A METHOD FOR DETERMINING THE ALTITUDES OF TERTIARY FLORAS

DANIEL I. AXELROD
University of California, Los Angeles 24, California

ABSTRACT

Effective temperature (*ET*) at lowland stations can be used to determine accurately the altitude of *ET* at stations in upland forests today. The *ET* of a Tertiary flora near sea level appears to provide a reliable basis for determining the altitude indicated by the *ET* of a contemporaneous upland flora because there was a more regular vertical distribution to *ET* zones in the Tertiary. This resulted from climates which were more broadly zoned and less diverse in type; from relief which was lower and which had less influence on the local distribution of temperature; and from temperateness (*M*) which was high over wide regions.

Since Tertiary climate was characterized by pronounced temperateness (*M*), the effective temperature (*ET*) of a Tertiary flora can be determined most accurately if inferences are drawn from analogous modern forests in areas of high temperateness (*M* 60+), the regions where forests have persisted with least change since the Tertiary (i.e. Szechuan, Yunnan, Puebla-Oaxaca, New Zealand, southern Chile, Canary Islands).

The method devised to determine altitudes of stations in modern upland forests is applied to Tertiary floras with the following results. (1) A late Eocene subalpine forest (Bull Run flora) in northeastern Nevada probably lived near 4,300 feet, contemporaneously with broad-leafed evergreen forest near sea level to the west (Montgomery Creek-Moonlight, Comstock floras). (2) Mixed deciduous hardwood forest, inferred by botanists to have occupied the ancestral Great Smoky Mountains during Eocene, probably had its lower margin near 2,500 feet, situated above the warm temperate broad-leafed evergreen forest that dominated the lowlands (Wilcox flora). (3) Middle Miocene floras of the Columbia Plateau and adjacent region display a gradient from a marginal ecotone to warm temperate broad-leafed evergreen forest (Wishkaw, Grand Coulee, Latah, Whitebird floras) extending up to about 500 feet, to deciduous hardwood forest (Succor Creek, Horseshoe Bend, Upper Cedarville, Mascall floras) from 500-1,500 feet, to montane conifer-deciduous hardwood forest (Blue Mountains, Trout Creek floras) ranging from 1,500-3,000 feet, to montane conifer forest (Trapper Creek flora) above 3,000 feet. (4) Analysis of Eocene to early Oligocene floras along the Pacific Coast (Lat. 40-65°) reveals a vertical zonation of forests and climates, with the cooler zones rising to higher altitudes at lower latitudes.

The data support the principles that (1) altitudinal zonation of Tertiary climate exerted a primary control on the distribution and composition of forests much as it does today, that (2) a rise in altitude during the Tertiary corresponds to time transgression because floras of younger aspect lived in the cooler uplands, and that (3) owing to altitudinal zonation of climate, analysis of the secular trend of Tertiary climate should be based on sequences of floras in local areas at or close to sea level, and not on fossil floras in widely separated regions for they will display pseudoclimatic fluctuations since they occur in different climatic zones.

INTRODUCTION

TERTIARY forests were zoned altitudinally with respect to decreasing temperature. A good example is provided by Depape's (1928) analysis of the Pliocene floras of the Rhone Valley which shows that a palm-oak forest of the strand was replaced by laurel forest on well-watered lower slopes, that it graded up into mixed deciduous hardwood forest at moderate altitudes, and that adjacent volcanic mountains supported montane conifer forest. Middle Miocene floras of the Columbia Plateau and adjacent region (CHANEY, 1959; AXELROD, 1964) also show altitudinal zonation. Those from the coastal strip and the low Columbia embayment that reached well into the interior are dominated by deciduous hardwoods, lowland conifers, and a few broadleafed evergreens which lived under marginally warm temperate climate. At moderate altitudes, forests are composed chiefly of deciduous hardwoods and conifers of mild temperate requirements, and were replaced at higher levels by a montane conifer-deciduous hardwood forest. The occurrence in the latter of occasional records of upland conifers makes possible the assumption that pure montane conifer forest occupied the adjacent higher, cooler slopes. A similar zonal arrangement existed in late Eocene to judge from floras in northeastern Nevada. One (Copper Basin) is a montane conifer-deciduous hardwood forest, the other (upper Bull Run) is a pure montane conifer forest of the subalpine zone. Since they lived at levels well above the broad-leafed evergreen forests which then clothed the coastal slope 350-400 miles west (Montgomery Creek, Comstock floras), the problem arises as to whether we can accurately determine the altitudes at which these and other upland forests lived.

Estimates of the altitudes of Tertiary floras have been based chiefly on the geographic (altitudinal-latitudinal) and climatic relations of modern forests similar to the fossil floras (BERRY, 1934, pp. 48-51; DEPAPE, 1928; MACGINITIE, 1953; AXELROD, 1957; CHANEY, 1936, 1959). However, if a flora had a moderately high altitude the method does not yield consistent results because different investigators analyzing the same flora usually arrive at considerably different estimates of its altitude. The imprecision is due in part to drawing inferences from modern forests which live under climates that differ appreciably from those of the Tertiary, and in part to the climatic factors which may be selected to estimate altitude. From a consideration of the relations of effective temperature and temperateness (BAILEY, 1960; 1964), a method has been devised which seems to provide a more reliable basis for determining altitude (AXELROD, 1964). Furthermore, it should yield generally similar results if different investigators apply it to the same problem. Since the underlying principles appear to be sound, the method is described in the hopes that others will use it and perhaps discover ways to improve it so that it can aid further in a solution of the difficult problem of determining the altitudes of Tertiary floras, and of the climatic zones which they represent.

ECOLOGIC PRINCIPLES

To reconstruct Tertiary forests and the climates under which they lived, past conditions must be inferred from those prevailing in similar modern environments. General inferences as to the latitudinal and altitudinal arrangement of the major Tertiary forest zones may be made from the distribution of present-day forests. Proceeding northward along the eastern sides of the northern continents, tropical rainforest is replaced gradually by broad-leafed evergreen forest of warm temperate requirements. It in turn merges into mixed deciduous hardwood forest, which is replaced to northward by conifer-hardwood forest, and it then gives way to boreal conifer (taiga) forest, and tundra is finally reached. The same sequence of forest types is encountered in ascending from sea level to higher altitudes, whether in China or Mexico. These changes in forest composition with latitude and altitude provided the basis for suggesting that the occurrence of a mixed deciduous hardwood forest of mild temperate requirements near sea level in Alaska during the Eocene makes possible the assumption that a somewhat similar forest probably inhabited the uplands of Oregon and Nevada some 25° Lat. farther south when the contemporaneous Goshen, Comstock, and other subtropical forests occupied the lowlands there (CHANEY, 1936). That such a relation probably existed is fully consistent with the composition of upland Eocene floras in northeastern Nevada. Representing conifer-deciduous hardwood forest, they differ in composition from those in Alaska chiefly because they lived under cool temperate climate in the uplands, above the mild temperate zone which is recorded near sea level to the north (see below).

Modern forest zones provide a basis for inferring the altitudes of Tertiary forests because they reflect differences in the climates to which they are adapted. In using climatic data which are available for modern forests to infer the altitudes of Tertiary forests, it is evident that certain restricted areas (Yunnan, Szechuan, Jalapa-Orizaba, central Honshu, Sonora, Canary Islands) approximate Tertiary climates more closely than do other regions (eastern United States, Oregon-Washington, Arizona, Spain) which support forests that are closely related to them historically, but which represent late Cenozoic segregates adapted to different climates. Forests in the former areas were less modified by climatic change during the later Cenozoic, and they now persist under climates which more nearly represent Tertiary conditions. Thus, in order to reconstruct the climates under which Tertiary forests lived, it seems appropriate to examine present conditions in these relict areas. The requirements of the living forests in terms of effective temperature (*ET*) and temperateness (*M*) are of major concern. Changes in the spatial and qualitative relations of *ET* and *M* during the Tertiary materially affected the composition of the forests, and the latitudes and altitudes at which they lived. Consideration of these factors provides a basis for determining the altitude of a fossil flora, and also that of the vegetation-climatic zone which it represents.

EFFECTIVE TEMPERATURE (*ET*)

Effective temperature (*ET*) is a measure of the warmth of climate. As noted by Bailey (1960), the principle may be understood by recalling the awakening pulse of life that starts at the edge of the tropics in spring, and which gradually marches poleward until the margins of polar regions are reached in early summer. In fall, ebbing life retreats from high to low latitudes, and reflects temperatures generally similar to those which existed in spring. The assumption is that the ebb and flow of life are related primarily to the waning and waxing of thermal environment. Since the principle is biased toward biologic responses, it naturally has considerable merit in terms of interpreting past climate from fossil evidence.

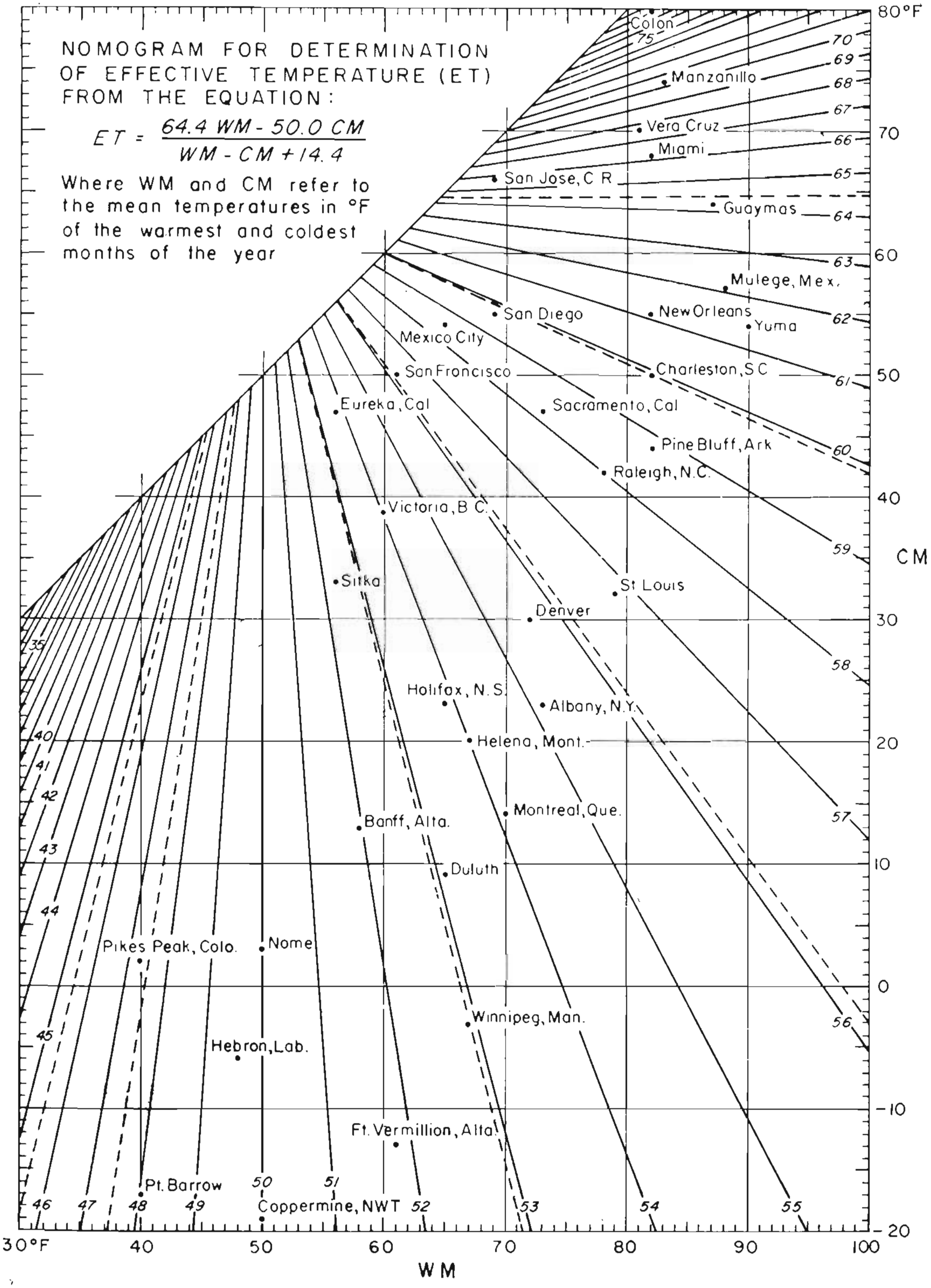
ET measures warmth by a scale that specifies temperature at the beginning and end of a warm period, and the duration of that period. Thus a principle of *seasonal* rather than annual warmth is expressed by *ET*. It is determined from the mean temperatures of the warmest (*WM*) and coldest (*CM*) months, factors which alternate in their control over *ET*. In a gradient from warm to cold climate, the appearance of a true winter marks the limit of tropical conditions, the margin of which is taken as 64·4°F (18°C) for the *coldest* month of the year. As winter increases in length and cold, a true summer finally disappears at the edge of the polar zone, the border of which coincides with 50°F (10°C) for the *warmest* month of the year. Bailey's climatic classification in terms of *ET* is reproduced in Table 1, and Text-fig. 1 shows the *ET* at a number of representative North American stations. As illustrated there, Colon, Manzanillo, Vera Cruz, and Miami are in the tropical zone for the mean temperature of the *coldest* month (*CM*) exceeds 64·4°F. On the other hand, Pikes Peak, Hebron, and Pt. Barrow are in the polar zone, where mean temperature of the *warmest* month (*WM*) is below 50°F. Figure 1 also shows that some stations with the same *ET* are widely spread across the nomogram. Those which are farthest from the upper left margin have greater ranges of mean temperature for the warmest and coldest months. Thus Eureka (*ET* 54) has temperatures of 56° and 47°F as compared with 70° and 14°F at Montreal (*ET* 54), and which express differences in the temperateness of climate.

