

# Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America

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## ABSTRACT

Comparisons of the physiognomy of leaves from modern vegetation of known climates with that of Eocene and Oligocene fossil leaf assemblages from middle latitudes of western North America indicate paleoaltitudes comparable or higher than those at present. Using canonical correspondence analysis, a multivariate statistical approach that includes nonlinear relationships between characters and environmental parameters, we relate leaf physiognomy of fossil samples to modern vegetation of known environmental parameters, including moist enthalpy of the atmosphere, a thermodynamically conserved quantity of the atmosphere that varies with altitude. By estimating enthalpy values for both lowland leaf assemblages and coeval interior leaf assemblages, altitudes for the interior assemblages can be estimated to  $\pm 890$  m. In northeastern Washington and southern British Columbia, the high Eocene altitudes indicate subsidence, or collapse, of an area undergoing crustal extension and may reflect an immediately preceding period of uplift that triggered the extension. Similarly, other areas that have undergone Cenozoic crustal extension appear to have been at least as high as they are at present. Three sites from the Rocky Mountains also indicate elevations at least as high as at present, and therefore suggest subsidence, either resulting from cooling of a hot upper mantle or erosion and isostatic compensation of surrounding terrain. High altitudes during Eocene and Oligocene time in western North America appear to have been normal, even in areas such as the Green River basin, and therefore cast doubt on the commonly inferred late Cenozoic uplift of that region.

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## INTRODUCTION

Throughout most of the Mesozoic Era and into the beginning of the Tertiary Period, the tectonic setting of western North America resembled that of the present-day Andes of South

America—by analogy, a high wide mountain belt. Granite batholiths intruded the crust near the coast, and crustal shortening by thrust faulting and folding dominated deformation inland, as it currently does within the Andes (e.g., Jordan et al., 1983). As has occurred in the Andes in

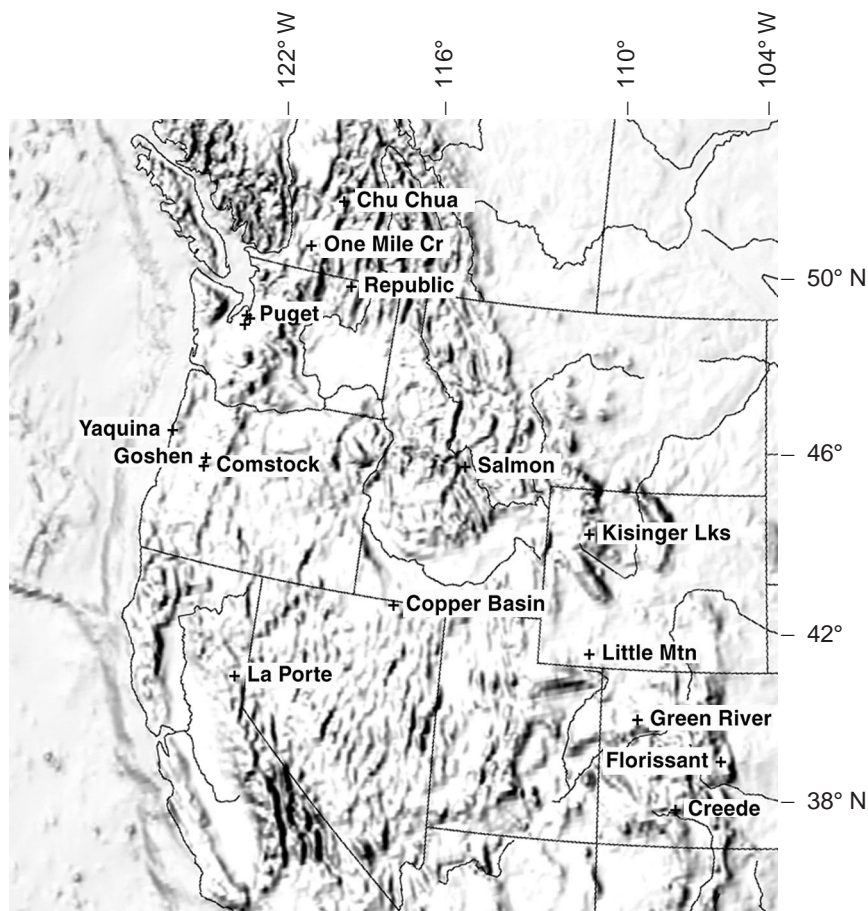
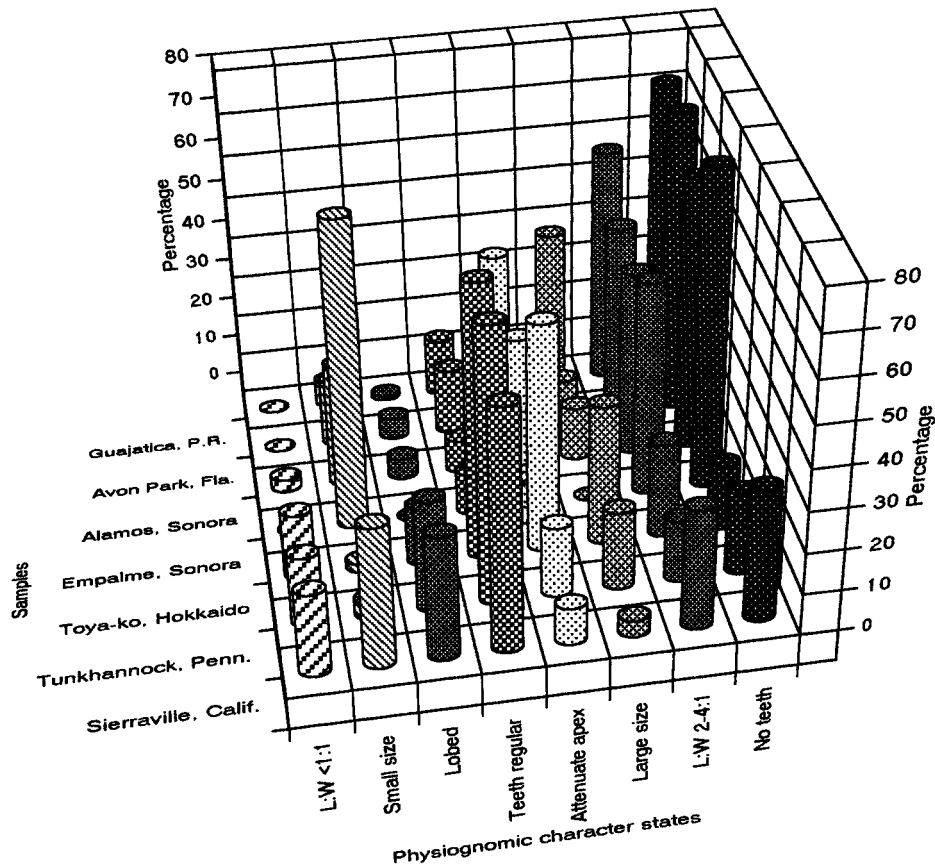


Figure 1. Map of middle-latitude western North America showing location of leaf assemblages analyzed in this report. The map is oriented obliquely to approximate the average latitudinal position of western North America during Eocene time.



**Figure 2.** Abbreviated physiognomic profiles for some modern samples in the climate-leaf analysis multivariate program (CLAMP) database. Guajatica, Puerto Rico, represents broad-leaved evergreen, multistratal rain forest (mean annual temperature [ $T$ ] = 24.0 °C, mean growing season precipitation [ $P$ ] = 195 cm); Avon Park, Florida, represents mixed broad-leaved evergreen and deciduous forest and scrub ( $T$  = 22.8 °C,  $P$  = 140 cm); Alamos, Sonora, represents short, tropical deciduous forest and scrub ( $T$  = 23.5 °C,  $P$  = 64 cm); Empalme, Sonora, represents Sonoran Desert ( $T$  = 23.3 °C,  $P$  = 18 cm); Toya-ko, Hokkaido, represents mixed northern hardwood (deciduous) forest ( $T$  = 8.2 °C,  $P$  = 65 cm); Tunkhannock, Pennsylvania, represents mixed northern hardwood (deciduous) forest ( $T$  = 8.6 °C,  $P$  = 56 cm); Sierraville, California, represents dry, mixed coniferous forest ( $T$  = 8.0 °C,  $P$  = 8 cm). Large leaves are those in the mesophyll 1 and 2 categories, and small leaves are those in the leptophyll 1 and 2 categories of Wolfe (1993). L:W is the length-to-width ratio.

Cenozoic time (e.g., Suárez et al., 1983), the locus of thrust faulting migrated eastward across the terrain now occupied by Nevada into that of western Utah and eastern Idaho, forming most recently the Sevier belt on the eastern edge of this deformed zone (Armstrong, 1968). Then, in Late Cretaceous time, concurrently with the final development of the Sevier belt, reverse faulting hundreds of kilometers farther east created the structures now exposed in the Rocky Mountains of Colorado, Wyoming, Utah, and Montana (e.g., Burchfiel et al., 1992; Wernicke et al., 1987). Since ca. 50 Ma, however, deformation throughout the Rocky Mountains has been mild. Farther west, the surface area of the terrain

where Mesozoic thrust faulting had been widespread has expanded, perhaps to as much as twice its initial width, by crustal extension associated with the normal faulting that created the Basin and Range province (e.g., Wernicke et al., 1987). As crustal extension is commonly associated with crustal thinning, the isostatic response of the decreasing crustal thickness implies that elevations should have decreased, at least in the Basin and Range province. Thus, simple physical arguments suggest that in the absence of additional processes and of evidence to the contrary, mean elevations in western North America east of the Basin and Range province should not have changed greatly in the past 50 m.y., while

those within the Basin and Range province should have decreased.

Conventional wisdom holds the contrary view, that “the present high elevation of the Colorado Plateau and most of the Cordilleran region occurred in late Cenozoic time” (Burchfiel et al., 1992). So widespread is this view, that studies of individual regions reporting details of Mesozoic and early Cenozoic historical geology commonly concluded, in some cases with little discussion, that significant uplift of the region occurred in late Cenozoic time (e.g., Atwood and Mather, 1932; Blackstone, 1975; Blackwelder, 1915, 1934; Deiss, 1943; Eaton, 1986, 1987; Forrester, 1937; Izett, 1975; Keefer, 1970; Love, 1970; McKee and McKee, 1972; Pardee, 1950; Scott, 1975; Tweto, 1975; Wahlstrom, 1947). Moreover, this view pervades the literature on climate change to the extent that not only are early and middle Tertiary elevations commonly assumed to be low (e.g., Barron, 1985; Sloan, 1994; Sloan and Barron, 1992; Greenwood and Wing, 1995), but late Cenozoic uplift has been assigned the cause of climate changes that include the Pleistocene Ice Age (e.g., Manabe and Broccoli, 1990; Ruddiman and Raymo, 1988; Ruddiman and Kutzbach, 1989).

