler, 1980]	22 33 35 54 58 61 68 69 77 86 92 93 98 125 143 146 151 153 157 168 169 173 184 193 213 216 221 228
Elk Creek (310 m) [Schankler, 1980]	169 213
Elk Creek (340 m) [Schankler, 1980]	77 103 213 228
Elk Creek (360 m) [Schankler, 1980]	17 22 33 35 54 58 60 61 68 77 86 92 93 98 99 125 143 146 151 153 157 168 169 183 184 193 213 216 221 228 229
Elk Creek (370 m) [Schankler, 1980]	17 33 35 54 58 61 68 77 86 92 93 98 125 143 146 153 157 168 169 173 184 193 213 216 221 229
Elk Creek (380 m) [Schankler, 1980]	13 77 92 168
Elk Creek (390 m) [Schankler, 1980]	33 35 51 54 58 60 61 69 77 92 121 143 157 168 169 183 184 193 213 221 228 229
Potala Bonanza [Bown et al., 1993]	16 33 35 46 52 54 58 60 61 77 90 92 93 121 125 148 168 169 183 184 193 216 221 224 227 228 229
Elk Creek (410 m) [Schankler, 1980]	35 51 58 61 77 92 93 168 169 193 221
Elk Creek (420 m) [Schankler, 1980]	35 51 54 58 61 77 92 93 153 157 168 169 193 221 224 228 229
Dry Cottonwood Bonanza [Bown et al., 1993]	1 11 33 46 54 58 60 61 77 92 93 121 125 153 168 193 221 224 228 229 233

Appendix A5 (continued)

Elk Creek (430 m) [Schankler, 1980]	1 51 58 77 92 93 121 143 148 229
Elk Creek (440 m) [Schankler, 1980]	1 33 35 58 61 65 77 92 93 143 168 205 229
Kraus Flats [Bown et al., 1993]	1 16 17 33 35 42 54 58 61 77 86 92 93 121 125 140 148 169 183 184 193 205 221 224 228 229
Elk Creek (450 m) [Schankler, 1980]	1 11 33 35 51 54 58 61 77 92 93 125 143 153 157 168 169 184 205 224 227 229
Elk Creek (460 m) [Schankler, 1980]	33 35 51 54 58 61 77 92 93 125 157 168 193 228 229
Elk Creek (470 m) [Schankler, 1980]	33 35 42 54 58 61 77 92 93 132 157 168 183 184 216 228
Elk Creek (480 m) [Schankler, 1980]	1 58 92 93
Elk Creek (490 m) [Schankler, 1980]	1 33 35 58 60 77 93 125 143 153 157 169 229
Elk Creek (520 m) [Schankler, 1980]	35 58 61 77 92 93 143 168 229
Elk Creek (530 m) [Schankler, 1980]	1 11 33 35 37 54 58 60 61 77 88 89 92 93 98 99 121 125 132 148 150 157 168 169 183 184 193 216 221 224 227 228 229
Reservoir Creek Bonanza [Bown et al., 1993]	1 11 13 16 33 35 46 54 58 60 61 69 77 88 90 92 93 114 121 125 140 143 148 150 168 169 184 193 216 221 224 227 228 229 233
Elk Creek (540 m) [Schankler, 1980]	33 35 58 77 92 93 121 143 168
Elk Creek (550 m) [Schankler, 1980]	1 11 35 92 93 125 157 168 193
Elk Creek (560 m) [Schankler, 1980]	1 11 17 33 35 46 51 54 58 61 77 88 92 93 98 114 121 125 132 143 150 153 157 164 168 169 193 221 224 227 228 229
PURple Hills [Bown et al., 1993]	1 11 33 35 46 51 54 58 60 61 77 92 93 121 125 150 153 168 169 193 221 224 227 228 229 233
Chriacus Locality [Bown et al., 1993]	1 11 16 17 33 35 46 51 52 54 58 60 61 77 88 92 93 114 121 125 148 153 157 168 169 184 193 216 221 228 229
Elk Creek (570 m) [Schankler, 1980]	1 11 17 33 35 46 52 54 58 60 61 77 84 88 92 93 98 121 125 132 143 150 157 168 169 193 224 228 229
Elk Creek (580 m) [Schankler, 1980]	1 10 11 33 35 46 51 52 58 60 61 77 88 92 93 98 99 121 125 132 140 143 150 157 168 169 193 221 224 228 229
Elk Creek (590 m) [Schankler, 1980]	1 11 33 35 52 58 61 77 88 92 93 114 121 143 153 157 168 169 183 193 216 224 228 229
Elk Creek (600 m) [Schankler, 1980]	1 33 35 54 58 61 69 77 84 88 92 93 121 125 132 143 150 153 157 168 169 193 221 224 228 229
Elk Creek (610 m) [Schankler, 1980]	1 33 35 52 54 58 61 69 77 88 92 93 98 121 125 137 140 143 148 150 157 168 169 193 224 227 228 229
Elk Creek (620 m) [Schankler, 1980]	1 33 35 51 52 54 58 60 61 69 77 84 88 92 93 98 114 121 125 143 150 157 168 169 180 193 221 224 228 229
Bobcat Draw Bonanza [Bown et al., 1993]	1 13 16 33 46 51 54 58 60 61 65 77 84 88 92 93 121 125 148 150 168 169 184 193 221 224 228 229
Elk Creek (630 m) [Schankler, 1980]	1 33 35 54 58 60 61 77 88 92 93 125 157 169 193 221 224 229
Elk Creek (640 m) [Schankler, 1980]	1 33 35 54 58 61 69 77 92 99 125 157 168 184 216 228 229
Elk Creek (650 m) [Schankler, 1980]	1 33 35 54 58 61 77 88 92 93 98 125 157 168 224 228
Elk Creek (670 m) [Schankler, 1980]	1 15 35 58 77 88 92 100 118 125 143 224 228 229
Elk Creek (680 m) [Schankler, 1980]	1 15 33 35 54 58 61 77 84 88 92 93 98 100 118 125 157 168 193 228 229
Elk Creek (690 m) [Schankler, 1980]	1 10 33 35 61 77 88 92 93 100 118 125 168 184
Elk Creek (710 m) [Schankler, 1980]	54 92 93 100 118 157

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