TEMPERATENESS (*M*)

Temperateness (*M*) rates the thermal regime in terms of its departure from 57·2°F (14°C), which represents conditions midway

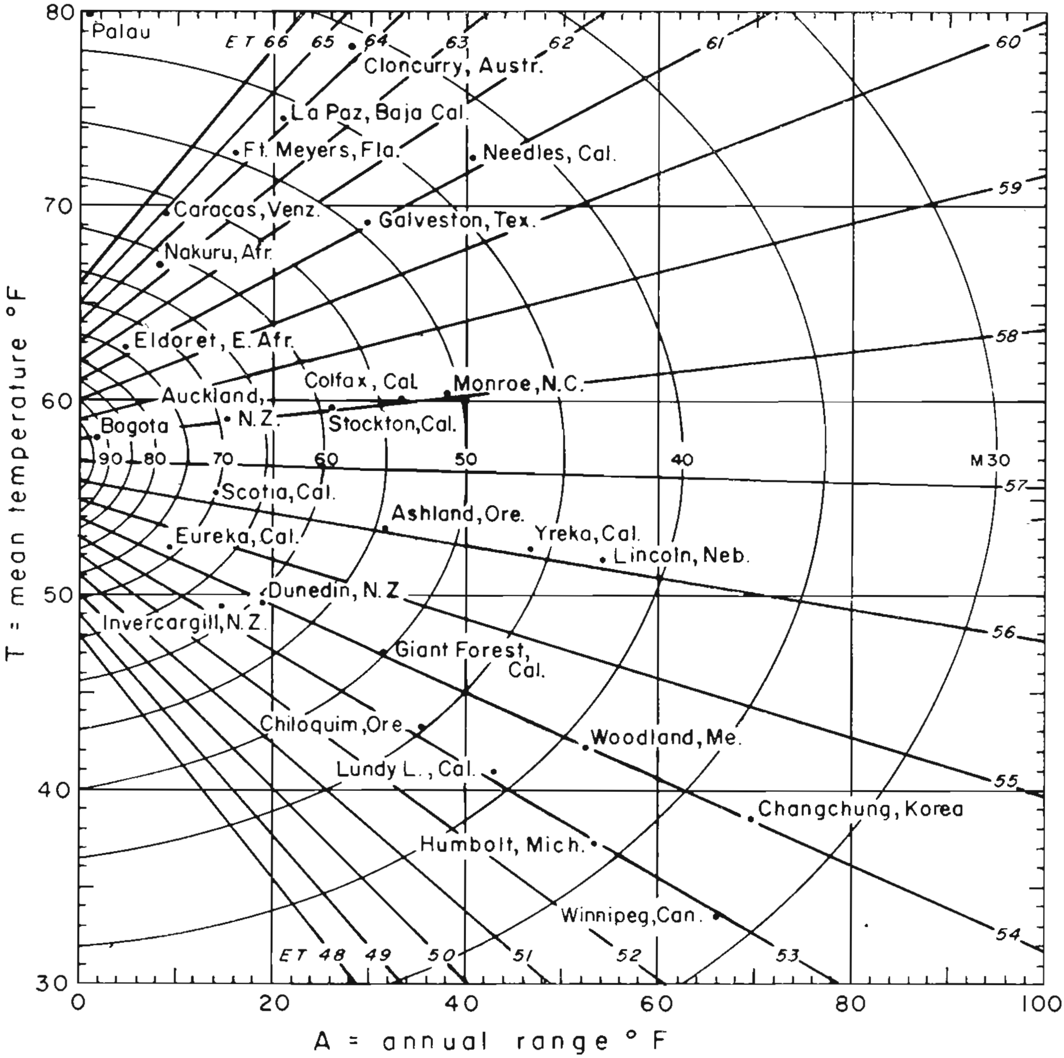
TABLE 1 — CLIMATIC CLASSIFICATION IN TERMS OF EFFECTIVE TEMPERATURE (BAILEY, 1960)

	MAJOR CATEGORY	*ET*		DAYS WITH AVERAGE TEMP. <*ET*	MINOR CATEGORY
		°C	°F		
TROPICAL	Climates of low latitudes				torrid
		24·1	75·4		
					hot
		20·8	69·4		
					very warm
		18·0	64·4	365	
TEMPERATE	Climates of middle latitudes				warm
		15·5	59·9	227 (7 1/2 mo.)	
					mild
		13·4	56·1	165 (5 1/2 mo.)	
					cool
		11·6	52·9	108 (3 1/2 mo.)	
					very cool
		10·0	50·0	0	
POLAR	Climates of high latitudes and altitudes				cold
		8·6	47·5		
					very cold
		7·5	45·5		
					glacial



TEXT-FIG. 1 — Nomogram showing distribution of some North American stations according to their effective temperature (*ET*). Nomogram by H. P. Bailey, 1960.

between the limits of polar and tropical climate, and which is also approximately the mean temperature of the earth (BAILEY, 1960, 1964). If a climate is colder or warmer than 57·2°F, or if seasonal fluctuations in temperature exist, then the variation can be expressed by a series of arcs nearly normal to the *ET* lines, and which decrease in value from 100 as climate becomes more intemperate. The concept of temperateness is illustrated in Text-fig. 2. The graph plots selected stations of similar effective temperature (*ET*) along the radii, and which display a wide spread in terms of temperateness. A sshown there, the degree of temperateness near the edge of the polar zone (*ET* 53) decreases in proceeding to stations of higher annual range (*A*). At Invercargill (*A* 14) temperateness is *M* 62+ (read from the arcs) as compared with Winnipeg (*A* 65) and its *M* 32 rating. Similarly, at the margins of the tropics (*ET* 64), Nakuru (*A* 4) in the uplands (alt. 6, 024 ft) of Kenya has a temperateness of *M* 63 as contrasted with *M* 42 at Cloncurry (*A* 28) in the tropical scrub of northern Australia. Text-fig. 2 also shows that stations which depart most from an annual temperature of



TEXT-FIG. 2 — Distribution of stations according to their temperateness (*M*) and effective temperature (*ET*). Nomogram by H. P Bailey, 1963.

T 57·2 (or 14°C), even though having a similar annual range (Ft. Myers=*A* 17, Auckland=*A* 16), have a lower temperateness (*M*) rating: Ft. Myers (*T* 73) has a temperateness of *M* 49, whereas at Auckland (*T* 59) it is *M* 68. The meaning of *M* is further emphasized by comparing conditions at Palau (Koror) with those at Bogota (Text-fig. 2). Palau has a mean annual temperature of 80·8°F, the mean temperatures of the warm and cold months are 81·1°F and 80·2°F, giving an annual range of ·9°F, and an *M* rating of 43. Bogota has a mean annual temperature of 58°F, mean temperatures of the warm and cold months are 59°F and 57°F, the annual range is 2°F, and it has a temperateness rating of *M* 92 (Text-fig. 2).

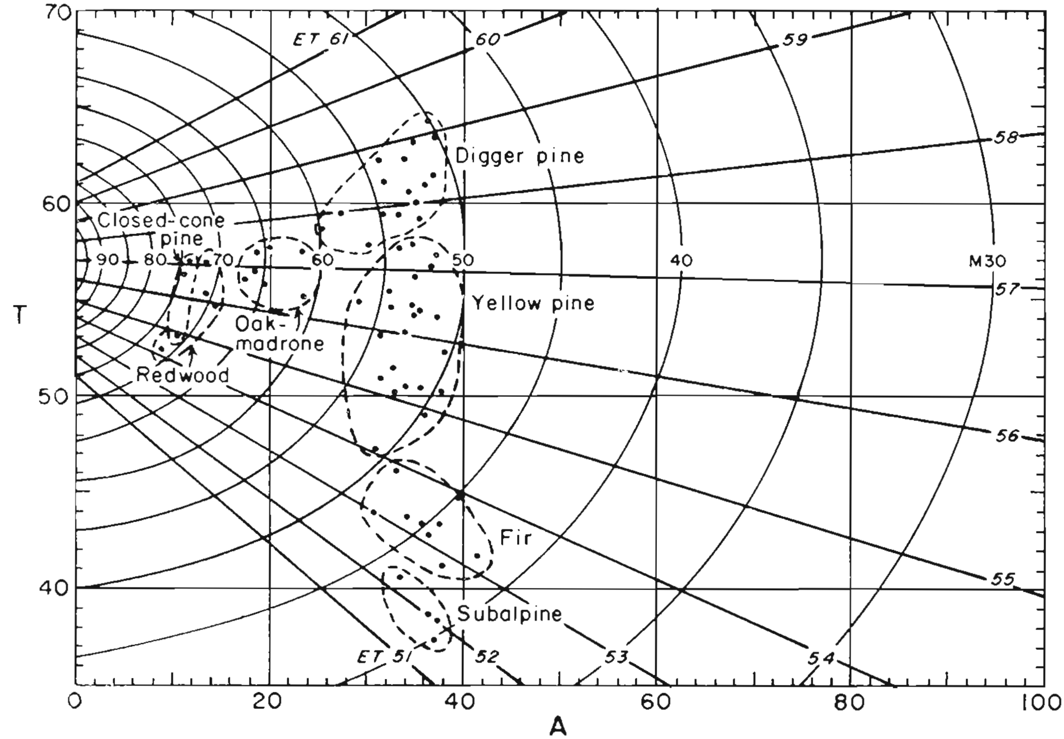
LIVING PLANT COMMUNITIES AND THEIR *TE-M* RELATIONS

That the concepts of warmth (*ET*) and temperateness (*M*) have meaning in terms of modern vegetation and climate can readily be demonstrated.

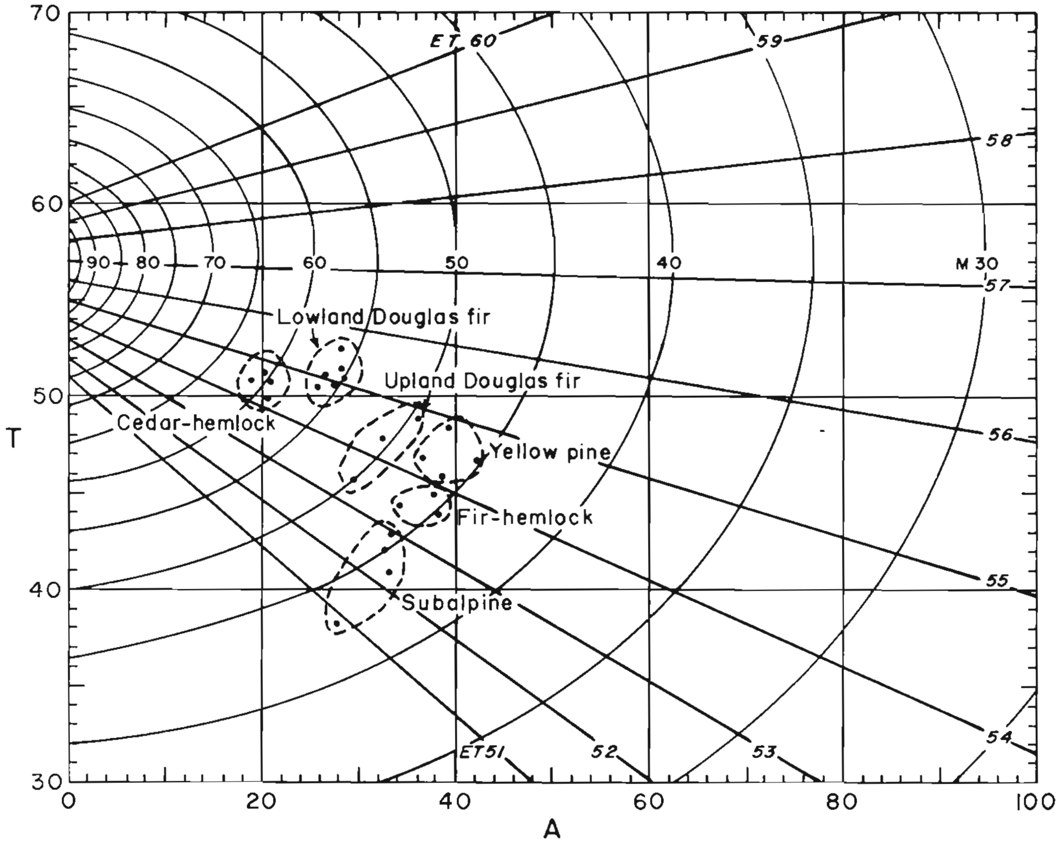
Text-fig. 3. Here are plotted the *ET* and *M* values for meteorological stations (Appendix 1) situated in the major forests of California, and which range from sea level to timberline. Segregation of the communities is apparent in terms of both factors, with closed-cone pine and redwood forests having the highest temperateness (*M*) ratings, subalpine forest the lowest.