The roots of the view that the high terrain developed in latest Cenozoic time seem to lie partly in (1) paleoclimatic indicators that suggest that temperatures were warmer than at present over much of this terrain; (2) the sharp erosion of the landscape of the western United States in late Pliocene and Quaternary time (e.g., Ruddiman et al., 1989); and (3) tilted ancient stream beds in the Sierra Nevada (e.g., Christensen, 1966; Dalrymple, 1963; Huber, 1981; Hudson, 1960; Lindgren, 1911). Neither (1) nor (2) is well founded, however (Molnar and England, 1990), and (3) applies only locally to uplift of the Sierran crest; moreover, tilting appears to result largely from erosional unloading of the crest and sediment loading on the western foothills (Small and Anderson, 1995). As we show herein, early to middle Cenozoic elevations throughout most of the western United States were generally comparable to, or higher than, present-day elevations; this calls for a reexamination of paleobotanical evidence for low altitudes during that time.

The early paleobotanical evidence was tailored to fit the putative geologic interpretations. Citing Blackwelder’s (1915) interpretations of the structural and geomorphic history of the Green River basin, Bradley (1929, p. 89) stated,

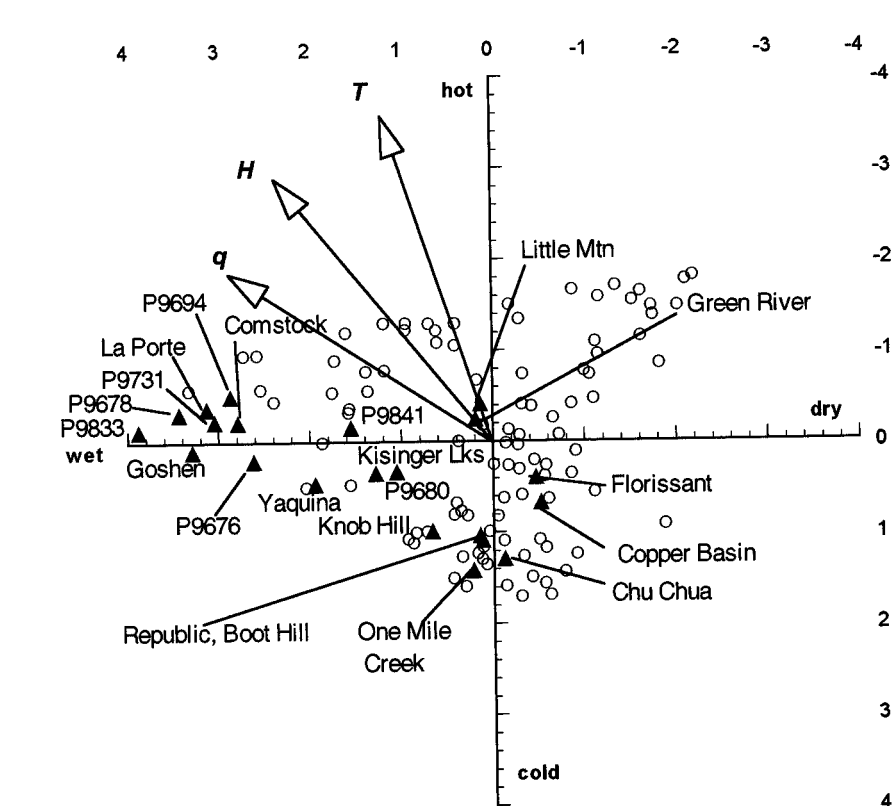
From this history it appears that the mountain ranges and high divides that form the rim of the Gosiute drainage basin were probably somewhat higher with respect to the floor of the basin during Eocene time than at present. The floor of the basin, however, in common with the general level of that part of the continent, was probably less than 1,000 feet above

sea level. Presumably the great regional uplift did not occur until some time late in the Tertiary period. The assumptions that follow and from which are deduced the features of the Eocene climate depend more or less directly upon this conception of the Eocene topography of the Green River Basin and the surrounding country.

MacGinitie's (1953) study of the floral assemblage from the late Eocene (ca. 35 Ma) Florissant beds of central Colorado (Fig. 1) seems to have served as fundamental evidence for the inference of low mid-Cenozoic elevations in the Rockies. In his study, MacGinitie (1953) assigned nearest living relatives to as many fossil species as possible, and from the habitats of the nearest living relatives inferred a paleotemperature that was distinctly higher than present (~18 vs. ~4 °C). He concomitantly interpreted the late Eocene to early Oligocene floras from the Mississippi Embayment as indicating only moderately warmer (~3 °C) temperatures than present at their respective latitudes. Assuming a typical variation of temperature with altitude, MacGinitie (1953) estimated a paleoaltitude of ~900 m. That elevation served as the reference for numerous subsequent studies that attempted to quantify Cenozoic paleoelevations (e.g., Eaton, 1986; Epis and Chapin, 1975; Trimble, 1980). In his later study of the Green River flora, MacGinitie (1969) arrived at an estimate of ~300 m for the altitude of the Green River lakes, citing part of the quote from Bradley (1929).

Roughly concurrently, Axelrod (1957, 1966; Axelrod and Bailey, 1969, 1976; Axelrod and Ting, 1960, 1961) assigned nearest living relatives to fossil species in floral assemblages from other parts of the western United States, particularly in western Nevada and California. Although they recognized that climate had changed throughout this period, Axelrod and his colleagues also inferred recent uplift from their assignments of nearest living relatives that live in climates much warmer than those of the high terrains from which the fossils came.

The assignment of nearest living relatives to fossil taxa—in particular to taxa assigned on the basis of only one plant organ, rarely from entire plants—and the association of that nearest living relative to a climate carries with it the implicit assumption that plants have not evolved in response to environmental changes. Although such an approach applied to late Quaternary plants would be reasonable, its application to plants that have become extinct or have evolved morphologically makes such ecological assignments untestable hypotheses. If plants have evolved in response to climate change, the nearest living relatives method lacks credibility as a method for inferring paleoclimate. As we discuss in more detail herein, the physiognomic characteristics of the plants of



**Figure 3.** Sample plots from canonical correspondence analysis of climate-leaf analysis multivariate program (CLAMP) database normal samples (white circles) and some Eocene and Oligocene samples (black triangles) projected onto the surface defined by the two largest eigenvalues of the analysis. The first eigenvalue is roughly parallel to mean annual temperature, and the second measures water stress. Fossil samples prefixed by P represent U.S. Geological Survey locality numbers for samples from the Puget Group. The arrows depict vectors of some environmental parameters: *T* (temperature), *H* (enthalpy), and *q* (specific humidity). The axes were partially constrained by these three parameters and by cold-month and warm-month mean temperatures, mean growing season length, mean annual precipitation (*P*), mean monthly growing season precipitation, three consecutive wettest months during growing season, three consecutive driest months during growing season, and relative humidity. *T* and *H* produce the longest vectors, which is an indication of their significance in ordering the samples. When samples are orthogonally projected to a given environmental vector and its extension, the samples are approximately ranked for that parameter (see Wolfe, 1995).

fer a more robust indicator of paleoenvironments than does taxonomy (Wolfe, 1979, 1993, 1995; Spicer, 1989).

In addition to the paleobotanical arguments for late Cenozoic uplift, uplift has been assumed to be the cause of the incised landscape of the Rocky Mountains (e.g., Scott, 1975) and of the abundant sediment in both adjacent basins (e.g., Love, 1970) and in the Gulf of Mexico, where sedimentation rates for the past 2 m.y. were four times more rapid than earlier (Hay et al., 1989). This period of rapid erosion and sedimentation correlates with a climate, replete with glaciation, very different from that of the preceding 250 m.y. It follows that climate change, rather than elevation change, provides

a simple mechanism for the relatively rapid Pliocene-Quaternary erosion and sediment transport (e.g., Molnar and England, 1990). A recent compilation of sediment transport and sedimentation rates from glaciated and glacier-free areas suggests that glacial erosion commonly (although not everywhere) is an order of magnitude more rapid than fluvial erosion (Hallet et al., 1996).

#### Recent Progress in Determining Paleoelevations

Even before arguments for a late Cenozoic uplift of the western United States were challenged, evidence to the contrary appeared. Avoiding near-

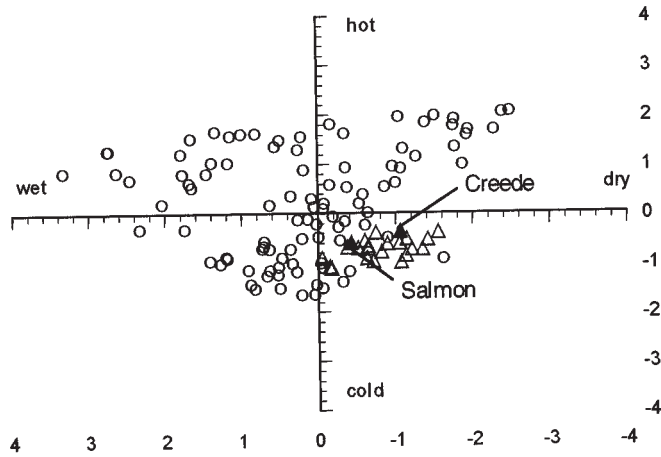


Figure 4. Sample plots from canonical correspondence analysis of climate-leaf analysis multivariate program (CLAMP) database normal samples (white circles), CLAMP subalpine and subarctic samples (white triangles), and the Salmon Eocene and Creede Oligocene samples (black triangles). The modern subalpine and subarctic samples plot as a contiguous inlier; the position of these inlier samples indicates greater warmth and dryness than actually occurs in the sampled areas. These samples should be analyzed separately from the normal samples (see Wolfe, 1995).

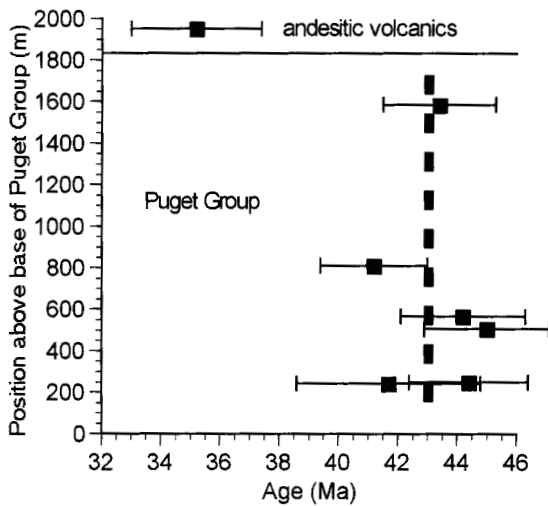


Figure 5. Potassium/argon ages and their stated errors for samples from ash partings of the Puget Group and from a flow from the overlying andesitic volcanic rocks (Turner et al., 1983). Whereas the indicated age of the andesitic volcanics is consistent with paleobotanical dating, the Puget ages all overlap at ca. 43 Ma (dashed vertical line) and suggest resetting by a thermal event.

est living relatives and using the physiognomic characteristics of the fossil leaves (cf. Wolfe, 1979), Meyer (1986, 1992) assigned paleotemperatures to fossil floral assemblages in New Mexico and Colorado. For example, Meyer (1986) inferred a somewhat lower mean annual temperature (14 °C) for the Florissant flora than did MacGinitie (1953). Relating this paleotemperature to paleoelevation, however, required another step.