Text-fig. 4. This shows the *ET* and *M* values at stations (Appendix 1) in the forests of southwestern Washington, with the coastal cedar-hemlock forest having the highest temperateness rating. The Douglas fir forest in the lowlands away from the coastal strip has nearly the same *ET*, but a lower temperateness due to slightly greater ranges of temperature.

Text-fig. 5. This illustrates the *ET* and *M* at stations (Appendix 1) in the principal forest regions of New England. The oak-pine forest of the coastal strip, here at its northern limit of distribution, has the highest effective temperature and temperateness. Note that both *ET* and *M* rapidly decrease inland as the oak-(chestnut)-tulip,



Text-fig. 3 — Illustrating the differences in the effective temperature (*ET*) and temperateness (*M*) requirements of California forests.



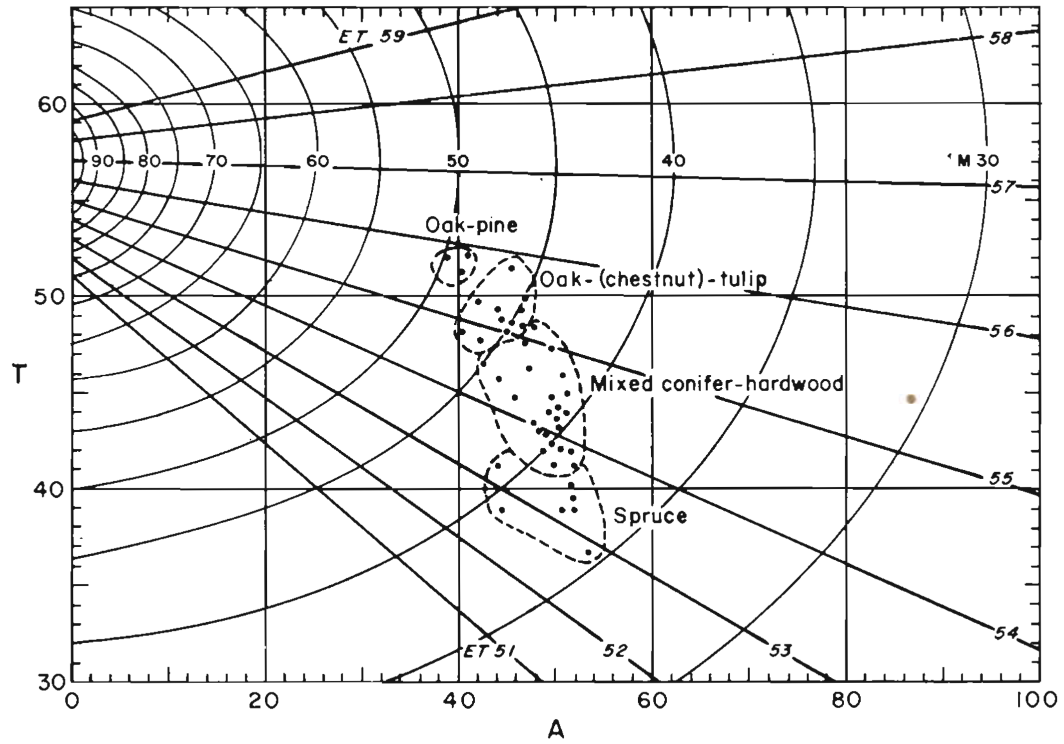
TEXT-FIG. 4 — Illustrating the differences in the effective temperature (*ET*) and temperateness (*M*) requirements of forests in south-western Washington.

conifer-hardwood, and spruce forests successively replace one another.

Text-fig. 6. Here are indicated the differences in *ET* and *M* requirements of the three principal desert floras of eastern California (Appendix 1). As noted by Shreve (1942), the Great Basin desert is composed of low shrubs which form communities that are simple in composition. The Mohave has more numerous and larger shrubs, and the communities are more complex. The Sonoran is an arboreal desert characterized by numerous succulents (cacti) and is a highly diversified flora.

Text-fig. 7. That there are important differences in the *ET* and *M* requirements of the major subdivisions of the desert floras in the western United States is shown in the figure (Appendix 1). The two principal divisions of the Sonoran desert of southwestern Arizona (NICHOL, 1937) are the *Larrea-Franseria* association of the low valleys, and the succulent desert of the bordering hillslopes which occupies areas of higher temperateness. In the Great Basin desert of west-central Nevada (BILLINGS, 1949), the lowlands support a shadscale desert whereas the adjacent hills have a sagebrush community which occupies areas of slightly lower temperateness.

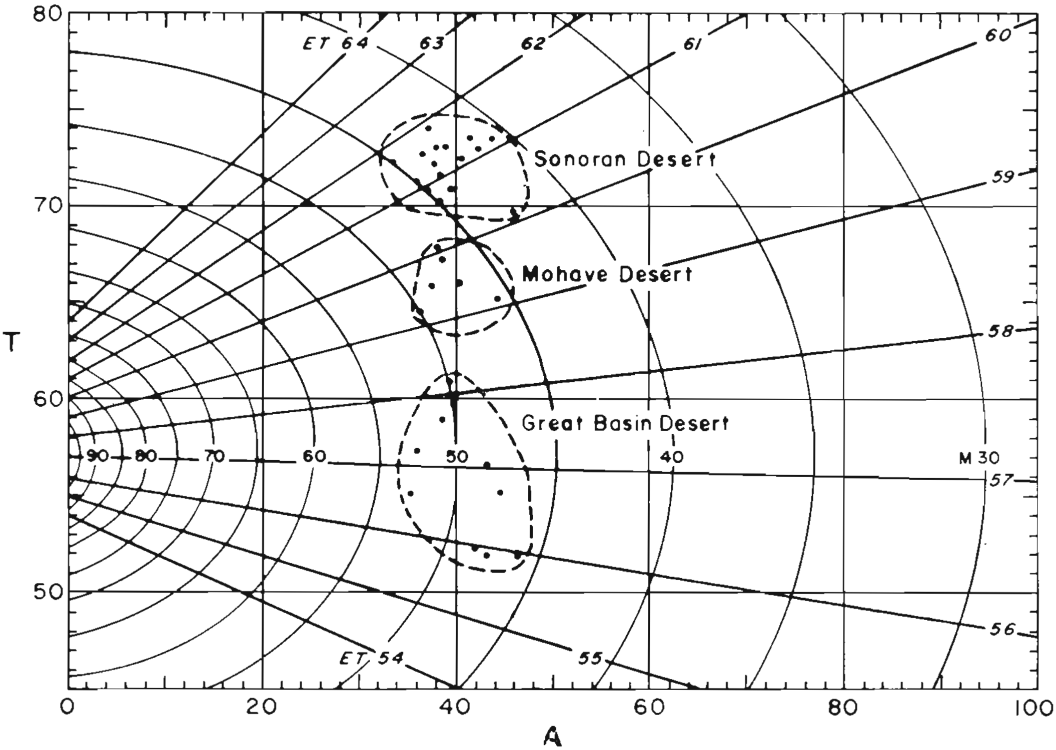
Text-fig. 8. Hopkins (1959) attempted to find a relation between the distribution of the three major vegetation types of Alaska (Sitka spruce-hemlock forest, white spruce-birch forest, tundra) and temperature. Using data for 70-odd stations, the parameters selected for study were (*a*) the number of days with temperature above 50°F, and (*b*) the mean temperature of the coldest month. When plotted graphically, the results showed a fair correlation though he noted 11 " anomolous " stations.



TEXT-FIG. 5 — Illustrating the differences in effective temperature (*ET*) and temperateness (*M*) requirements of forests in New England.

The stations were evaluated according to their *ET* and *M* values (TEXT-FIG. 8), and it is evident that they not only display a better segregation in terms of the three major vegetation types, each major community divides into subordinate units in terms of their *M* requirements. Both forests have rather similar heat requirements (*ET* 51-52) as noted by Hopkins, but as figure 8 shows the chief difference is in their temperateness: *M* 36-52 for Sitka spruce-hemlock forest, *M* 23-36 for white spruce-birch forest. The Sitka spruce-hemlock forest divides into two parts, with stations in the interior or in ecotone with White spruce-birch forest having a lower *M* rating than those along the southeast coast. The White spruce-birch forest also has two phases in terms of temperateness, with stations at the head of Cook Inlet or on the coast to the west having a higher *M* rating than the forest in the interior. Figure 8 shows that there are four major subdivisions to tundra vegetation in terms of *M* values, with temperateness decreasing northward as range of temperature (*A*) becomes greater. There are only three " anomolous " stations. Two of them (Dillingham, Middleton) are in the tundra zone which overlaps Sitka spruce-hemlock forest, and the other (Palmer) is in White spruce-hemlock forest, which overlaps Sitka spruce-hemlock forest. All of them may be explained by their relatively short record from the late ‘thirties on, and which reflects the warming trend at middle and higher latitudes. Since these stations are near the ecotones to other communities, it is the increased summer warmth that makes them appear anomolous because they now have *ET* values like adjacent, relatively stabilized forest communities which have not yet had time to supplant tundra in these " anomolous " areas.

It is apparent from these examples (TEXT-FIGS. 3-8) that the concepts of *ET* and *M* provide a sound basis for expressing accurately the major climatic requirements of living plant communities. They also seem sufficiently sensitive to discriminate



TEXT-FIG. 6 — Illustrating the differences in effective temperature (*ET*) and temperateness (*M*) requirements of desert vegetation in south-eastern California.

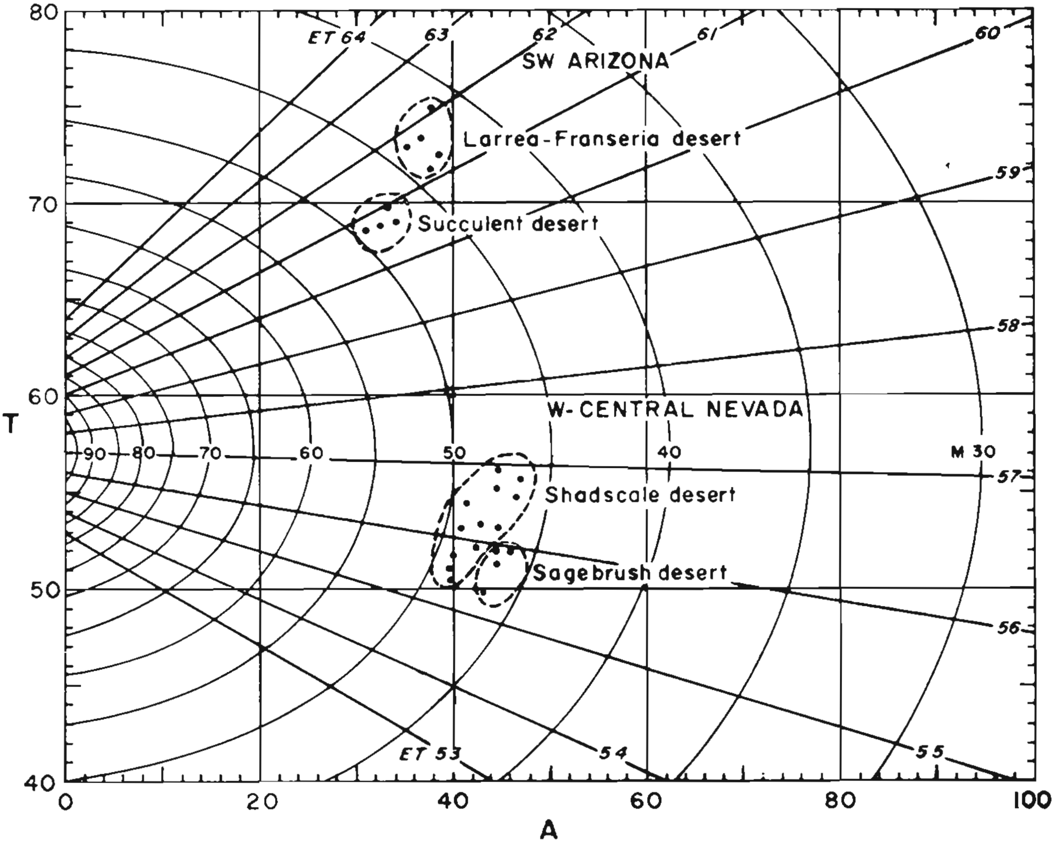
between minor communities of major vegetation types which heretofore have not readily been assessable in terms of climate. *ET* and *M* thus appear to provide a more reliable basis for interpreting the climatic conditions under which Tertiary floras lived.

SOME RELICT TERTIARY FORESTS AND THEIR *ET*-*M* RELATIONS

Warm Temperate Forests

I. The warm temperate broad-leafed evergreen forests of southeastern Asia (WANG, 1961) and eastern Mexico (MIRANDA & SHARP, 1950) represent the nearest modern analogues of most of the early Tertiary lowland floras of middle northern latitudes. In upland areas these living forests persist under high temperateness. In Yunnan, at Tengchung (alt. 5,300 ft.) and Kunming (6,200 ft.), *M* is 63 and 62, and *ET* is 57·6 and 58·2, respectively. By contrast, lowland stations in the forest (Kweilin, Kian, Chanting, Yunkia) have a higher *ET* (58·7-59·4) and temperateness is appreciably lower (*M* 45-50). Similar relations are displayed by the forest of the east Mexican escarpment. For example, at Huachianango, Puebla (alt. 5,100 ft.), *ET* is 59 yet it is a frostless climate (*M* 68), and tropical and temperate plants are well intermixed (MIRANDA & SHARP, 1950). This area is " cooler " than New Orleans (*ET* 61·4) which supports a mixed deciduous hardwood forest in which evergreens are rare, and *M* is only 48. Thus it becomes understandable that at times of high temperateness, as in the early and middle Tertiary, the *ET* of a Tertiary flora may have been appreciably lower than that which might be inferred from some analogous modern lowland forests.

II. A good part of the sclerophyll vegetation which contributed to the Madro-Tertiary Geoflora of southwestern North America (AXELROD, 1958) has survived in regions of high temperateness. Outstanding among these areas is the Channel Islands off the coast of southern California, where temperateness is pronounced (*M* 70+),



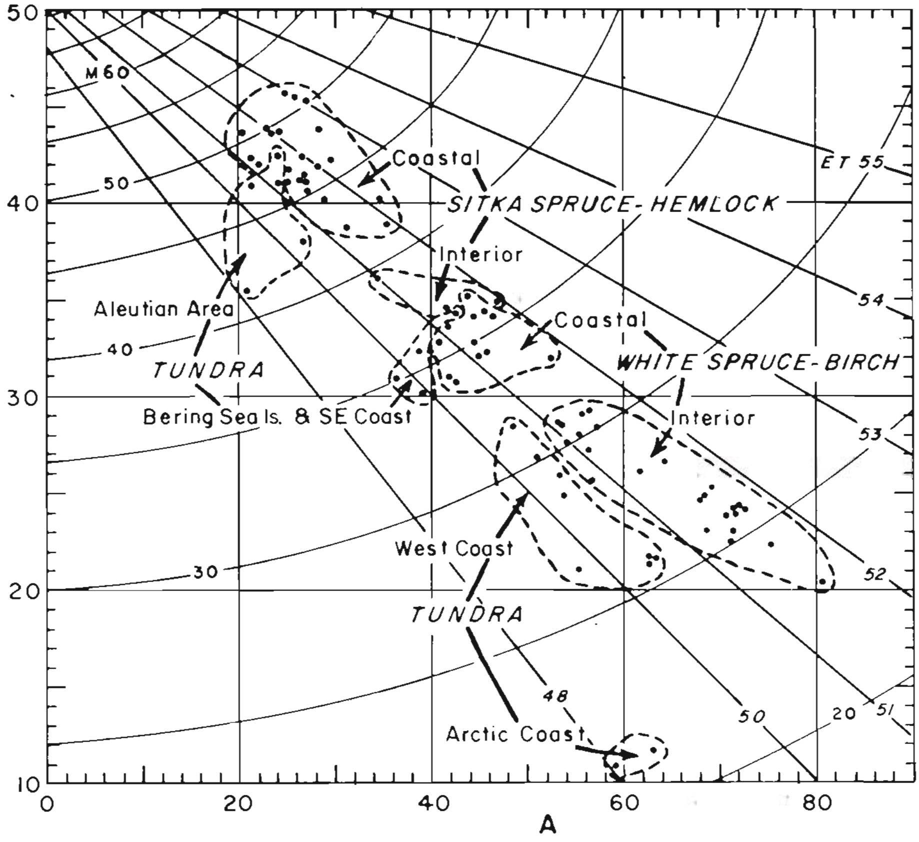
TEXT-FIG. 7 — Illustrating differences in effective temperature (*ET*) and temperateness (*M*) requirements of two major divisions of the Great Basin desert in west-central Nevada, and of the Sonoran desert in south-western Arizona.

and where relicts of the Tertiary persist which no longer occur on the continent. Similar relations are displayed by woodland vegetation in the uplands of the Cape Region of Baja California where relict endemics survive in an area of high temperateness (*M* 60+). Similar conditions occur also at middle altitudes in northwestern (Sonora, Sinaloa) and in northeastern (Nuevo Leon) Mexico, in the oak zone which interfingers with subtropical forest at lower levels, and with pine forest above, and which contains many endemics whose Tertiary relatives had a wider distribution on the continent. Other segregates of the woodland and scrub vegetation derived from the Madro-Tertiary Geoflora occur now in areas where temperateness is not as high as in the insular region. In southern California, oak woodland and chaparral inhabit areas where *M* is 60-65, but in the closely related vegetation in central Arizona it is *M* 55-50. It is apparent that these latter segregates became adapted to climates of lower temperateness during the later Cenozoic.

III. The laurel forest which is richly represented in the later Tertiary of southern Europe persists in scarcely modified form in the Canary and Madeira islands, where it lives in the uplands (4,000 ft.) under high temperateness (*M* 65). The forest was eliminated from southern Europe and adjacent Africa at the close of the Tertiary in response to the extreme — more intemperate — climates which accompanied glaciation.

Temperate Forests

I. The mixed deciduous hardwood forest of Szechuan and western Hupeh in



TEXT-FIG. 8 — Illustrating the differences in effective temperature (*ET*) and temperateness (*M*) of three major vegetation types in Alaska.

central China comprises the richest temperate forest in the Northern Hemisphere which has survived from the Tertiary. Its regional relations and composition have been described (CHENG, 1939; WANG, 1961), and its affinity with the Arcto-Tertiary Geoflora is well established (CHANEY & HU, 1940). Judging from fossil floras in the Arcto-Tertiary province, the Tertiary forest was richer than the surviving, for it included more numerous genera of hardwoods and conifers, and also evergreens, which are now found in widely separated regions.

Of primary interest is the nature of the climate which has enabled the forest to persist in a relatively unaltered state. The region is well watered, with precipitation distributed in all months of the year, and concentrated in the warm season. A large part of the hilly terrain in the upper Yangtze basin where the richest part of the flora occurs is essentially frost-free: it is subjected to only light freezing, which implies a temperateness rating near *M* 60. High temperateness results from the winter cloud cover which forms as adiabatically warmed westerlies pour off the Tibetan plateau, creating a " lid " over moister air trapped in the basin (HARE, 1961, p. 146). Not only does the cloud cover largely protect the region from severe freezing in winter, the surrounding topography is highly favourable for it forms a barrier to cold air which might otherwise drain into the area from the frigid interior (CHU & COOPER, 1950).

II. The coast redwood forest of northern California lives in an area of pronounced temperateness (*M* 65-70+), and it grades into the cedar-hemlock forest at the north which also lives under high temperateness

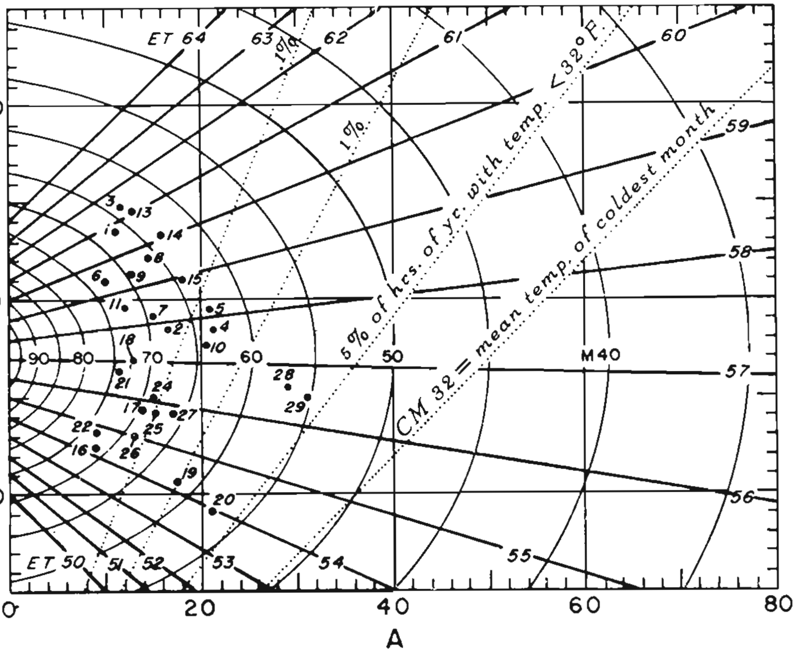
(*M* 55-70). The species of *Abies, Chamaecyparis, Sequoia, Thuja,* and their associates, whose close fossil relatives formed an important part of the Arcto-Tertiary Geoflora, have survived in a favourable environment created by (*a*) the dense fog that reduces high temperatures in summer, and by (*b*) the mountains to the east (Coast Ranges, Cascades, Sierra Nevada) which substantially shelter them from invasions of cold winter air from the interior. Some of their associates in the western Tertiary floras which have survived in scarcely modified from in the nearby region, and contribute to the forests of the Sierra-Cascade axis, live in a climate of lower temperateness (*see* TEXT-FIGS. 3, 4), a condition to which they gradually became adapted during Pliocene and later times.

III. Members of the *Nothofagus* forests, now typical of the Fuegan and Tasman regions, formed a major element of the Antarcto-Tertiary Geoflora which ranged across high southern temperate latitudes during the Cretaceous and Tertiary when wider land areas were present (AXELROD, 1960). These forests also survive under conditions of high temperateness, created in large part by their maritime position. In southern Chile *M* is 65-70, and in much of New Zealand, southeastern Australia, and Tasmania temperateness is also pronounced (*M* 60-75).

Summarizing, essential freedom from frost, or only light frost, typifies areas where relict vegetation most like that of the Tertiary now lives, as shown in Text-fig. 9 (see Appendix for stations). In reconstructing paleoclimate by comparing Tertiary floras with similar modern communities sounder inferences may be made if conditions of *ET* and *M* prevailing in such areas are used as a basis for analogy. Furthermore, in using climatic data (*ET*) to estimate altitude, conditions in forests that live under high temperateness provide a more reliable basis for inference.

ALTITUDES OF MODERN FORESTS CALCULATED FROM *ET*

Altitude may be determined from effective temperature. This is evident from the following examples (TABLES 2-9) which



TEXT-FIG. 9 — Illustrating pronounced temperateness (*M*) which exists in areas where relict forests of the Tertiary now live. Compare with figures 2-8 in terms of temperateness (*M*). Stations with *M* less than 60 are Aberdeen, Wash. (20), Highlands, N. C. (28), and Logan, W. Va. (29). See Appendix for stations.

show calculations from *ET* at lowland stations of the altitude of *ET* at stations situated in different upland forests today. In Table 2, the temperatures at Lodi, Madera, and Visalia near sea level in the central and southern Great Valley of California are used to calculate the altitude of *ET* at station in the forest zones at higher levels in the Sierra Nevada to the east. The data show Twin Lakes (alt. 8,720 ft.) is 43·5 ft. too low, the altitude at Huntington Lake (alt. 7,296) is exact, and that for Giant Forest (alt. 6,334 ft.) is 43·6 ft. too low.

Table 3. Here the temperatures for Marysville in the northern Great Valley of California are used to determine the altitude of *ET* at stations at higher levels in the Sierra Nevada to the east. The results are not as exact as those in the preceding example, and for the obvious reason that Nevada City and Norden are situated in valleys that have cold air drainage in summer, and which depresses the temperature of the warm month. Even so, the altitudes calculated are within the height of tall trees (83 ft. for Nevada City, 125 ft. for Norden), whereas the altitude of Blue Canyon is precisely correct.