With estimates of sea-level paleotemperature and paleotemperature of isochronous interior assemblages, the fundamental methodology proposed initially by Axelrod is based on

$$Z = \frac{T_{sl} - T_{int}}{TLR}, \quad (1)$$

where Z is altitude,  $T_{sl}$  is mean annual temperature at sea level,  $T_{int}$  is mean annual temperature of the interior assemblage of unknown paleoaltitude, and TLR is the (assumed) gradient of surface temperature with altitude, or terrestrial lapse rate, as opposed to the lapse rate in the free atmosphere. Although the worldwide average terrestrial lapse rate is ~5.5 °C/km (Axelrod, 1966), this value varies widely today, especially with local geography (Meyer, 1986). In the western conterminous United States today, the lapse rate determined

from equation 1 varies; e.g., ~1–2 °C/km in much of the Basin and Range province, ~3 °C/km in most intramontane basins of the Rocky Mountains, and >5 °C/km uncommonly in the Cascade Range of Washington (Wolfe, 1992).

Meyer (1985, 1992) recognized the large variations in terrestrial lapse rate in the western United States and used the present-day distribution of mean annual surface temperatures as a function of height and position in the western United States, and the knowledge that sea-level temperatures along the Pacific coast were considerably warmer than those at present, to estimate what temperatures would have characterized interior parts of western North America were they to have been at sea level in Oligocene–Miocene time. His estimated “sea-level” temperature for Florissant (29 °C) differs from what MacGinitie (1953) had assumed (22 °C) by 7 °C. The combination of Meyer’s lower paleotemperature and higher expected sea-level temperature yielded a paleoelevation similar to that at present. Assigning a meaningful uncertainty to Meyer’s (1986, 1992) inferred paleoaltitudes, however, is difficult, because his inferred paleotemperatures were estimated qualitatively and his assumptions leading to his inferred sea-level temperature ~2000 km from the coast lacked a meteorologically sound physical basis.

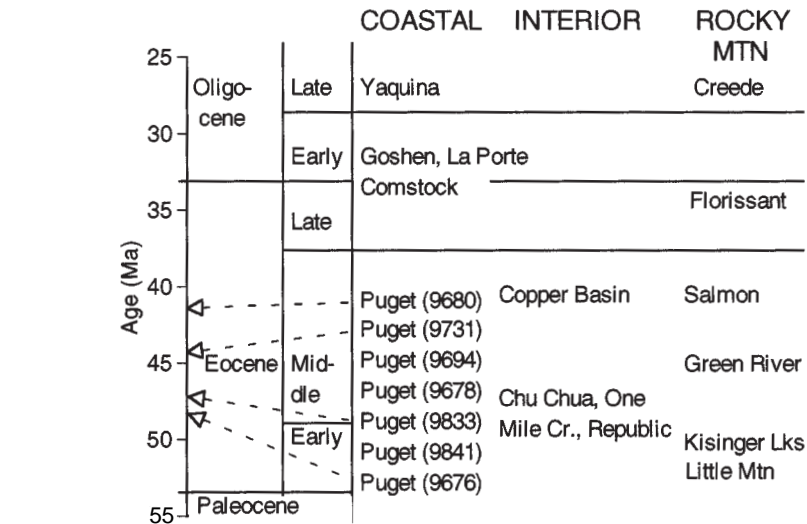
The development of a multivariate approach to leaf physiognomy (Wolfe, 1990) led to a quantitative calibration of physiognomy of leaf samples from modern environments with environmental parameters. Using an early version of the multivariate database (only ~60 modern samples had been collected), Wolfe and Wehr (1991) reported on analyses of three early middle Eocene leaf assemblages from the Republic, Washington, area and an isochronous assemblage from the Puget Group. The analyses indicated that the Puget assemblage had a mean annual temperature of ~17–18 °C, in contrast to the ~10–11 °C estimated for the Republic assemblages; these estimates were based on correspondence analysis, so the relations of samples to environmental parameters were subjective. Also subjective was the use of a low estimate of the decline in temperature to higher altitudes, which led Wolfe and Wehr (1991) to suggest a paleoaltitude of ~2.3 km.

Gregory and Chase (1992) exploited a subset of the available foliar physiognomic database (we use here an expanded version, discussed in the following) and used linear multivariate statistics to determine relations between leaf physiognomy and mean annual temperatures. Their statistics applied to fossil leaf physiognomy of the Florissant flora refined and quantified the estimate of the mean annual paleotemperature. Two estimates of paleoaltitude were made; one followed the method of Meyer (1986), and the sec-

ond used an assumed terrestrial lapse rate and applied it to estimates of differences in mean annual temperature between the coast and the Florissant. Gregory and Chase (1992) corroborated a paleoelevation indistinguishable from that at present.

The paleoaltitudinal estimates made by Axelrod (1957, 1966a, 1966b, 1987), Meyer (1992), Gregory and Chase (1992), and Wolfe (1994a; Wolfe and Wehr, 1991) all depend on an assumption of terrestrial lapse rate. Implicit in such estimates of sea-level temperatures in the past is the assumption that water vapor in the atmosphere, which depends strongly on temperature, had varied in time in such a way as to have no effect on spatial variations in surface temperature across western United States, although temperatures had changed uniformly by many degrees. With no supportive evidence, we consider that these previous paleoaltitudinal estimates are suspect and need reevaluation.

In addition, the abundances of stable isotopes, in particular  $\delta^{18}\text{O}$ , but also deuterium, are now being used to infer paleotemperatures in continental settings. Much of global climate is based on oxygen isotopic variations in marine microfossils, where the rapidly mixed seawater provides a homogeneous source of  $\delta^{18}\text{O}$ , which different microorganisms fractionate differently. In principle, the variations of  $\delta^{18}\text{O}$  in meteoric water precipitated over continents should allow inferences of paleotemperatures, but uncertainties in the source of the water later precipitated make the technique qualitative (Cerling, 1984). Nevertheless, the differences in isotopic ratios between those typical of present-day conditions and those measured from fossils reveal a surprising pattern; large negative values of  $\delta^{18}\text{O}$  (and  $\delta\text{D}$ ) suggest that early Cenozoic temperatures associated with precipitation in localities in the western United States were comparable to those at present; for example, ca. 50–51 Ma in Idaho (Seal and Rye, 1973) and in parts of Wyoming during Eocene time (Dettman and Lohman, 1993; Koch et al., 1995). Such low temperatures during a period of unusual warmth in oceanic regions are clearly consistent with high altitudes. Norris et al. (1996) reported relatively low concentrations of  $^{18}\text{O}$  deposited in lacustrine sediments of the middle Eocene Green River Formation in southwestern Wyoming. Allowing for enrichment of  $^{18}\text{O}$  by evaporation in lakes filling internally drained basins, they used their measurements of  $\delta^{18}\text{O} \approx -12\text{‰}$  to  $-16\text{‰}$  to infer that yet lower values,  $\delta^{18}\text{O} \approx -18\text{‰}$ , characterized the source waters to the lake. Norris et al. (1996) inferred that snow, not rain, was probably the dominant form of precipitation in the surrounding mountains. Assuming a paleoaltitude of only 150–300 m for the Green River Formation and a lapse rate of the free atmosphere of  $6.5\text{ }^\circ\text{C}/\text{km}$ , Norris et al.



**Figure 6.** Correlation chart for some Eocene and Oligocene floras from midlatitudes of western North America. Puget (9680) includes material from 9836 and 9837. Puget (9676) includes material from 9677.

(1996) deduced that altitudes as high as 3000 m in the surrounding mountains would have been necessary to collect significant snowfall. Our inferences about the paleoelevation of the Eocene Green River lakes suggest that the basin was quite high.

## METHODS

Because of the role played by evaporation and precipitation in the energy balance of the Earth's atmosphere, Forest et al. (1995) sought a thermodynamic parameter, different from mean annual temperature, to use for inferring paleoelevations, in particular, one that does not ignore water vapor in the atmosphere. Moist static energy, a thermodynamically conserved parameter of the atmosphere, quantifies the total energy content per unit mass of a parcel of air, excluding the negligible kinetic energy:

$$h = c_p' T + L_v q + gZ = H + gZ, \quad (2)$$

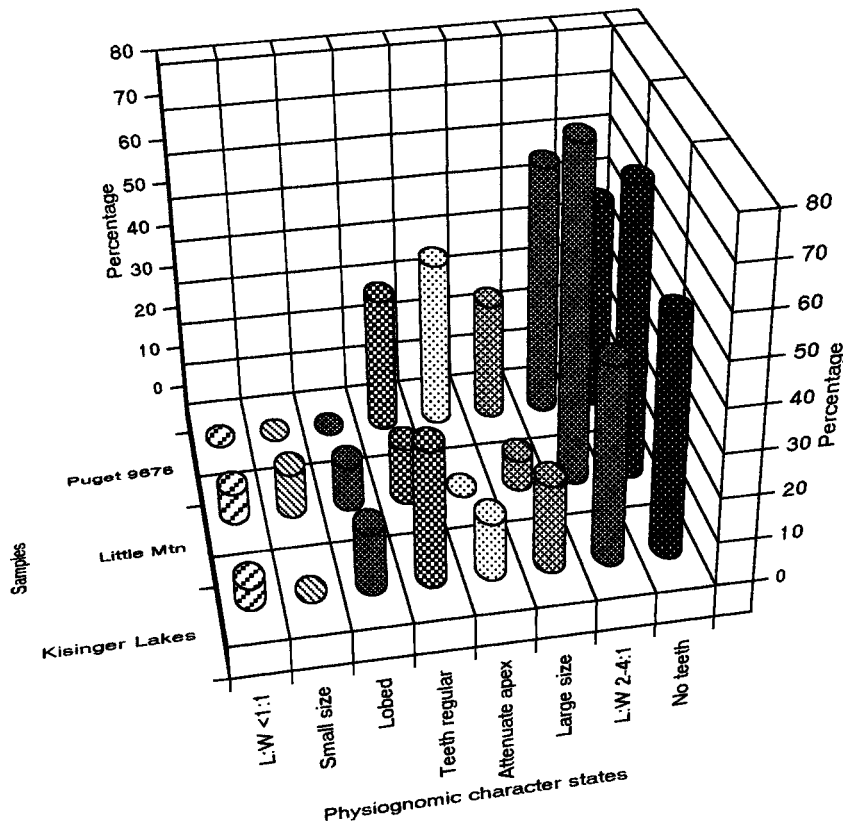
where  $c_p'$  is the specific heat capacity of moist air at constant pressure,  $T$  is temperature (Kelvin),  $L_v$  is the latent heat of vaporization,  $q$  is specific humidity,  $g$  is gravitational acceleration,  $Z$  is height, and  $H (= c_p' T + L_v q)$  is enthalpy. With the assumption that moist static energy is zonally invariant, the difference between two estimates of enthalpy for sites at similar paleolatitudes should yield an estimate of their difference in potential energy,  $gZ$ .

Air masses can gain or lose potential energy (elevation), latent heat (water vapor), or thermal energy (temperature), but their sum is conserved over time scales that are large compared with the time

for the air to move across a continent at midlatitudes. Because air usually moves from west to east at midlatitudes, moist static energy should be conserved along lines of latitude. Thus, if we can infer enthalpy at two sites, one near the coast and the other inland, we can estimate their difference in heights from their differences in enthalpy. Some error will be introduced by moist static energy having some longitudinal variation, an error ( $d_h$ ) that is estimated at  $4.5\text{ kJ kg}^{-1}$  (Forest et al., 1997).

If differences in measurements of enthalpy can yield estimates of altitude, the problem becomes how to obtain estimates of enthalpy. Inferences of enthalpy for fossil floras can be made from leaf physiognomy of the woody dicotyledons, specifically from CLAMP (climate-leaf analysis multivariate program). Wolfe (1993, 1995) analyzed samples of leaves from >100 sites proximal to meteorological stations. Each sample comprises at least 20 species of woody dicotyledons, all vouchered and collected to contain the full range of observed physiognomic variation for each species in the sampled site. Each species was scored for physiognomic variation of 31 character states, which include characters of margin, size, apex, base, and general shape (see Wolfe, 1993, Figs. 8 and 9). The totals (as percentages) for each character state in a given sample constitute the sample profile.

As seen in Figure 2, the percentage of species that have particular character states varies markedly in modern samples, from rain forests to deserts and from hot to cold climates: an analogy can be made to the distribution of species along environmental gradients. Because the distribution of species is generally related to envi-



**Figure 7.** Abbreviated physiognomic profiles for an early middle Eocene (ca. 48 Ma) leaf assemblage from the Puget Group and late early Eocene (ca. 49–51 Ma) leaf assemblages from the Rocky Mountains. The Puget assemblage represents lowland vegetation in western Washington, and the Kieinger Lakes and Little Mountain assemblages represent vegetation from western Wyoming. Analysis of the Kieinger Lakes assemblage is based on MacGinitie (1974); analysis of the Puget Group assemblage is based on a collection in the U.S. National Museum; and analysis of the Little Mountain assemblage is based on collections in the University of California Museum of Paleontology. The Little Mountain physiognomy has character states that indicate both drier (e.g., small leaf size, few attenuate apices) and cooler (e.g., more lobes and broader leaves) conditions than the Puget physiognomy. The Kieinger Lakes physiognomy has character states that indicate moister (e.g., larger leaf size) and cooler (e.g., more regularly spaced teeth) conditions than the Little Mountain. L:W is the length-to-width ratio.

ronmental factors in a nonlinear fashion, ecologists have developed methods to analyze species and environment relations. One such method is ordination by canonical correspondence analysis, in which species data for samples are related to supplied environmental variables; the ordination axes are constrained by these environmental variables, and the relative significance of each environmental variable to species distribution can be evaluated. As in species distributions, the physiognomic character states also have nonlinear relations to environmental variables (Wolfe, 1995), and thus canonical correspondence analysis is an appropriate tool. Our multivariate analysis of leaf physiognomy by canonical correspondence analysis was carried out using ter Braak's (1992) CANOCO software.

Ordination of the modern climate-leaf analysis multivariate program samples is related primarily to temperature and secondarily to water stress (Wolfe 1993, 1995; Fig. 3). Moist enthalpy is a factor second only to mean annual temperature in ordering the samples. A significant anomaly occurs, however, in ordering the subalpine samples, which include those from the subarctic (including samples from areas of >300 cm precipitation). They plot as a nest, or inlier (Fig. 4), within samples that are dry and cool (but not cold). Recognition of this inlier from leaf physiognomy is simple: the samples in the subalpine nest have anomalously high scores on axes 3 and/or 4, which in turn reflect a peculiar combination of physiognomic character states; e.g., species in these samples typically have small leaves that have rounded

apices (as in warm, dry species), but the leaves are not emarginate as in the warm, dry species. In two-dimensional space, the subalpine and subarctic samples form a contiguous nest, and they plot warmer and drier than they are; in multidimensional space, the subalpine nest forms a cluster removed from samples of normal vegetation. The most accurate calibration of environmental parameters for non-subalpine and non-subarctic samples is obtained by removal of the samples in the subalpine nest (see Wolfe, 1993, 1995). If subalpine and subarctic samples are not removed from the analysis, the temperature parameters (including the temperature-dependent enthalpy) for all the normal samples typically appear cooler than when the subalpine and subarctic samples are retained. In the present context, inclusion of the subalpine and subarctic samples for calibration of the non-subalpine and non-subarctic samples will lead to overestimating paleoaltitude for these samples.

For non-subalpine and non-subarctic fossil samples, the uncertainty in the difference in estimated paleoaltitudes between two sites was placed at ~760 m (Wolfe et al., 1997); however, this estimate used the mean error (4.2 kJ kg<sup>-1</sup>) for predicting enthalpy from canonical correspondence analysis. The standard error ( $\sigma_H$ ) for this prediction is 5.3 kJ kg<sup>-1</sup>, which is about the same as the 4.5 kJ kg<sup>-1</sup> error ( $\sigma_h$ ) introduced by longitudinal variation in enthalpy. When applied to two coeval sites, the combination of the two independent errors produces a standard error in the estimated difference in altitude of ~890 m:

$$\sigma Z = \sqrt{\frac{2\sigma_H^2 + \sigma_h^2}{g^2}} = 890 \text{ m.} \quad (3)$$

However, much of the standard error for estimating enthalpy from vegetation is in the samples from southern Sonora and southern Baja California, which represent thorn scrub. If these samples are excluded from the regression, the standard error is reduced to 4.3 kJ kg<sup>-1</sup> and the standard error for altitude is reduced to 770 m. Because none of the lowland coastal vegetation during Eocene and Oligocene time represents thorn scrub, the estimate of a standard error of 770 m is reasonable.

Most of the fossil samples analyzed here are within the normal group, and only two (Salmon, Idaho, and Creede, Colorado) are within the subalpine nest. Calibration of subalpine samples with environmental parameters is less precise than for the non-subalpine and non-subarctic samples (see Wolfe, 1993, 1994b), especially relative to enthalpy. All the subalpine and subarctic samples have a short growing season; if the growing season is defined as all consecutive days that have mean temperature >10 °C, samples in the subalpine and subarctic nest typically have a growing

TABLE 1. FOSSIL LEAF ASSEMBLAGES ANALYZED

Assemblage	No. spp.	Age (Ma)	$Z_p$ (km)	P. lat. ( $^{\circ}$ N)	$T$ ( $^{\circ}$ C)	$H$ (kJ kg $^{-1}$ )	$\delta H$ (kJ kg $^{-1}$ )	$Z_{i,T}$ km	$\delta Z$ km
<u>Late Oligocene</u>									
Yaquina, Oregon	35	24–29	0.01	47.0	15.4	317.9	0	<0.1	0.0
Creede, Colorado, 1	24	27.2	2.7	40.0	10.8	296.7	25.4	2.6	+0.1
Creede, Colorado, 2	24	27.2	2.7	40.0	4.2	<295.0	27.1	>2.8	-0.1
<u>Latest Eocene to earliest Oligocene</u>									
Goshen, Oregon	44	~33–34	<0.1	48.0	20.1	333.8	0	<0.1	0.0
Comstock, Oregon	25	~34–35	<0.1	48.0	21.2	332.7	0	<0.1	0.0
La Porte, California	37	33.2	1.5	43.0	23.0	337.9	0	<0.1	0.0
Florissant, Colorado	99	~35	2.6	40.0	11.8	300.9	37.6	3.8	-1.2
<u>Late middle Eocene</u>									
Puget Group, Washington									
9680	30	39–42	<0.1	52.0	14.9	313.8	0	<0.1	0.0
Copper basin, Nevada	25	40.2	2.2	45.0	10.5	298.3	19.2	2.0	+0.2
Salmon, Idaho, 1	28	<41	1.2	50.0	10.2	297.2	17.8	1.8	-0.6
Salmon, Idaho, 2	28	<41	1.2	50.0	2.6	295.0	20.0	2.0	-0.8
<u>Middle Eocene</u>									
Puget Group, Washington [mean]									
9731	45	43–46	0.1	53.0	22.8	338.7	0	<0.1	0.0
9694	44	43–46	0.1	53.0	23.3	337.0	0	<0.1	0.0
9678	43	43–46	0.1	53.0	21.8	335.3	0	<0.1	0.0
9833	24	43–46	0.1	53.0	22.8	342.2	0	<0.1	0.0
Green River, Colorado	58	~45	2.4–2.9	43.0	16.4	311.1	28.0	2.9	-0.5
<u>Late early to early middle Eocene</u>									
Puget Group, Washington [mean]									
9841	28	48–50	0.1	53.0	18.2	323.8	0	<0.1	0.0
9676, 9677	31	48–50	0.1	53.0	18.1	326.4	0	<0.1	0.0
Chu Chua, British Columbia	24	48–50	1.0	56.5	8.4	296.0	27.5	2.8	-1.8
One Mile Creek, British Columbia	29	48–50	0.8	54.0	8.3	297.1	27.9	2.9	-2.1
Republic, Washington [mean]									
48–50			0.8	54.2	10.0	300.8	24.5	2.5	-1.7
Downtown	80	48–50	0.8	54.2	9.8	299.7	25.6	2.6	-1.8
Boot Hill	27	48–50	0.8	54.2	9.5	299.1	26.2	2.7	-1.9
Knob Hill	43	48–50	0.9	54.2	10.7	303.5	21.6	2.2	-1.3
Kisinger Lakes, Wyoming	34	~50	2.7	46.0	14.6	312.2	17.2	1.8	+0.9
Little Mountain, Wyoming	30	50–51	2.7	42.0	17.2	312.3	20.7	>2.1	-0.6

Notes:  $Z_p$  = present-day altitude, P. lat. = paleolatitude,  $T$  = mean annual temperature,  $H$  = estimated enthalpy,  $\delta H$  = difference between sea level and estimated enthalpy,  $Z_{i,T}$  = estimated altitude from enthalpy difference,  $\delta Z$  = difference between present-day altitude and estimated paleoaltitude. For Creede and Salmon, first estimates assume that the assemblages are not subalpine, and the second estimates assume that the assemblages represent subalpine; the estimates are thus maximal enthalpy and minimal altitude.

season of <4.3 months. In the present context, however, we emphasize that the mean annual enthalpy for all modern samples that fall within the subalpine nest is <295 kJ kg $^{-1}$ , and we assume that any fossil sample that falls within the nest can be assigned this as a maximum value. Mean annual temperature for the subalpine samples can be calibrated with a standard error of 1.3  $^{\circ}$ C (Wolfe, 1993); if we have an estimate of an appropriate terrestrial lapse rate, mean annual temperature differences between sea level and interior assemblages can yield a general estimate of paleoaltitude for the subalpine assemblages. However, the combination of errors, first in calculating a terrestrial lapse rate from fossil assemblages of a particular period, and second in estimating  $\delta T$  for a sea level and interior assemblage, is so great that simply using a maximum estimate of 295.0 kJ kg $^{-1}$  of  $H$  for any subalpine sample seems to us a simple and effective way of estimating a minimal altitude for the few fossil assemblages that plot in the subalpine nest.