Table 4. The altitudes of stations in the humid forests of the southern Cascades of Oregon are determined from data at Glendale (alt. 1,441 ft.) in the Rogue River Valley in this example. Here there is again a nearly exact correlation with calculated altitude of *ET* at upland stations because they occur in sites which more

TABLE 2 — CALCULATIONS FROM LOWLAND STATIONS IN VALLEY OF CALIFORNIA OF *ET* AT STATIONS IN UPLAND FORESTS OF SIERRA NEVADA*

STATION	VEGETATION	ALT.	WM	CM	ET	ERROR IN FEET
Lodi	Grassland	50 ft.	73·3	46·2	58·1	
Twin Lakes	Subalpine forest	8,720	56·0	23·7	51·9	
,, *calculated from Lodi*	,, ,,	,,	55·4	28·3	52·0	−43·5
Madera	Grassland	296	78·9	44·4	58·4	
Huntington Lake	Fir forest	7,296	61·4	29·5	53·7	
,, *calculated from Madera*	,, ,,	,,	62·8	28·2	53·7	0
Visalia	Grassland	296	80·3	46·4	59·0	
Giant Forest	Sierra redwood forest	6,334	65·7	33·1	54·8	
,, *calculated from Visalia*	,,	,,	66·5	32·6	54·9	−43·5

*Calculations based on lapse rate of 2·3°F./1,000 ft. WM = mean temp. of warmest month; CM = mean temp. of coldest month.

TABLE 3 — CALCULATIONS FROM A LOWLAND STATION OF SUCCESSIVE CHANGES IN *ET* AT HIGHER ALTITUDES IN NORTHERN SIERRA NEVADA, CALIFORNIA*

STATION	VEGETATION	ALT.	WM	CM	ET	ERROR IN FEET
Marysville	Grassland	67	79·1	45·5	58·7	
Nevada City	Lower Yellow pine forest	2,600	68·7‡	40·9	56·4	
,, *calculated from Marysville*	,,	,,	72·8	39·2	56·8	−83·4
Blue Canyon	Upper Yellow pine forest	4,700	66·8	36·5	55·4	
,, *calculated from Marysville*	,,	,,	67·8	34·2	55·4	0
Norden	Fir forest	6,640	61·4‡	29·5	53·6	
,, *calculated from Marysville*	,,	,,	63·1	29·5	53·9	−125·1

*Calculations based on lapse rate of 2·4°F./1,000 ft.; WM = mean temp. warmest month; CM = mean temp. of coldest month.

‡Anomaly probably due to cold air drainage since stations are in deep canyons.

TABLE 4 — CALCULATIONS FROM A LOWLAND STATION OF SUCCESSIVE CHANGES IN *ET* AT HIGHER ALTITUDES IN SOUTHERN CASCADES, OREGON*

Station	Vegetation	Alt.	WM	CM	ET	Error in feet
Glendale	lower Douglas fir—yellow pine forest	1,441	68·1	39·5	56·1	
Prospect	upper Douglas fir—yellow pine forest	2,473	65·8	35·1	55·1	
,, *calculated from Glendale*	,,	,,	65·4	36·8	55·2	−40
Fish Lake	Fir forest	4,800	60·5	29·0	53·3	
,, *calculated from Glendale*	,,	,,	59·6	31·0	53·3	0
Crater Lake	Subalpine forest	6,400	56·5	25·2	52·0	
,, *calculated from Glendale*	,,	,,	55·6	27·0	51·9	+40

*Calculations based on lapse rate of 2·5°F./1,000 ft., WM = mean temp. of warmest month; CM = mean temp. of coldest month.

TABLE 5 — CALCULATIONS FROM LOWLAND STATIONS OF ALTITUDES OF *ET* AT STATIONS IN UPLAND AREAS, NORTH CAROLINA*

Station	Alt	WM	CM	ET	Error in feet
Plymouth	21 ft.	78·1	46·2	58·7	
Chapel Hill	500	78·9	42·5	58·2	
,, *calculated from Plymouth*	,,	76·4	44·5	58·3	−27·8
Hickory	1,165	76·9	41·4	57·8	
,, *calculated from Plymouth*	,,	74·0	42·1	57·5	+83·4
Hendersonville	2,253	73·2	39·7	56·9	
,, *calculated from Plymouth*	,,	70·1	38·2	56·3	+164·4
Parker	4,075	66·8	34·0	55·2	
,, *calculated from Plymouth*	,,	63·5	31·6	54·3	+250·2
Mt. Mitchell	6,684	59·2	28·7	52·9	
,, *calculated from Plymouth*	,,	54·2	22·3	51·4	+417·0

*Assuming a normal lapse rate, 3·6°/1,000 ft.

nearly reflect normal terrain than do those of the preceding example. As shown in the table, the altitudes for Prospect (alt. 2,473) and Fish Lake (alt. 4,800 ft.) are both 40 feet too low, whereas that for Crater Lake (alt. 6,400 ft.) is exact.

Table 5. In the eastern United States, calculations were made from a sea level station (Plymouth) in North Carolina for the altitudes of *ET* at stations distributed westward to the crest of the Great Smoky Mountains. Assuming a normal lapse rate, there is a high correspondence between the actual and calculated levels for *ET* at stations up to moderate altitudes, with departures of only -27·8 ft. for Chapel Hill, +83·4 ft. for Hickory, and +164·4 ft. for Hendersonville. At the higher stations (Parker, Mt. Mitchell), the temperatures for both the warmest and coldest months calculated from Plymouth are cooler than the observed, and hence these upland stations differ somewhat more in calculated and observed altitude for *ET*; estimates for Parker (alt. 4,075 ft.) and for Mt. Mitchell (alt. 6,684 ft.) are 250·2 ft. and 417·0 ft. too high, respectively. Even so, the calculated altitudes of the highest forest zones are not affected.

In order to ascertain the basis for the greater discrepancy in the levels calculated for *ET* in the uplands in this area as compared with other regions, estimates were made using lapse rate 3·0. As shown in

Table 6, this gives nearly the correct values at all stations between observed and calculated *ET* and latitude: the departures are 33·3 feet low for Chapel Hill and Hickory, and 66·6 feet too high for Hendersonville, Parker and Mt. Mitchell. The data suggest that the Bermuda high pressure system may have a greater effect on lapse rate in this region than is generally assumed, making it somewhat less than 3·6°F per 1,000 feet, usually considered as the standard lapse rate.

Table 7. Here are shown calculations for altitudes of *ET* at upland stations in three areas in Japan. The calculation from Tu (alt. 15 ft.) for the altitude of Odaigahara (alt. 5,139 ft.) is 27·8 feet too high; calculations from Huisiki (alt. 439 ft.) for Matumoto (alt. 1,732 ft.) and Oiwake (alt. 3,282 ft.) are 111·2 and 55·6 feet too low, respectively. From Numadu (alt. 24 ft.) determination of the altitudes of Kohu (alt. 856 ft.) and Otiai (alt. 3,686 ft.) are 166·8 and 55·6 feet too low, respectively.

TABLE 6 — RECALCULATIONS FROM LOWLAND STATIONS OF ALTITUDES OF *ET* AT STATIONS IN UPLAND AREAS, NORTH CAROLINA*

STATION	ALT.	WM	CM	ET	ERROR IN FEET
Plymouth	21 ft.	78·1	46·2	58·7	
Chapel Hill	500	78·9	42·5	58·2	
,, *calculated from Plymouth*	,,	76·7	44·8	58·3	−33·3
Hickory	1,165	76·9	41·3	57·8	
,, *calculated from Plymouth*	,,	74·7	42·8	57·7	+33·3
Hendersonville	2,253	73·2	39·7	56·9	
,, *calculated from Plymouth*	,,	71·4	39·5	56·7	+66·6
Parker	4,075	66·8	34·0	55·2	
,, *calculated from Plymouth*	,,	66·0	34·1	55·0	+66·6
Mt. Mitchell	6,684	59·2	28·7	52·9	
,, *calculated from Plymouth*	,,	58·2	26·3	52·7	+66·6

*Assumes a lapse rate of 3·0°F./1,000 ft.

TABLE 7 — CALCULATIONS FROM LOWLAND STATIONS OF ALTITUDE OF *ET* AT STATIONS IN UPLAND AREAS, CENTRAL JAPAN*

STATION	ALT.	WM	CM	ET	ERROR IN FEET
I. Tu (34°44′, 136°31′)	15 ft.	79·2	39·4	57·7	
Odaigahara (34° 11′, 136° 06′)	5,139	62·9	20·1	52·9	
,, *calculated from Tu*	,,	60·7	19·9	52·8	+27·8
II. Husiki (36° 47′, 137° 03′)	439	78·2	36·1	57·2	
Matumoto (36° 14′, 137° 59′)	1,732	73·0	28·2‡	55·6	
,, *calculated from Husiki*	,,	73·5	31·4	56·0	−111·2
Oiwake (36° 20′, 138° 33′)	3,282	68·2	23·5	54·4	
,, *calculated from Husiki*	,,	68·0	25·9	54·6	−55·6
III. Numadu (35° 06′, 138° 51′)	24	78·6	41·7	58·0	
Kohu (35° 38′, 138° 34′)	856	77·7	43·2‡	56·9	
,, *calculated from Numadu*	,,	76·7	39·8	57·5	−166·8
Otiai (Kai) (35° 48′, 138° 49′)	3,686	66·0	24·8	52·2	
,, *calculated from Numadu*	,,	65·4	28·5	52·4	−55·6

*Assumes a normal lapse rate, 3·6°F/1,000 ft.
‡Departures from calculated values probably due to local terrain.

These results are within the height of trees.

Table 8. To test the method in the Southern Hemisphere, calculations for the altitudes of *ET* at stations in New Zealand are presented here. On North Island, the *ET* at Napier (alt. 5 ft.) was used to determine the altitudes of *ET* at Kariori (alt. 2,125 ft.) and Chateau Tongariro (alt. 3,670 ft.), and the results are 27·8 feet too low and 83·4 ft. too high, respectively. The *ET* at Hastings (alt. 451 ft.) used to determine the altitude of Taihape (alt. 2,157) gives a figure 27 feet too high.

On South Island the results are surprisingly accurate considering that the stations are more scattered and that high relief exerts an important control on the distribution of temperature. As shown in Table 8, using Akaroa (alt. 150 ft.) the calculations for the altitudes of *ET* at Rudstone (alt. 1,217 ft.) and Hermitage (alt. 2,510 ft.) are 111·2 and 166·8 feet too high. With Alexander (alt. 520 ft.) as a base, Ophir (alt. 1,000 ft.) is 27·8 ft. too high, and Manorburn Dam (alt. 2,448 ft.) is 111·2 ft. too low — all within the height of trees.

Table 9. Finally, to test the method in a tropical region the altitudes of several stations in eastern India were determined from the data at Calcutta (alt. 21 ft.). Here we find that Cherrapunji (alt. 4,309 ft.) is 63·4 ft. too low, Shillong (alt. 4,920 ft.) is 55·6 ft. too low, and Darjeeling (alt. 7,376 ft.) is precisely correct.

Such close correspondence between *ET* at higher altitudes, and that calculated there from lowland stations, cannot always be expected today because diverse climatic conditions may exist in local areas. For example, the persistent, dense summer fog in the lowlands of western Washington depresses the temperature of the warm month to a low level. As a result, calculations from a lowland station do not portray accurately the altitudes of cool upland

TABLE 8 — CALCULATIONS FROM LOWLAND STATIONS OF ALTITUDE OF *ET* AT UPLAND STATIONS, NEW ZEALAND*

STATION	ALT.	WM	CM	ET	ERROR IN FEET
NORTH ISLAND					
I. Napier (39° 29′, 176° 55′)	5 ft.	65·5	47·3	56·8	
Kariori (39° 28′, 175° 31′)	2,125	57·6	40·4	53·4	
,, *calculated from Napier*	,,	57·9	39·7	53·5	−27·8
Chateau Tongariro (39° 12′, 175° 32′)	3,670	53·1	36·0	51·4	
,, *calculated from Napier*	,,	52·3	34·1	51·1	+83·4
II. Hastings (39° 39′, 176° 51′)	451	65·3	45·9	56·5	
Taihape (39° 39′, 175° 49′)	2,157	59·2	41·4	54·1	
,, *calculated from Hastings*	,,	59·1	39·7	54·0	+27·8
SOUTH ISLAND					
III. Akaroa (43° 46′, 172° 56′)	150	62·0	44·6	55·3	
Rudstone (43° 333′, 171° 42′)	1,217	59·2	40·8	54·1	
,, *calculated from Akaroa*	,,	58·2	40·8	53·7	+111·2
Hermitage (Mt. Cook) (43° 43′, 170° 07′)	2,510	56·1	34·5	52·3	
,, *calculated from Akaroa*	,,	53·5	36·1	51·7	+166·8
IV. Alexander (45° 15′, 169° 24′)	520	61·7	36·3	54·2	
Ophir (45° 07′, 169° 36′)	1,000	60·2	34·8	53·7	
,, *calculated from Alexander*	,,	59·9	34·5	53·6	+27·8
Manorburn Dam (45° 22′, 169° 36′)	2,448	53·6	30·0	51·3	
,, *calculated from Alexander*	,,	54·7	29·3	51·7	−111·2

*Assumes a normal lapse rate, 3·6°F/1,000 ft.