#### LOW-ALTITUDE ASSEMBLAGES

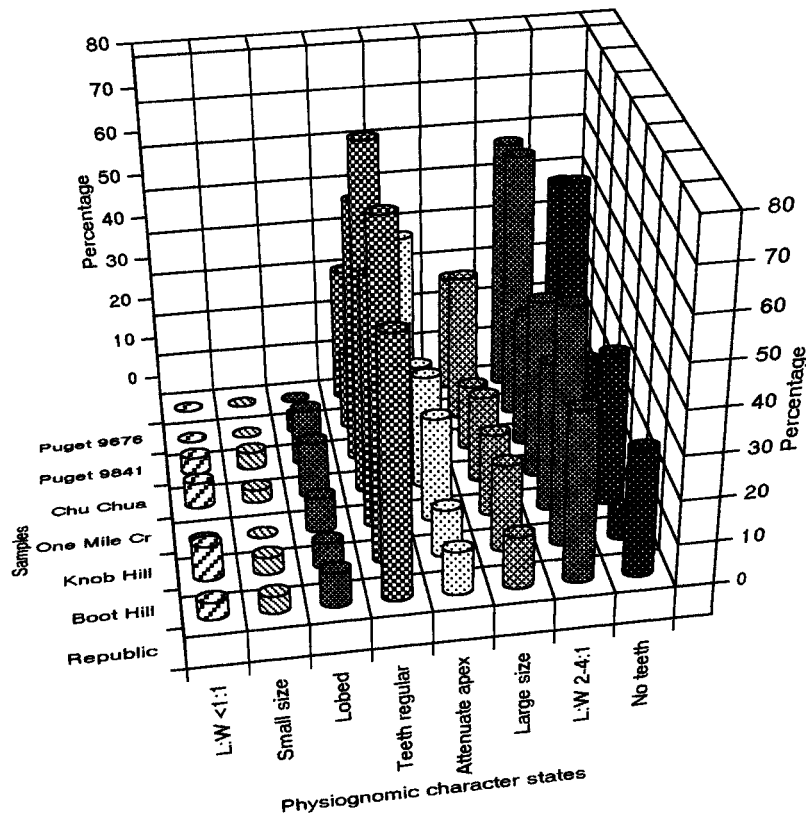
The analysis of near-coastal, low-altitude leaf assemblages that are isochronous with the interior

assemblages is critical to the method used here. That mean annual temperatures in coastal regions in the western United States have fluctuated markedly during Eocene and Oligocene time is clear (Wolfe, 1978, 1994a). To compare, for example, an interior flora from a warm interval of Eocene time with a coastal flora from a cool interval of Eocene time might indicate little difference in either temperature or physiognomy and hence little difference in paleoaltitudes. Conversely, to compare an interior flora from a cool interval with a coastal flora from a warm interval could grossly overestimate the paleoaltitude of the interior flora.

With the exception of the Comstock, all the near-coastal Eocene assemblages analyzed were collected from the Puget Group of western Washington, and thus the ages of the various Puget assemblages need to be considered. Wolfe (1968) used the leaf floras from the Puget Group as the basis for five formal stage ages: the oldest of these—the Franklinian stage—was equated approximately to early Eocene time; Ful-tonian time was approximated to middle Eocene time; Ravenian time was approximated to late Eocene time; and Kummerian time was approximated to early Oligocene time. Further analysis of the relations of marine and nonmarine biostratigraphic units

along the Pacific Coast (Wolfe, 1981) indicated that (1) the time of the Eocene-Oligocene boundary was at ca. 32 Ma, (2) the Kummerian was ca. 32–37 Ma and late Eocene, (3) the Ravenian and the Ful-tonian were ca. 37–49 Ma and middle to early late Eocene, and (4) the Franklinian was 49–52 Ma and late early Eocene.

In contrast, K/Ar age determinations based on material from ash partings from the Puget Group coals were interpreted to indicate that the almost 2 km of sedimentary rocks—including numerous thick coal beds—of the Puget Group in the type sections of the paleobotanical stages were deposited in a period of no more than 4 m.y. and represented only middle Eocene time (Turner et al., 1983). Results from K/Ar analyses from the conformably overlying volcanic rocks (part of the type section of the Kummerian stage) placed the volcanic unit at ca. 35 Ma (early Oligocene, as then thought) and therefore consistent with the paleobotanical correlations of the Kummerian. The Puget ages are not internally consistent relative to stratigraphy; some sampled units yield K/Ar ages older than those of underlying units. The stated experimental errors on the radiometric ages permit the various ages to be stratigraphically consistent, but all the Puget ages overlap at



**Figure 8.** Abbreviated physiognomic profiles for some early middle Eocene (47–49 Ma) leaf assemblages. The Puget assemblages represent lowland vegetation in western Washington, the Chu Chua and One Mile Creek represent vegetation in southern British Columbia, and the remaining assemblages represent the Republic vegetation in northeastern Washington. Analyses of the Puget assemblages are based on collections in the U.S. National Museum; analyses of the One Mile Creek and Republic assemblages are based on collections in the University of Washington Burke Museum; and analysis of the Chu Chua assemblage is based on collections now at the University of Arizona but to be deposited in the Geological Survey of Canada collections. Although the physiognomies of both Puget assemblages indicate cooler temperatures than in the four succeeding Puget assemblages, the interior assemblages have smaller leaf size, numerous species are lobed, and a preponderance of species that have regularly spaced teeth. L:W is the length-to-width ratio.

about 43 Ma (Fig. 5), which could be evidence of resetting by a single thermal event. The K/Ar analyses of the Puget ash partings (1) are stratigraphically and internally inconsistent, (2) are especially variable in the lower part of the Puget section, (3) overlap at about 43 Ma, (4) are anomalous relative to the thickness of the sequence (especially considering the included thick bituminous coals), requiring extremely high depositional rates, and (5) are inconsistent with the paleobotanical correlations. We conclude that the K/Ar analyses of the Puget Group ash partings only indicate a thermal event at ca. 43 Ma and that the suggested paleobotanical correlations (Newman, 1981; Wolfe, 1981) are approximately correct.

The Chalk Bluffs flora, which is the major correlative flora of the lowest (Franklinian) stage of

the Puget Group, was considered on the basis of stratigraphic relations to marine units to be ca. 49–52 Ma (Wolfe, 1981). The marine unit (Ione Formation) has been assigned to the Penutian stage of the benthic foraminiferal sequence, and the Penutian is approximately equivalent to planktic foraminiferal zone P8 (ca. 50–50.5 Ma). The Penutian, however, is time transgressive, ranging from 49 to 55 Ma (e.g., Miles, 1981). Palynostratigraphy of the lower Puget (Newman, 1981) suggests that this section is no older than 49 Ma. This suggests that the oldest known Puget Group floras are no older than 48–49 Ma and are thus of early middle Eocene age.

The ages of the near-coastal floras of Kumerian (late Eocene and earliest Oligocene) and late Oligocene ages are unequivocal. The Com-

stock and stratigraphically higher Goshen assemblages are from nonmarine lateral equivalents of the marine Spencer and Eugene Formations (Armentrout, 1981), which are overlain conformably by a thin unit that has a K/Ar age of 31 Ma (Evernden and James, 1964). The La Porte flora in California has been dated by K/Ar at 33.4 Ma (corrected from the date reported by Evernden and James, 1964), although this assemblage needs an age based on  $^{40}\text{Ar}/^{39}\text{Ar}$  analyses. No radiometric ages are known from the late Oligocene Yaquina Formation, but the flora is present in a deltaic unit between the lower and upper marine tongues of the formation (McClammer, 1978), which is assigned to the marine Galvinian stage on the basis of marine fossils (ca. 24–29 Ma; Armentrout, 1981).

## INTERIOR ASSEMBLAGES

The ages of most interior floras analyzed are based on radiometric dating and/or a combination of stratigraphy and radiometric dating (Fig. 6). Ages for the Creede, Florissant, Little Mountain, Kisinger Lakes, Green River, Copper basin, Republic (including all three major assemblages), and One Mile Creek (Princeton) assemblages are based on K/Ar dating (see discussions in MacGinitie, 1969, 1974; Wolfe and Tanai, 1987), although we stress the need for new single-crystal  $^{40}\text{Ar}/^{39}\text{Ar}$  dating. No independent ages are known for the Chu Chua assemblage, and all that is certainly known for the Salmon assemblage is that it is younger than 41 Ma (M. L. Statz, *in* Wolfe and Tanai, 1987).

## RESULTS

The inferences of the paleoaltitudes of the oldest Rocky Mountain leaf assemblages analyzed depend in part on the ages of these assemblages relative to the Puget assemblages. As summarized in MacGinitie (1974), the Kisinger Lakes flora should be about 48.5 Ma using the old K/Ar constants, and about 49.8 Ma using current constants. Similarly, the Little Mountain flora was assigned a K/Ar age of 49 Ma (Culbertson, cited *in* MacGinitie, 1974), which is 50.3 Ma using current constants. If so, then we suggest that the Little Mountain and Kisinger Lakes floras are probably ~1–2 m.y. older than the oldest analyzed Puget leaf assemblage; in Table 1, therefore, comparison is made only to the oldest Puget assemblage (Fig. 7).

Because of the early Eocene thermal optimum, the older an assemblage within the early Eocene, the more probable that the enthalpy value at sea level would be higher and, consequently, the greater the altitude that would be estimated for interior assemblages. This is particularly applicable to the Little Mountain assemblage, which is

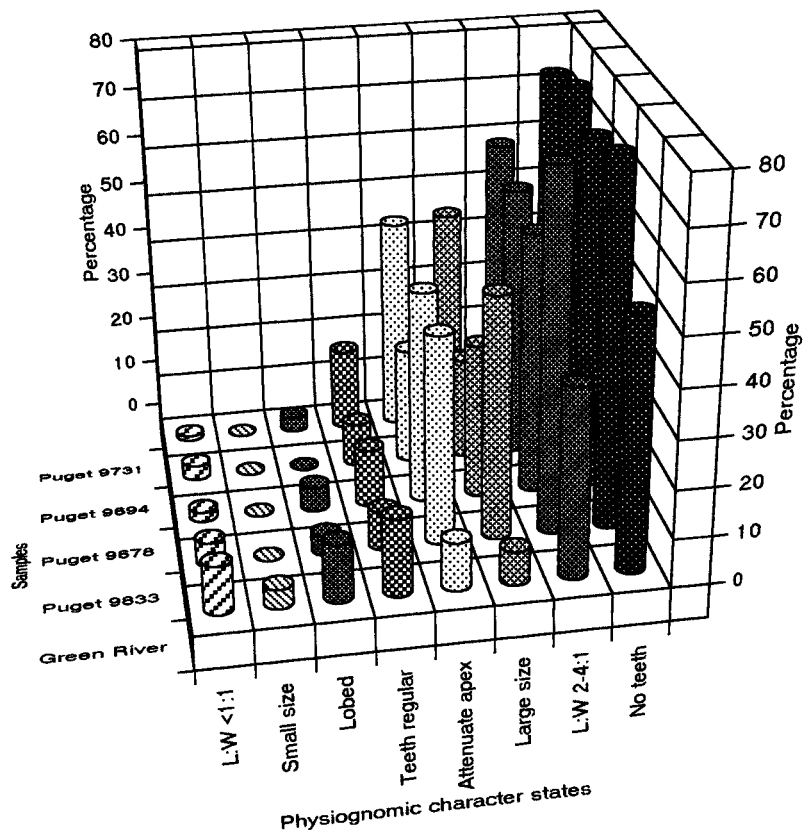


from the lower part of the Green River Formation, and has an estimated paleoaltitude of  $2.1 \pm 0.8$  km, which should be considered a minimal estimate. The CLAMP estimate of  $1.8 \pm 0.8$  km for the Kisinger Lakes assemblage may also represent a minimal estimate, but, being closer in time to the lowest Puget assemblage, may be valid. The Kisinger Lakes assemblage was significantly higher than the 0.3 km estimate suggested by MacGinitie (1974).

Leaf physiognomy of the early middle Eocene assemblages from northeastern Washington and southern British Columbia is markedly different from physiognomy of the Puget assemblages (Fig. 8). These upland assemblages all indicate substantially higher (~2 km) altitudes during Eocene time than at present; the estimates for the Republic assemblages are about the same as the estimate of 2.3 km made previously on the basis of temperature differences (Wolfe and Wehr, 1991). The depositional settings for these assemblages are lakes that occupied grabens following the initiation of normal faulting in these areas. Note that if these assemblages were older than early middle (possibly latest early) Eocene age (>49 Ma), they would have lived during the early Eocene thermal optimum, when sea-level enthalpy would have been even higher than that estimated for the Puget Group. Thus, the inferred paleoaltitudes would be substantially higher. Similarly high paleoelevations would be deduced if these assemblages lived later in middle Eocene time and were thus isochronous with the next four stratigraphically higher Puget assemblages.

For the warm interval of middle Eocene time, ca. 43–46 Ma, physiognomic differences between four coastal floras and the one interior flora analyzed are significant (Fig. 8), although some differences (e.g., leaf sizes and attenuate apices) may be largely the result of differences in precipitational regimes. The physiognomies of the four assemblages from the Puget Group all yield very similar estimates for both  $T$  and  $H$ ; their plots far to the left in Figure 3 indicate abundant precipitation with no dry season. In contrast, the earlier Puget leaf assemblages (9676, 9841), although indicating moist conditions, are less wet; noteworthy too are coals, which are thinner and fewer from the lower part of the Puget section than from the section containing these younger leaf assemblages (9833, 9878, 9694, 9731).

The only interior flora of the middle middle Eocene (43–46 Ma) interval that we have analyzed is from the upper part of the Green River Formation, which is dated ca. 45 Ma by a combination of stratigraphy and radiometric data (MacGinitie, 1969). Traditionally, the Green River lakes have been placed at low altitudes (e.g., Greenwood and Wing, 1995), partly because consensus assigns large interior lakes to



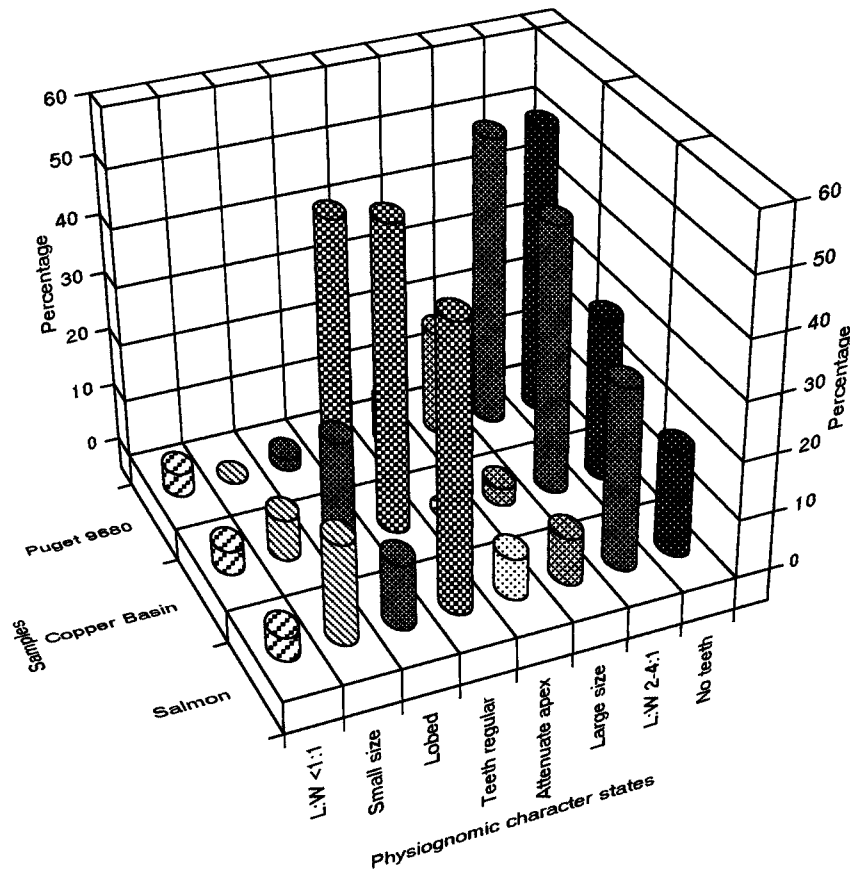
**Figure 9.** Abbreviated physiognomic profiles for some middle Eocene (ca. 43–46 Ma) leaf assemblages. The Puget assemblages represent lowland vegetation in western Washington, and the Green River assemblage represents vegetation in northwestern Colorado and adjacent Utah. Analysis of the Green River assemblage is based primarily on MacGinitie (1969), and analyses of the Puget Group assemblages is based on collections in the U.S. National Museum. The Puget assemblages all have character states indicative of high temperature (species typically have no teeth and are unlobed) and rainfall (large leaf size and many species have attenuate apices), in contrast to the Green River physiognomy. Dryness in the Green River physiognomy is also indicated by the many species that have linear (“stenophyllous”) leaves (i.e., length-to-width ratio,  $L:W > 4:1$ ).

low altitudes. Large lakes can persist in continental interiors at high altitudes, as in the Andes and on the Tibetan Plateau. Compared to the Puget assemblages (Fig. 8), the Green River assemblage has fewer untoothed species that are linear, large, and have attenuate apices. Such differences yield an estimated paleoaltitude of 2.9 km for the Green River flora, which differs little from the present-day altitudes at the fossil localities.

For the succeeding cool interval of late middle Eocene time (late Ravenian of Wolfe, 1968), we combined the flora from three localities in the Puget Group in order to have a taxonomically diverse sample. The combined Puget assemblage has a high proportion of species that have leaves with untoothed margins and are unlobed, large, and have attenuate apices; note that the Puget and the interior assemblages all have moderate repre-

sentation of regularly toothed species (Fig. 9). From nearest living relatives, Axelrod (1966b) inferred the Copper basin flora to have lived at <1.2 km compared to the present-day altitude of ~2.1 km; however, the physiognomic differences imply that the Copper basin flora lived at ~2.0 km (Table 1), i.e., about the same as the fossil locality today. If the Copper basin were isochronous with the older Puget flora from locality 9731 or with the younger Comstock flora, the estimated paleoaltitude would be substantially higher.

The Salmon flora is not well dated. It is present in lacustrine sediments deposited in a graben after the initiation of normal faulting of the Challis Volcanics. The Salmon flora has some taxa in common with the later Eocene floras in western Montana, and, like Wolfe and Tanai (1987), we consider the Salmon flora to be of late middle



**Figure 10.** Abbreviated physiognomic profiles for some late middle Eocene (ca. 39–42 Ma) leaf assemblages. The Puget assemblage includes material from three localities (9680, 9836, 9837) and represents lowland vegetation in western Washington; the Salmon assemblage represents vegetation in east-central Idaho; and the Copper basin assemblage represents vegetation in northeastern Nevada. Analysis of the Copper basin assemblage is based on Axelrod (1966b), and analyses of the other assemblages are based on collections in the U.S. National Museum. Although of cooler aspect (e.g., fewer species have no teeth and many have regularly spaced teeth) than the four preceding assemblages, the combined Puget late Ravenian physiognomy is of warmer aspect than the Copper basin, which has fewer untoothed and more lobed species. The Salmon physiognomy would appear to indicate drier conditions than the Copper basin, as indicated by the higher proportion of small leaves; the higher incidence of attenuate apices in the Salmon assemblage, however, indicates wetter conditions, suggesting that—as in modern subalpine physiognomy—the small leaf size is primarily related to coldness rather than to dryness. As in the Creede assemblage (see Fig. 12), large-leaved dicotyledonous evergreens are absent in the Salmon assemblage, despite the putatively mild winter climates of Eocene time. L:W is length-to-width ratio.

Eocene age and approximately coeval with the Copper basin and upper Ravenian floras (Fig. 10). Whatever the exact age of the Salmon flora, the CLAMP analysis places the vegetation as subalpine; as is typical for many subalpine samples, the Salmon assemblage has a generally small leaf size, but indicators of true drought (e.g., an emarginate apex) are absent. This places the Salmon paleoaltitude at  $>2.0$  km, if the Salmon assemblage is of late Ravenian age; this estimate is

based on a maximal enthalpy value of  $295 \text{ kJ kg}^{-1}$  for any subalpine assemblage. If the Salmon assemblage is considered as non-subalpine and non-subarctic, the paleoaltitude would have been 1.8 km. If the Salmon is somewhat older or younger than suggested here, paleoaltitudes would be substantially higher.

Assemblages stratigraphically above upper Ravenian assemblages in the Puget and overlying volcanic unit are represented by small collections,

none of which is sufficiently diverse for CLAMP analysis. These collections could be combined, as were the late Ravenian Puget assemblages, but the large assemblages at Goshen, Comstock, and La Porte farther south are available for analysis as sea-level assemblages for comparison to the inland Florissant flora (Fig. 11).