TABLE 9 – CALCULATIONS FROM A LOWLAND STATION OF ALTITUDE OF *ET* AT UPLAND STATIONS, EASTERN INDIA

STATION	ALT.	WM	CM	ET	ERROR IN FEET
Calcutta	21	87·8	68·3	66·1	
Cherrapunji	4,309	68·6	53·6	59·2	
,, *calculated from Calcutta*	,,	72·4	52·9	59·5	−63·4
Shillong	4,920	70·2	49·6	58·4	
,, *calculated from Calcutta*	7 ,,	70·2	50·7	58·6	−55·6
Darjeeling	37,6	61	40	54·5	
,, *calculated from Calcutta*	,,	60·5	40·5	54·5	0

stations in the nearby Cascades to the east. A somewhat different situation occurs in southern California. Using interior stations to determine the altitude of upland stations (San Bernardino for Arrowhead at 5,150 ft.; San Jacinto for Idyllwild at 5,250 ft.) the levels are 300 feet too low because the inversion in summer gives upland stations higher temperatures than normal.

These small departures, as well as those noted above for terrain influence (cold air drainage, etc.), clearly reflect the sensitivity of *ET* to local changes in climate (warmth). Environmental variation of this sort may reasonably be supposed to have been reduced or absent in the early and middle Tertiary, and of only slight significance in the late Tertiary. During most of the period climates were broadly zoned, high latitudes had a temperate climate, hot dry interior regions were restricted in area, and upwelling did not produce fog-bound coastal strips in summer. Furthermore, with generally lower continents and the absence of high relief like that of today there would be a more even distribution to temperature over wide regions and local anomalies (cold air drainage, warm sites, temperature inversions) would have been rarely present. As a result of the more regular and even gradient of temperature, temperateness was high over broad regions during the Tertiary. It was chiefly near the close of the period, and during the Quaternary, as continents increased in altitude, as major mountain systems were elevated, as climates became more prominently zoned, as *new* regional climates (polar, tundra, steppe, etc.) developed, that temperateness was greatly reduced over wide areas. In terms of figure 10 (see below), during most of the Tertiary *ET-M* relations were to the left of the line 1·0 per cent freezing, and even at latitudes above 70° probably were not much below 10 per cent freezing (TEXT-FIG. 10) in the early Tertiary to judge from the floras in Greenland, Grinnell Land and other high latitude stations. They shifted to the right — to lower temperateness — in the later part of the period and during the Quaternary chiefly, as greater ranges and extremes of temperature developed.

Since vegetation zones can be distinguished accurately by their *ET-M* relations (TEXT-FIGS. 3-8), and since climatic data at lowland stations (TABLES 5-12) can be used to determine closely the altitudes of upland stations today, it seems probable that calculations of altitudes of Tertiary floras would have been no less accurate because gently zoned climates of high temperateness resulted in a more regular vertical distribution of the *ET* zones.

· ALTITUDES OF TERTIARY FLORAS

With these principles in mind, we turn now to illustrating how effective temperature (*ET*) may be used to estimate the altitudes of Tertiary floras, and of the climatic zones which they represent. Most of the floras under consideration have been described, so they need not be reviewed here. The first example, however, is based on a flora now under study so a few remarks are presented to indicate its geologic occurrence, composition, and age.

EOCENE SUBALPINE FOREST NEVADA

A flora from the Bull Run basin, northeastern Nevada, is preserved in lake beds at six localities near the middle of the exposed Tertiary section which rests on Paleozoic rocks and on biotite rhyolite lapilli tuffs dated as 42 million years old (Geochron

Laboratories Inc., Report No. 30439, 1964). The plant bearing section is overlain conformably by ashy shales which contain biotite rhyolite ash beds dated as 35 million years (Geochron Laboratories Inc., Report No. B0124, 1962). The latter is overlain unconformably by Jarbidge rhyolite, which in the area to the south is overlain unconformably by the Humboldt formation, the lower part of which yields middle Miocene early Barstovian-Temblor) mammals.

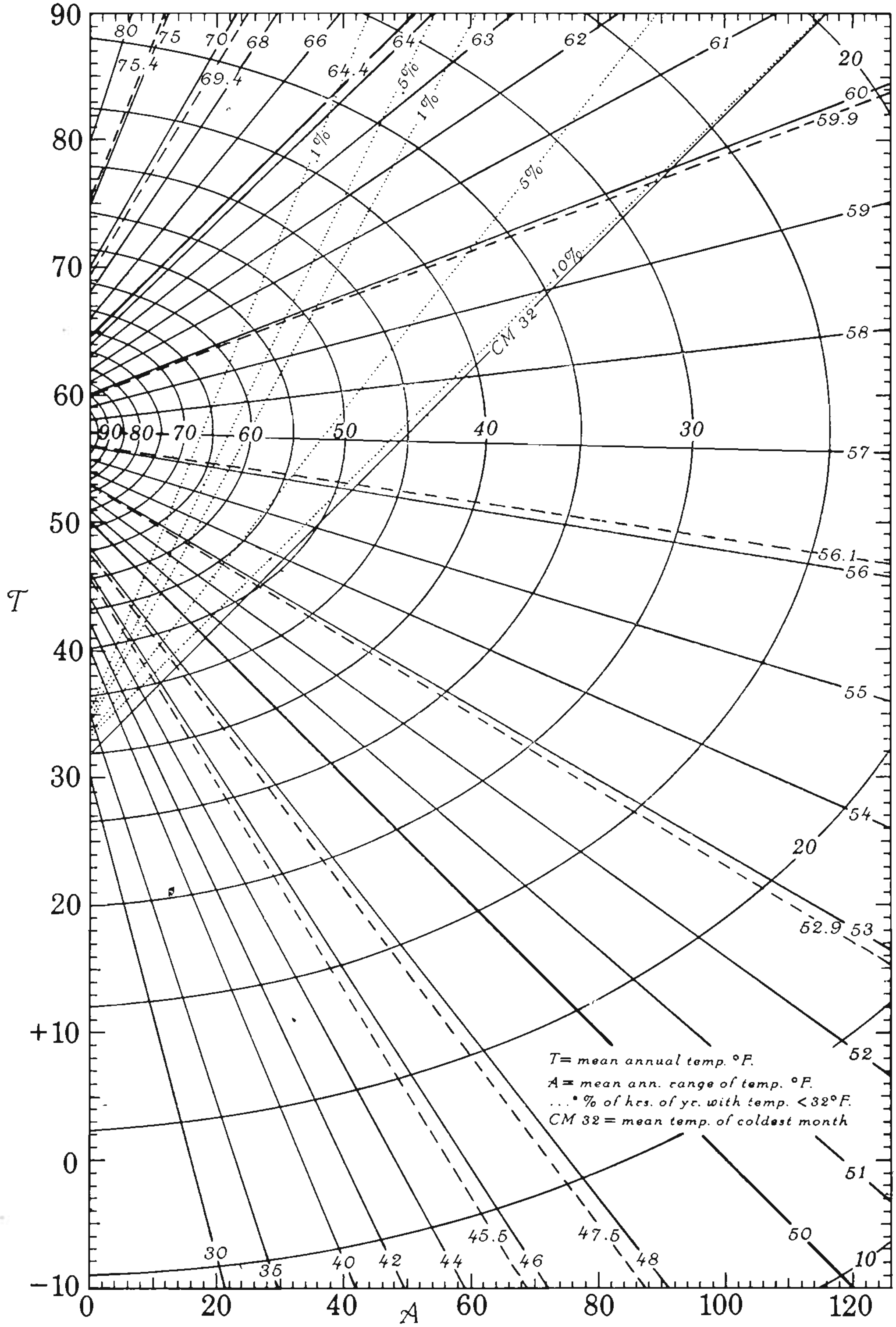
The three florules representing the upper Bull Run flora include more than 7,000 specimens of which montane conifers — *Abies* (2 spp.), *Picea* (3 spp.), *Pinus* (3 spp.), *Larix*, *Thuja*, and *Tsuga* — comprise 99 per cent of the sample. Angiosperms are represented by only a few shrubs, in such genera as *Mahonia*, *Pachystima*, *Prunus*, *Ribes* and *Vaccinium*. The flora represents a montane conifer forest, and it probably lived near the margin of the subalpine zone (*ET* 53) to judge from the complete absence of deciduous hardwoods in it.

The upper Bull Run flora is approximately contemporaneous with the late Eocene Montgomery Creek-Moonlight (California) and Comstock (Oregon) floras in the coastal region 350-400 miles west and northwest, and which represent warm temperate broadleafed evergreen forests. It is estimated that they lived under a climate with an *ET* of about 62, and annual range of temperature was near 10°F. By turning to figure 10, and finding the intersection of *ET* 62 with *A* 10, measure the vertical distance between *ET* 64·4 and *ET* 50. Scaling off this distance on the temperature scale at the left margin of the figure, we find that 24·5°F of mean annual temperature separates the tropical (*ET* 64·4) and polar (*ET* 50) zones. Assuming a normal lapse rate (3.6°F/1,000 ft., or 1°/278 ft.), this amounts to a vertical separation of 6,811 feet ($24{\cdot}5 \times 278 = 6{,}811$ ft.). By constructing a graphic scale (TEXT-FIG. 11), it is possible to measure and to visualize immediately the altitudes of the zones between *ET* 64·4 and 50. Using *ET* 62 (Montgomery Creek-Moonlight flora) as the datum for sea level, we see that *ET* 53 — the upper Bull Run flora — had an altitude of 4,300 feet. If *ET* in the coastal strip was somewhat higher (*ET* 63) or lower (*ET* 61), altitude would be increased or decreased by approximately 500 feet. If annual range of temperature (*A*) was slightly higher (*i. e.* 11) or lower (*i. e.* 9), then the altitude would be increased or decreased by about 250 feet.