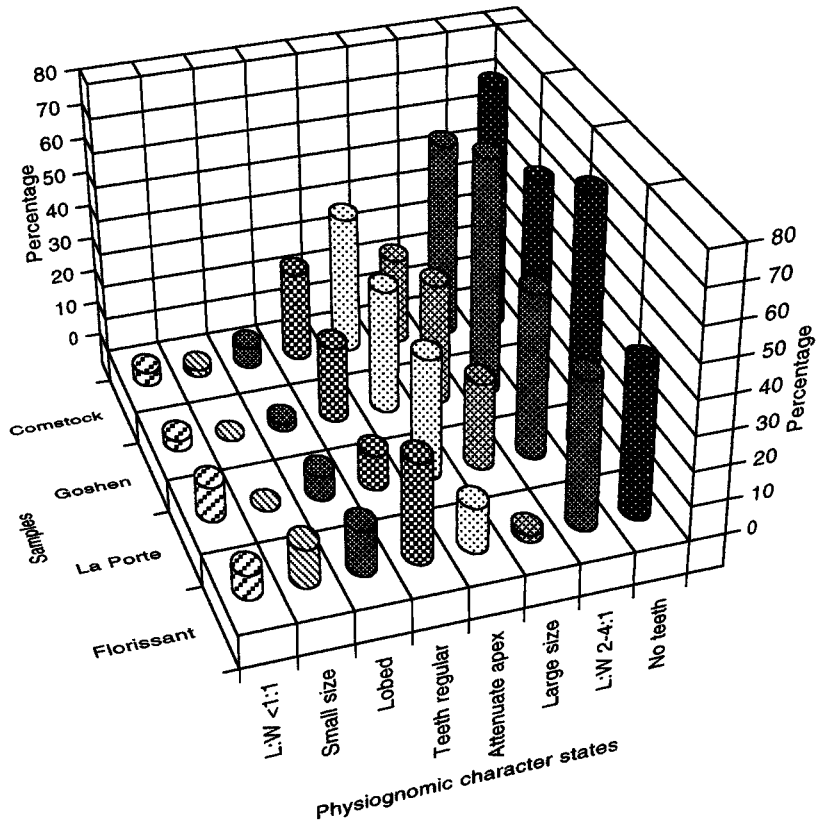
As noted previously, most recent estimates of paleoaltitude for the Florissant area during the latest Eocene are  $\sim 2.4$  to  $2.7$  km, which is about present-day altitude. Our analysis suggests a paleoaltitude about 1 km higher than these estimates, but Gregory and MacIntosh (1996) revised the Florissant paleoaltitude, still assuming a terrestrial lapse rate, upward to 3.1 km. Forest et al. (1995) were the first to estimate paleoaltitude from differences in moist enthalpy as derived from leaf physiognomy, and suggested a paleoaltitude for the Florissant area similar to that suggested by Gregory and Chase (1992). The differences in estimates of  $H$  between those of Forest et al. (1995) and our analysis stem, in part, from the use of linear statistics in one case and nonlinear canonical correspondence analysis in the other. More important, the absence of samples from western Mexico in the CLAMP database used by Forest et al. (1995) may account for a lower  $H$  ( $321.1$  vs.  $333.5 \text{ kJ kg}^{-1}$ ) for the coastal floras. This difference, in turn, is partially offset by the inclusion of the subalpine nest in the calibration of CLAMP by Forest et al. (1995), which accounts for a lower  $H$  ( $294.6$  vs.  $300.1$ ) for the Florissant assemblage and other fossil assemblages that plot near the subalpine nest. These two factors combined to yield a difference in  $H$  of 6.9, which represents most of the difference in estimate of paleoaltitude.

The youngest interior flora under consideration is the Oligocene Creede flora (Fig. 12), which was monographed by Axelrod (1987) and revised by Wolfe and Schorn (1990). The Creede flora is in lacustrine moat deposits of a late Oligocene caldera (Axelrod, 1987); on the basis of nearest living relatives, Axelrod estimated the surface of the lake to have been at  $\sim 1.2$ – $1.4$  km. This is in contrast to the higher altitude ( $\sim 2.2$ – $2.5$  km) suggested by Wolfe and Schorn (1989), who based their conclusions on general physiognomic principles. However, this estimate suggested so little subsequent uplift in southern Colorado that Wolfe and Schorn thought that the estimate was anomalous, and thus adopted an ad hoc explanation (Molnar and England, 1990) related to speculative winter temperature inversions to explain the low  $T$  estimate ( $0$ – $2.5$  °C) for the Creede assemblage. The robustness of CLAMP relative to differing taxonomic treatments is well exemplified by the Creede assemblage: the estimated  $T$  and  $H$  for the Creede assemblage based on the taxonomic treatment by Axelrod (1987), who determined  $>50$  woody di-

cotyledon species, versus that of Wolfe and Schorn (1990), who reduced this number to 24, are within the standard errors for  $T$  and for  $H$ .

Creede  $T$  is estimated from (1) recognizing that the Creede sample plots in the subalpine zone (Fig. 4), and (2) regression of  $T$  for only the subalpine samples (see Wolfe, 1993). This CLAMP subroutine yields an estimate of  $T$  of 4.2 °C. The association of the Creede sample with the subalpine nest indicates that enthalpy was  $<295 \text{ kJ kg}^{-1}$  and paleoaltitude was  $>2.8 \pm 0.8 \text{ km}$ . If we try to use  $\delta T$  of 10.6 °C between sea level and the Creede flora to estimate paleoaltitude, the result is an uncertain terrestrial lapse rate. At about 35 Ma, the Florissant  $T$  indicates a terrestrial lapse rate of  $2.9 \text{ °C/km} \pm$  and at 15.5–16.0 Ma, the estimated terrestrial lapse rate between the coast and western Nevada was  $2.0\text{--}3.3 \text{ °C/km}$  (Wolfe et al., 1997). Using the highest terrestrial lapse rate ( $3.3 \text{ °C/km}$ ) yet estimated for the time from 15 to 35 Ma in western United States yields an estimate of  $\sim 3.9 \text{ km}$  paleoaltitude for the Creede lake surface, and the volcanic plateau  $\sim 1 \text{ km}$  above could have been  $\sim 5 \text{ km}$  altitude. The higher-than-present paleoaltitudinal estimates for this area of southern Colorado during late Oligocene time might be expected, because of uplift due to underplating of magma and therefore crustal thickening associated with the volcanism at the surface. Like modern subalpine samples, the Creede assemblage has generally small-leaved species, but ones that are not emarginate, and a low incidence of lobed species; we thus think that the Creede plots in the subalpine nest. Nevertheless, as with the Salmon, if the Creede leaf assemblage were treated as non-subalpine and non-subarctic rather than subalpine, the enthalpy difference between the Creede and Yaquina assemblages would indicate a paleoaltitude for the Creede of  $2.6 \pm 0.8 \text{ km}$ , approximately that of the present.

The uncertainty of terrestrial lapse rates in western North America during the Eocene and Oligocene makes previous paleoaltitudinal estimates of uncertain validity when these are based on an assumed particular lapse rate. The largely independent estimates of paleoaltitudes and of  $T$  given in Table 1 allow gross estimates to be made of past terrestrial lapse rates. On the basis of differences in  $T$  between the Puget Group and the uplands of Washington and southern British Columbia, estimated lapse rates for early middle Eocene time are  $3.4 \text{ °C/km}$  (mean of all three Republic assemblages),  $3.5 \text{ °C/km}$  (One Mile Creek), and  $3.3 \text{ °C/km}$  (Chu Chua). The relations between the Puget and Green River suggest a lapse rate of  $2.8 \text{ °C/km}$ ; relations between the Puget and Copper basin suggest a rate of  $3.3 \text{ °C/km}$ ; and relations between the coastal assemblages and Florissant suggest a rate of  $3.1 \text{ °C/km}$ . These gross estimates are similar to



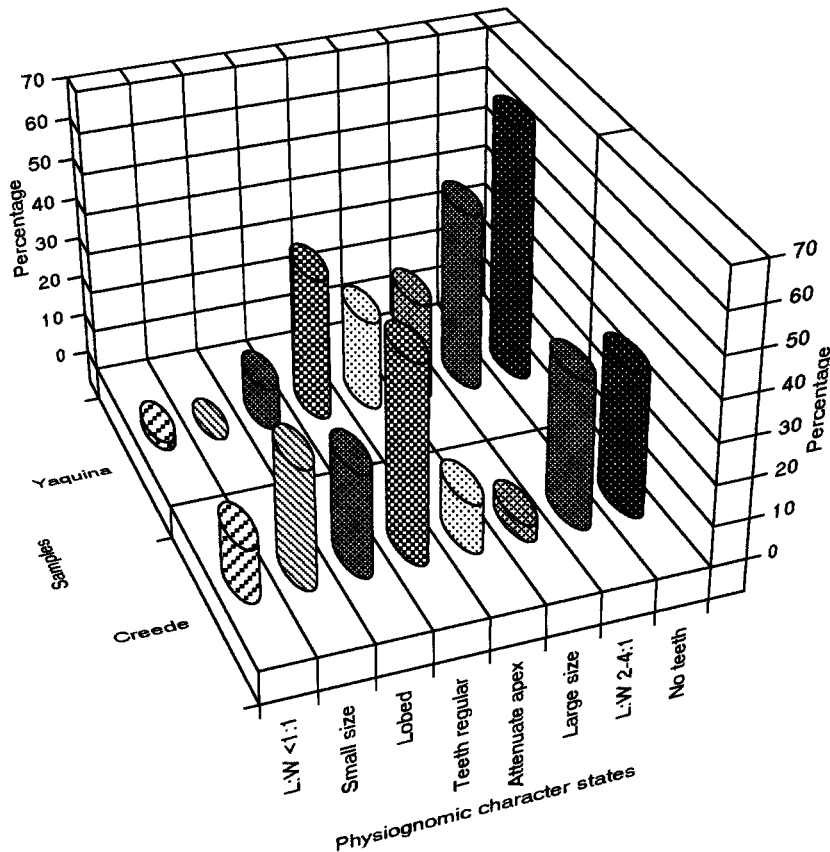
**Figure 11.** Abbreviated physiognomic profiles for some late Eocene to earliest Oligocene (ca. 33–35 Ma) leaf assemblages. The Comstock and Goshen assemblages represent lowland vegetation in west-central Oregon, the La Porte assemblage represents vegetation in eastern California, and the Florissant assemblage represents vegetation in central Colorado. Analysis of the Goshen assemblage is based on Chaney and Sanborn (1933), analysis of the Comstock is based primarily on Sanborn (1935), analysis of the La Porte is based on Potbury (1935), and analysis of the Florissant is based on MacGinitie (1953). The Florissant physiognomy is of both drier (e.g., small leaf size, few attenuate apices) and cooler (higher proportion of regularly toothed and lobed leaves) aspect than physiognomy of the near-coastal assemblages. L:W is length-to-width ratio.

the empirically derived terrestrial lapse rate of  $\sim 3.0 \text{ °C/km}$  in present-day western North America (Wolfe, 1992).