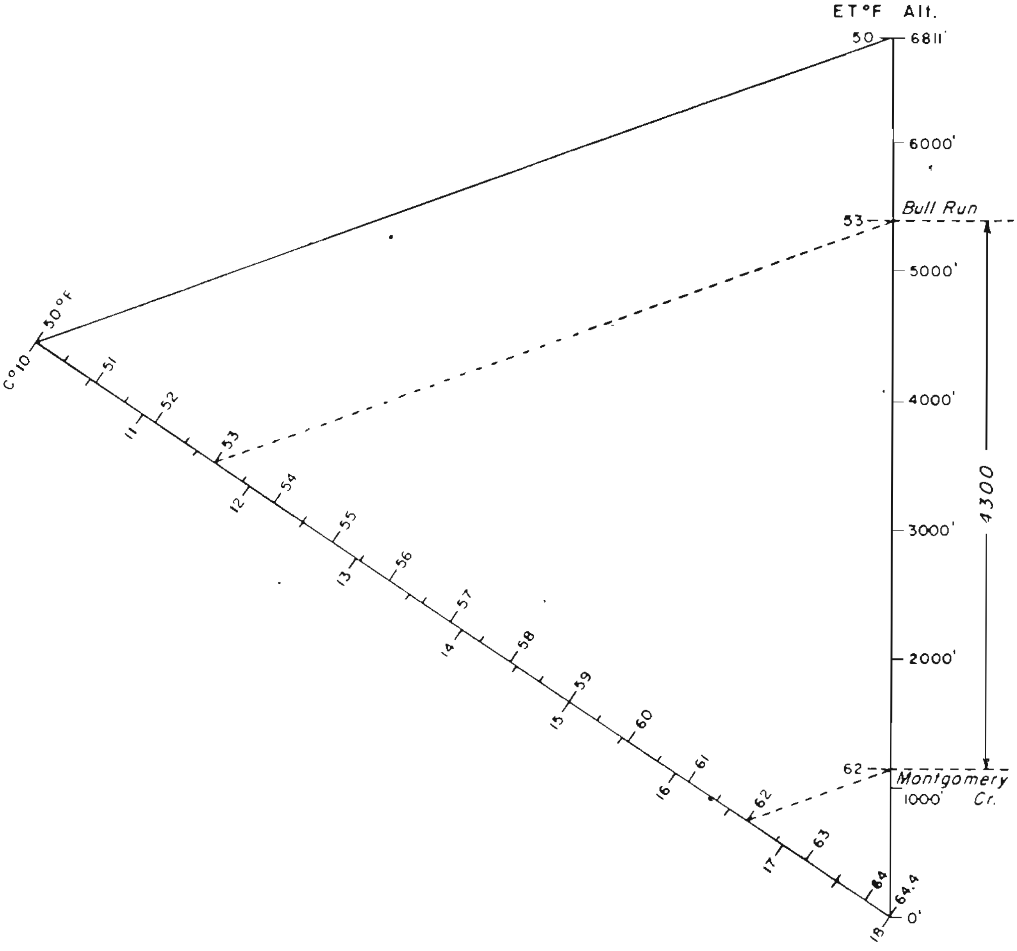
No doubt some readers will be skeptical that a montane conifer forest could have lived at an altitude only 4,300 feet above warm temperate broad-leafed evergreen forest in the Eocene at Lat. 41°N, yet comparable relations exist today in areas of high temperateness. On the eastern escarpment of Mexico warm temperate broad-leafed evergreen forest, which shows high relationship to the Eocene floras of northern California and Oregon, ranges up to about 5,000 feet near Jalapa (alt. 4,700 ft.), where conditions are *ET* 60·7 and *M* 67. Continuing up the slopes of the adjacent volcano Nauchampotepetel, montane conifer forest is reached at an altitude of 8,600 feet where *ET* is close to 53 as judged from the data at Las Vigas (alt. 8,187 ft., $WM = 56{\cdot}1$, $CM = 46{\cdot}4$, $ET = 53{\cdot}7$). Since the zone of *ET* 62 lies about 600 feet below Jalapa, the altitudinal separation of *ET* 62 and 53 is approximately 4,400 feet. Similar relations with respect to zones of warmth exist in southern Brazil, in the Serra da Mantiqueria 100 miles northwest of Rio de Janeiro. In this area broadleafed evergreen forest extends up to timberline which is at approximately 6,400 feet (CLAUSEN, 1963), a relation consistent with the pronounced temperateness there (*M* 72). Subalpine conifer forest is not represented here, though its lower margin would correspond with *ET* 53. Climatic data at Itatiaia (alt. 7,150 ft., $WM = 56{\cdot}5$°F, $CM = 46{\cdot}7$°F, $ET = 53{\cdot}8$) show that the zone of *ET* 53 lies close to 7,600 feet, or about 5,000 feet above the level of *ET* 62 in this region which can be calculated from Petropolis (alt. 2,667 ft., $WM = 70{\cdot}1$°F, $CM = 59{\cdot}5$°F, $ET = 61{\cdot}7$°). Thus in these modern examples from areas of high temperateness the zones of *ET* 62 and 53 are separated by approximately 4,400 (Jalapa) and 5,000 (Itatiaia) feet. When we note that they are near Lat. 20° and that the Bull Run flora is at Lat. 41°, an estimate of 4,300 feet for the Bull Run flora seems reasonable in view of the pronounced temperateness of early Tertiary climate.

EOCENE MIXED DECIDUOUS HARDWOOD FOREST, GREAT SMOKY MOUNTAINS

Cain (1943) assembled paleobotanical evidence to support Fernald's (1931) suggestion that a temperate deciduous hardwood



TEXT-FIG. 10 — Nomogram showing relations of effective temperature (radii), temperateness (arcs), and frost frequency lines, and which is used to calculate altitudes of modern and fossil floras. Nomogram by H. P. Bailey, 1964.



TEXT-FIG. 11 — Graphic scale illustrating how altitude of Bull Run flora may be calculated from *ET* at sea level.

forest probably occupied the higher parts of the Great Smoky Mountains during the Eocene, at which time the surrounding lowlands were covered with subtropical forests, as shown by the Wilcox and Claiborne floras (BERRY, 1924, 1930). The inference that mixed deciduous hardwood forests probably lived in the mountains was based on the occasional presence of leaves of temperate genera in the lowland Eocene floras. Brown (1940, 1944, 1946, 1960) partially revised the list of temperate plants that Cain assembled from Berry's studies, and recognized temperate species of *Acer*, *Betula*, *Cercidiphyllum*, *Comptonia*, *Eucommia*, *Fagus*, *Sassafras*, *Staphylea*, *Leitneria* and *Zelkova* in the otherwise largely subtropical Wilcox flora. From outcrops of the Wilcox group in southcentral Arkansas, Jones (1961) identified pollen of a number of genera which commonly occur in warm temperate areas. Apart from *Pinus*, which ranges up to 10 per cent in some of the samples, *Carya*, *Engelhardtia*, *Quercus* and *Myrica* are represented in the shales which yield a leaf flora composed preponderantly of subtropical plants. Gray (1960) reports that pollen of such temperate genera as *Abies*, *Alnus*, *Carya*, *Castanea*, *Fagus*, *Juglans*, *Liquidambar*, *Liriodendron*, *Nyssa* and *Tilia* occurs in the somewhat younger middle Eocene Claiborne flora of Alabama, an assemblage previously considered subtropical on the basis of its leaf fossils.

Since the Wilcox, Claiborne and related floras are composed of ferns, palms, and broad-leafed evergreens whose nearest relatives live in the tropics and subtropics, the lowlands were marginally tropical. The well-preserved leaves of most of the temperate plants need not have been transported from trees that lived in the distant cooler highlands, as has been suggested, but may well have been contributed to the record by occasional deciduous hardwoods associated with the broadleafed evergreen forest in the lowlands. Deciduous hardwoods regularly occur in these forests today, as on the escarpment of eastern Mexico (MacGinitie, 1941; Leopold, 1950; Miranda & Sharp, 1950) and also in central to southern China (Cheng, 1939; Wang, 1961) and in Japan (Takeda, 1913). Nonetheless, to judge from (*a*) the altitudinal relations of modern forests which show that a zone of deciduous harwood forest lies above broadleafed evergreen forest, from (*b*) the nature of the pollen record in the Wilcox and Claiborne floras, and from (*c*) the composition of the temperate Eocene floras to the north (Fort Union, Yellowstone, Disko I., E. Greenland) which are dominated by deciduous hardwoods, and which may be presumed to have ranged southward in upland areas of temperate climate (Chaney, 1936), we may infer that deciduous hardwoods increased in numbers at higher cooler levels in the nearby ancestral Great Mountains, grading up into a mixed deciduous hardwood forest. Hence the problem arises as to the minimum level which would be required for the community.

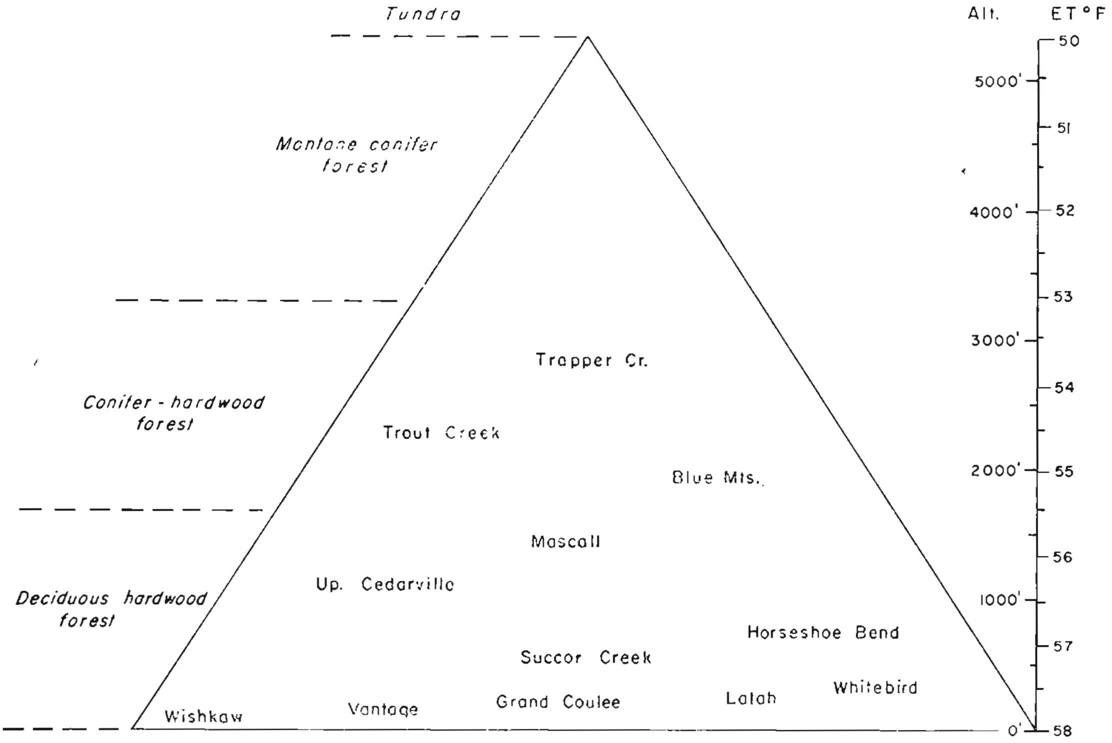
In view of its composition, the early Eocene Wilcox flora was north of the margin of the nonmarine tropics. On this basis, *ET* was about 63 (or 62) in the lowlands, and the annual range of temperature was approximately 10° at Lat. 35 (Tennessee). From the intersection of *ET* 63 with *A* 10 (Text-fig. 10), by measuring the vertical distance between *ET* 64·4 and *ET* 50 we find that 24·5° of mean annual temperature separates tropical and polar climate. In terms of altitude this implies a vertical separation of about 6,800 feet (24·5 × 278= 6,811 ft.), assuming a normal lapse rate. It is apparent that broad-leafed evergreen forest would have ranged up to near 2,500 feet where it would be replaced by a mixed deciduous hardwood forest in a zone where *ET* was approximately 58 (or 57·5). Thus if the higher parts of the Great Smoky Mountains stood near 2,500-3,000 feet during the early Eocene — and geologic evidence for its Eocene altitude is not conclusive — the area would have supported a temperate deciduous hardwood forest. To judge from the composition of the temperate Eocene forests to the north, and also from the nature of the rich mixed deciduous hardwood forest of China (Wang, 1961), it may be suggested that the upland forest which is inferred to have occupied the higher parts of the Great Smokies probably would have differed from the relict cove forests in that area today in having more numerous dominants among the crown trees, more frequent evergreens (both trees and shrubs), more lianes and epiphytes, and probably was richer in composition than any living forest since temperate deciduous hardwood genera (*Cercidiphyllum*, *Eucommia*, *Zelkova*) no longer native to North America are recorded in the region.

MIDDLE MIOCENE FLORAS, COLUMBIA PLATEAU AND ADJACENT REGION

The method can be used to determine the altitudes of the diverse Middle Miocene floras of the Columbia Plateau and adjacent region referred to earlier. Recent reports concerning their geologic occurrence, composition, physical conditions, and age are presented elsewhere (Chaney, 1959; Axelrod, 1964).

The Wishkaw (Astoria) and slightly older Miocene floras in and near the coastal strip are dominated by deciduous hardwoods, lowland conifers, and also by moderate numbers of broadleafed evergreens. They suggest a climate with *ET* near 58 (or 57·5), and a mean annual range of temperature of about 20°F. Following down line *ET* 58 to *A* 20 (Text-fig. 10) and measuring vertically we find that 34·5°F of mean annual temperature separates the tropical (*ET* 64·4) and polar (*ET* 50) zones. Assuming a normal lapse rate (3·6°F/1,000 ft., or 278 ft./1°F), this represents a vertical separation of about 9,600 feet (278 × 34·5=9,591 ft.) Using *ET* 58 as the base for sea level, we see in figure 12 an idealized mountain in which the altitudes of the middle Miocene floras as judged from their inferred *ET* requirements are shown, as is the altitudinal range of the vegetation zones which they represent.