## DISCUSSION AND CONCLUSIONS

Two basic processes lead to large changes in mean elevations ( $\sim 1 \text{ km}$  or more) over large areas in relatively short times ( $<10 \text{ m.y.}$ ). First, changes in crustal thickness will, via isostasy, yield changes in mean elevations of roughly 15% of the change in crustal thickness. Thus, crustal shortening or extension at rates of a few millimeters per year over regions as wide as 100 km will yield elevation changes of  $\sim 1 \text{ km}$  in 10 m.y. Similarly, the addition of material by magmatic processes to the base of the crust should cause surface uplift of comparable amounts,  $\sim 15\%$  of the thickness of added crustal material. Second, an alteration of the thermal structure of the upper mantle by mass transfer,

such as by delamination of the entire mantle lithosphere (e.g., Bird, 1978, 1979) by convective removal of thickened, and therefore unstable, lower lithosphere (e.g., England and Houseman, 1989; Houseman et al., 1981), or by heating by erosion of the basal lithosphere by the impingement of a newly developed zone of hot upwelling, can cause rapid uplift of the Earth's surface ( $1\text{--}2 \text{ km}$  in a few million years). Most other processes require longer periods for comparable elevation changes. Erosion lowers mean elevations on a longer time scale, because isostasy compensates for material that is removed. For a relatively high average erosion rate of  $0.3 \text{ mm/yr}$ , mean elevations should decrease at  $0.05 \text{ mm/yr}$ , corresponding to 500 m of subsidence in 10 m.y. More typical erosion rates of  $0.1 \text{ mm/yr}$  require proportionally longer periods for substantial lowering of the surface. Similarly, thermal alteration by conductive heating or cooling is a slow process, dictated by the thermal time



**Figure 12.** Abbreviated physiognomic profiles for some late Oligocene (ca. 24–27 Ma) leaf assemblages. The Yaquina assemblage represents lowland vegetation in west-central Oregon, and the Creede assemblage represents vegetation in the San Juan Mountains of south-central Colorado. Analysis of the Yaquina assemblage is based on McClammer (1978), and analysis of the Creede assemblage is based on Wolfe and Schorn (1990). All physiognomic character states of the Yaquina assemblage indicate warmer and wetter conditions than the Creede. As in present-day subalpine environments, Creede physiognomy mimics physiognomy of dry, slightly warm environments (e.g., moderately small leaf size, a moderate proportion of untoothed species, and a moderate proportion of lobed species). The apparent dryness is, however, contradicted by general absence of emarginate (notched) apices, and the apparent warmth is contradicted by absence of large-leaved dicotyledonous (“broad-leaved”) evergreens. L:W is length-to-width ratio.

constant of the lithosphere of 30 to 100 m.y., for lithosphere 100 to 200 km in thickness.

Recognizing that much of the western United States underwent crustal shortening in Late Cretaceous and early Cenozoic time, we might expect paleoelevations in general to be greater than present-day elevations. Yet, because volcanism became widespread in both the Basin and Range province and in parts of the Rocky Mountains in Cenozoic time (e.g., Armstrong and Ward, 1991), we cannot ignore the possibility that the upper mantle beneath these areas was transformed from relatively cold to relatively hot, with the consequence that surface elevations increased during Cenozoic time.

With the exception of the Little Mountain and

Kisinger Lakes floras, all the interior floras analyzed indicate paleoaltitudes at least as high as the present-day altitudes of the fossil localities. As these localities represent different tectonic settings, we treat them first spatially, and then consider the implication of the temporal evolution.

Many of the localities we studied are from regions that have undergone normal faulting and crustal extension in Cenozoic time. These include areas where normal faulting has ceased (or is very minor, e.g., Washington and British Columbia) and others from the Basin and Range province, where active normal faulting is widespread and occurs rapidly compared with most other continental settings.

Early middle Eocene (ca. 49–50 Ma) paleo-

altitudes in northeastern Washington and southern British Columbia appear to have been 1–2 km higher than those at present. These localities are within grabens that apparently formed just after initiation of normal faulting at about 55–50 Ma (e.g., Carr et al., 1987; Parrish et al., 1988; Wernicke et al., 1987). Thus, it appears that these areas, which underwent Eocene crustal extension after a long period of crustal shortening (Burchfiel et al., 1992; Parrish et al., 1988; Price and Mountjoy, 1970; Wernicke et al., 1987), were high, and therefore their tectonic setting was similar to that of other high terrains of active normal faulting and crustal extension; i.e., the Basin and Range province farther south, the Tibetan Plateau (e.g., Molnar and Tapponnier, 1978), and the Andes (e.g., Sébrier et al., 1985, 1988). Our results cannot address the elevation history that preceded the onset of crustal extension, but they clearly support the contention that high terrains are susceptible to extension, or collapse. Moreover, our data from Washington and British Columbia cannot define the duration or rapidity of subsidence, but the pattern is similar to what we have determined for a part of the Basin and Range province (Wolfe et al., 1997), where rapid subsidence of a terrain as high 3000 m occurred shortly after normal faulting began at ca. 18 Ma. Thus, although the change in boundary conditions or internal state that initiated normal faulting in the southern Canadian Rocky Mountains and Washington and therefore initiated the Eocene Tectonic Transition of Parrish et al. (1990), cannot be deduced with confidence, the results presented here demonstrate that a large source of energy, gravitational potential energy stored in thick crust, existed when the normal faulting occurred.

The onset of normal faulting in a large high terrain (where shear traction on its base can be ignored) requires a change of some kind (e.g., England and Molnar, 1993). One candidate is convective removal of some or all of the thickened mantle lithosphere beneath a region that has undergone crustal thickening (England and Houseman, 1989). Thickening of mantle lithosphere creates a convective instability that leads to removal of relatively cold, dense material. The resulting removal of a cold lithospheric root and replacement by hotter asthenospheric mantle leads to uplift of the overlying crust and provides a trigger for the normal faulting. The distributions of ages and compositions of volcanic rocks from the Basin and Range province permit such an explanation for volcanism and the onset of normal faulting (e.g., Platt and England, 1994), but they do not require such an explanation.

The inferences from both Copper basin, Nevada, and Salmon, Idaho, suggest that paleoaltitudes were comparable to or higher than present-day altitudes. The more reliable estimate

is from Copper basin, where normal faulting is less active than elsewhere in the Basin and Range province; it implies little change in altitude since middle Eocene time. The Salmon flora, inferred to be within the subalpine nest, suggests a higher paleoelevation, perhaps as high as 4 km or more.

The other fossil localities that we studied are within the Rocky Mountains; the last phase of major faulting occurred there in early Cenozoic time, before ca. 50 Ma (e.g., Wernicke et al., 1987; Burchfiel et al., 1992). Thus, in general, the only obvious processes that might seem likely to have affected elevations in such areas are erosion and transport of sediment away from the region. In the absence of other deeper process that affected isostatic balance, isostatic compensation of the rock removed by erosion and transport would cause slow subsidence.

We examined floras from five sites from within the Rocky Mountains: the late early Eocene Little Mountain flora from southwestern Wyoming, the slightly younger Kisinger Lakes flora from northwestern Wyoming, the middle Eocene Green River flora from eastern Utah and northwestern Colorado, the latest Eocene–earliest Oligocene Florissant flora from central Colorado, and the late Oligocene Creede flora from south-central Colorado. Three of these yield paleoelevations higher than present, and all three are quite high. The inferred paleoaltitude of the Green River formation of  $2.9 \pm 0.8$  km is higher than at present and supports the inference of Norris et al. (1996), that mountains surrounding the lake were at elevations of 3 km or more. Moreover, as most of the Green River Formation was deposited in large lakes within the Rocky Mountains, these results imply that a large area must have been at high elevations at ca. 45–50 Ma. Similarly, the inferred paleoelevations for Florissant ( $3.8 \pm 0.8$  km) and Creede ( $\sim 4.2$  [±?] km) imply that the Southern Rocky Mountains were significantly higher than at present. It follows that these areas have subsided since 25–40 Ma. These paleoaltitudes cannot rule out the widespread belief that the Rocky Mountains underwent late Cenozoic uplift. Nevertheless, to be consistent with paleoaltitudes based on moist enthalpy changes would require substantial subsidence to precede such uplift.

What cannot be asserted with confidence is that these three localities have merely subsided because of erosion since high mountains formed in or surrounding these regions in Late Cretaceous to early Eocene time. Yet, perhaps most diagnostic here is the recognition that isostatic compensation of the present-day Rocky Mountains results not from thick crust, but from a hot upper mantle (Sheehan et al., 1995). The time that cold mantle lithosphere was replaced by hotter material is not clear, but the abundant Oligocene volcanism in Colorado indicates

thermal perturbation and therefore may mark a period of regional uplift, at least of the Florissant and Creede areas, associated with a marked thermal change of the underlying upper mantle. Subsequent subsidence would result from both erosion of surface material and cooling of mantle lithosphere. If as much as 1000–1500 m of subsidence has occurred since 25–40 Ma, as the differences in paleoaltitudes and present-day altitudes suggest, cooling of the upper mantle must have played an important role.

An abrupt change in the thermal structure of the upper mantle may account for the one flora that yields a lower paleoelevation than its present-day elevation, the late early Eocene Kisinger Lakes flora from the Central Rocky Mountains of western Wyoming, only ~50 km west-southwest of Yellowstone Lake. There seems little doubt that the volcanism and geothermal activity of the Yellowstone area are associated with localized upwelling in the underlying mantle plume beneath Yellowstone. Yellowstone is commonly considered to be typical of hotspot volcanism within a continental region; upwelling beneath it is less vigorous than beneath Hawaii, but comparable with that beneath Iceland (Sleep, 1990). Brott et al. (1981) estimated that the underlying thermal structure has caused an uplift of the Earth's surface of ~1 km, and Pierce and Morgan (1992) suggested 0.5–1 km of such late Cenozoic uplift, both comparable to that of other such hotspots (e.g., Sleep, 1990). Thus, that the present-day elevation of such an area is greater than paleoelevation should be no surprise. The Little Mountain flora may also be from an area that has undergone uplift, but the uncertainty of the valid coastal enthalpy at the time the flora lived makes the paleoaltitudinal estimate a minimum; furthermore, the estimated paleoaltitude is within the standard error and may indicate little, if any, altitudinal change.

The simplest deduction to be drawn from this comparison of present-day and paleoaltitudes is that most of the western United States and southern Canada was higher in elevation in early Cenozoic time than now. Moreover, where normal faulting has been intense, paleoelevations commonly suggest a subsidence of the region. The sparse distribution of localities and the different ages of the floras, however, call attention to the possibility that such generalities oversimplify the pattern and obscure, or ignore, other processes. In particular, widespread volcanism in the western United States implies that the upper mantle has not been cold and may have affected the elevation of the overlying crust. Correspondingly, thermal alteration of the upper mantle structure may have affected elevations in ways that our sparse data cannot expose. For example, some areas might have subsided substantially since the floras lived and then risen to their present-day elevations.

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