The existence of montane conifer forest on the slopes immediately above the dominant conifer-deciduous hardwood forest at Trapper Creek is shown by the presence in it of hemlock, larch, fir, and pine which



TEXT-FIG. 12 — Estimated altitudes of fossil floras of Columbia Plateau and adjacent region, and of the vegetation zones which they represent.

resemble trees that are confined chiefly to that upland forest zone today. They have not previously been recorded from the Miocene floras at lower altitudes except for the pine and fir which occur at Trout Creek, and which are much rarer there. At Trapper Creek they probably lived on nearby cooler slopes from which they contributed not infrequently to the accumulating record (AXELROD, 1964). This paleoecologic interpretation is fully consistent with the estimates of the altitude of the lower margin of the conifer forest zone (*ET* 53·5) as calculated from conditions at sea level (*ET* 58). As shown in Text-fig. 12, cold temperate climate suitable for montane conifer forest was about 500 feet above the basin. If *ET* was 57·5 instead of 58 and, there is reason to believe that it is an equally good estimate for sea level conditions, then the edge of the conifer forest zone was 250 feet lower. In either case, conditions suitable for it probably reached to somewhat lower levels on cooler north-facing slopes because the forest regularly displays such a distribution today. It is apparent that determination of the altitude of the basin from conditions at sea level are in accord with the relative abundance of plants that formed the major communities in the flora. Representing the upper part of a conifer-deciduous hardwood forest, it lived under a cooler climate than the Blue Mountains or Trout Creek floras which are samples of the lower and middle part of that zone as judged from the more numerous deciduous hardwoods in them which suggest milder climate. If the Trapper Creek flora had a somewhat higher altitude, it would be in the montane conifer forest zone and thus would have a more abundant representation of upland conifers. A slightly lower altitude would place it so remote from montane conifers that their structures probably would have a much lower (or no) representation in the flora.

EO-OLIGOCENE FOREST ZONES, WESTERN NORTH AMERICA

From an analysis of essentially contemporaneous floras which are distributed across many degrees of latitude, it is feasible to infer climatic conditions over a broad region. The procedure involves inferring *ET* and *A* values for floras at sea level, as well as for those at higher altitudes, and calculating the levels of the successively higher *ET* zones at each site. Altitudes with similar *ET* are then connected by lines which represent climatic boundaries defined by warmth. In regional reconstructions of this sort, the comparisons appear to yield a more accurate picture of regional paleoclimate than is otherwise possible. Paleotemperatures (*ET*) are more precise than those suggested by individual floras because they are being evaluated in terms of *several ET* boundaries at different altitudes which extend across a broad region. The procedure is somewhat analogous to the method by which a pan-balance may be brought into equilibrium by selecting from several pebbles (i.e. *ET*) which have nearly the proper weight only those which give it perfect balance. Ideally, the calculated boundaries should fall on nearly parallel, gently curved lines at times of high temperateness when climates were gently zoned and when high relief and diverse extreme (polar, desert, tundra) climates were not present over wide regions.

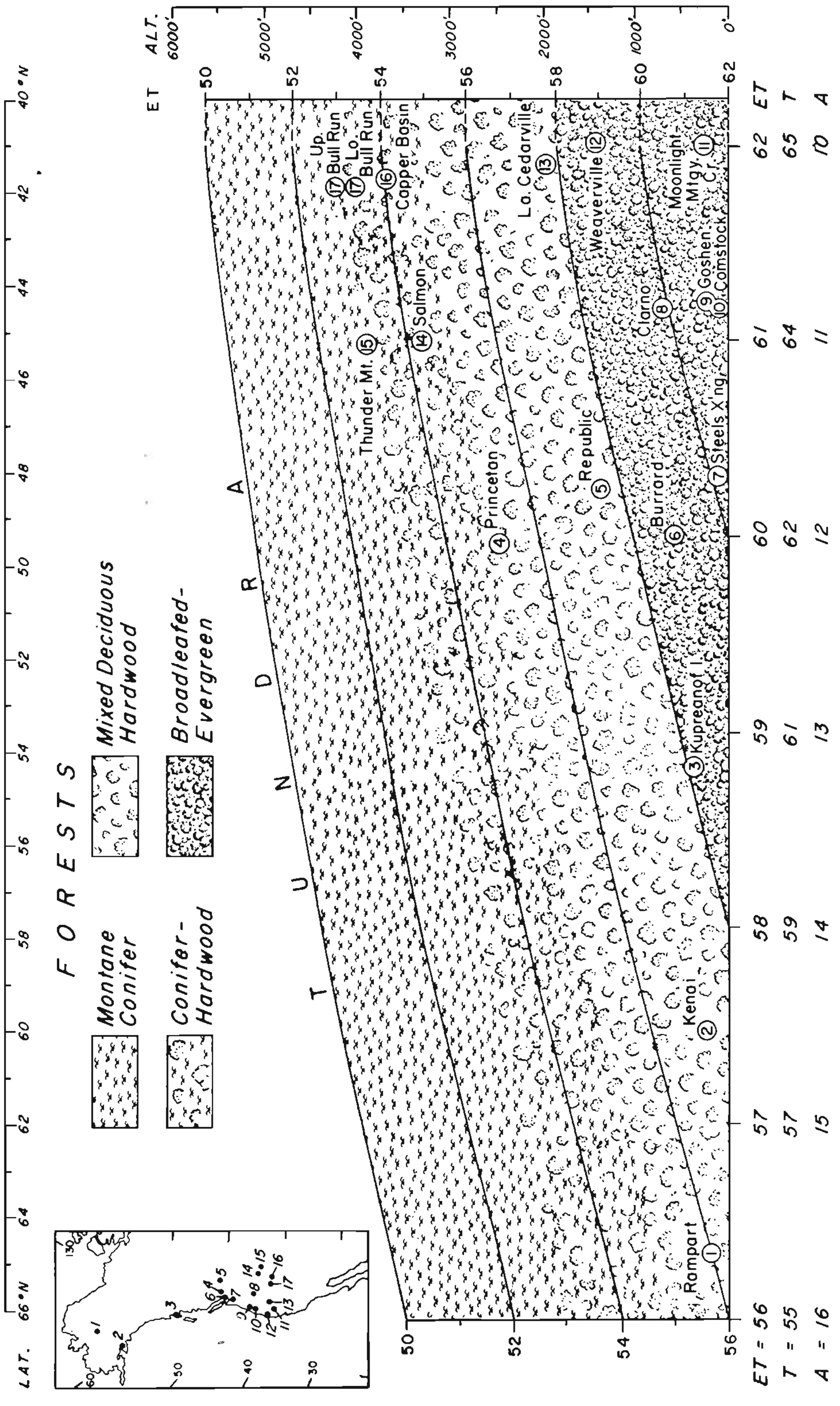
In Text-fig. 13, the Eocene-early Oligocene floras distributed from northern California (Lat. 40°) to central Alaska (Lat. 65°) are evaluated in terms of their regional altitudinal relations as judged from their composition and inferred *ET* requirements. Details concerning the ages of the upland floras near Lat. 40-44° and their inferred *ET* values are discussed elsewhere (AXELROD, 1965). Estimates of effective temperature (*ET*) as well as mean annual temperature (*T*) and annual range of temperature (*A*) are indicated for the floras near sea level, and from them the altitudes of the zones were calculated as in the preceding examples. The data suggest a gentle zonation of climate, and an altitudinal control on the distribution of forests, with the zonal *ET* boundaries flattening out at lower latitudes as annual range of temperature decreased. It is emphasized that the altitudes depicted for the floras represent the levels at which they would occur when all of them are reduced to a common age, transitional Eo-Oligocene.

LIMITATIONS TO THE METHOD

Determination of altitude by the method outlined here is subject to certain limitations. They introduce uncertainties that are expressed in terms of altitude estimated, and which may yield divergent results to different investigators.

AGE

In order to ascertain altitude, age must be known because the altitude of an upland flora is calculated from the effective temperature (*ET*) of a flora of similar age at or near sea level. For most floras that lived at generally low to moderate levels, there is now sufficient information available so that their ages may be established with a fair degree of accuracy. However, if a flora had a high altitude there may be considerable uncertainty as to its age. Early Tertiary floras which lived in upland areas under cool to cold temperate climate have the aspect of much younger floras. As discussed elsewhere (AXELROD, 1964, 1965), the Copper Basin and Bull Run floras of northeastern Nevada were initially considered by me (and others) to be late Miocene, yet they are late Eocene according to radiometric evidence (Geochron Laboratories Inc., Samples B-0124 and B-0094, February 1962). Furthermore, the Thunder Mountain flora, also previously considered Miocene (BROWN, 1937), evidently is middle Eocene (K/Ar age=49±2·0 million years (Geochron Laboratories Inc., Sample R-0411, June 1964). By any paleobotanical criteria now used for age analysis, a later Tertiary age is indicated for all these floras because they include numerous (50-85 per cent) genera which are native to the nearby region, they contain small-leafed species like those in later Tertiary floras, and they reflect cool temperate climate. In terms of the general trend toward cooling during the Tertiary, they have the aspect of later Tertiary floras that lived at low to moderate altitudes. Since we still have little information about the composition of upland floras of older Tertiary age, species or groups of species which may provide a general index to age have not yet been recognized in them. Hence in these cases it may not be clear from paleobotanical evidence alone whether a flora composed of montane conifers and deciduous hardwoods had (*a*) a high altitude and is of early Tertiary age, or whether (*b*) it had a generally moderate altitude and is of later Tertiary age. For this reason supplementary evidence — stratigraphic position,



TEXT-FIG. 13 — Altitudinal distribution of forest zones in the Pacific Northwest as determined from estimated *ET* requirements of Paleogene floras.

mammalian faunas, radiometric data — must be used to establish age. In the case of older Tertiary floras stratigraphic position may be of little help in ascertaining age because they often occur in formations which rest on a Pre-Tertiary granitic or metamorphic terrain, or on Paleozoic rocks. While this may suggest an older Tertiary age, such a conclusion may not be warranted because younger volcanic sequences also lap into older basement rocks.

ESTIMATES OF *ET* AND *A*

Determination of altitude is based on effective temperature (*ET*) and annual range (*A*) of temperature as deduced from conditions in modern forests most similar to the fossil flora. Two different investigators may well infer somewhat different *ET* and *A* values for a fossil flora, and hence arrive at divergent estimates of its altitude. This personal equation may be reduced if we recognize that temperateness (*M*) was high during most of the Tertiary. There is good evidence to suggest that climates were characterized by high temperateness and were essentially frost-free at middle latitudes well into the Pliocene (MacGinitie, 1962; Hibbard, 1960; Axelrod, 1950). As emphasized earlier, since Tertiary floras that represent deciduous hardwood and warm temperate broad-leafed evergreen forests lived under conditions of pronounced temperateness, they had a much " cooler " climate (i.e. *ET* 58 vs. 61) than would occur if temperateness was in the medium range over wide areas, as it is today (i.e. *M* 65+ vs. *M* 40-55). A temperateness rating of about 65 (implying no more than 0·5 per cent of hours of year with frost, see figures 9, 10) probably was a minimum value over wide areas at middle latitudes well into the Pliocene to judge from the regular intermingling of " temperate " and " tropical " plants in the later Tertiary, and from the nature of the vertebrate record as well (Hibbard, 1960). It is evident that recognition of pronounced temperateness will greatly reduce differences in the personal equation in determining the altitudes of most Tertiary floras as based on estimates of *ET* and *A*. Slightly different assumptions as to *ET* (i.e. 61° vs 62°) or *A* values (10° vs 12°) by different investigators are to be expected, and will yield differences in altitude of about 500 feet.

The procedure followed above has assumed constancy of *A* in the vertical column. Observational data indicate that today *A* decreases with altitude in free air, and that it increases toward the interior of a land mass. The contrary effects of altitude and distance from the sea are assumed to have largely neutralized one another in the early to middle Tertiary for at least moderate distances inland, as in the examples presented above. This assumption appears to be valid for topography was much lower than it is at present, and the broadly zoned climates of high temperateness which extended far into the interior would have moderated significantly any tendency for a notable increase in *A* there. This inference is consistent with the composition of floras in the interior (Yellowstone, Ft. Union, Rampart) as compared with those in coastal areas (Chalk Bluffs, Puget, Kenai). They are sufficiently alike in composition to suggest that a significant increase in temperature fluctuation seems unlikely for it presumably would be accompanied by important changes in floral composition which are not now apparent. To judge from the nature of the upper Green River flora of Wyoming-Colorado, which represents a subhumid warm temperate savanna that replaced mesophytic warm temperate broadleafed evergreen forest (Wind River, Tipperary floras) during late Eocene, the factor of increasing *A* with distance from the sea probably began to assume some importance there, an area 800 miles in the interior.

SAMPLE

In order to reconstruct the environment under which a Tertiary flora lived, it is apparent that an adequate sample is required. As for deciding whether a collection is representative or not, I have assumed that a flora is properly sampled when, after the collection is presumed to be adequate, no additional species can be recovered after another two days further digging. With an adequate sample for study, it is apparent that differences in estimates of effective temperature (*ET*), temperateness (*M*), and annual range of temperature (*A*) by two or more investigators will be reduced because the composition of the flora will indicate approximately its relations to adjacent (higher or lower) vegetation zones. Since an adequate sample will make possible more accurate inferences as to *ET* and *A*, determination of altitude should also be more reliable.

At the present time many investigators are combining palynological evidence with that supplied by megafossils in order to reconstruct Tertiary forests and the environments under which they lived. Such a procedure may lead to serious errors in the interpretation of climate, altitude, and age because some of the microfossils have been transported to the basin of deposition from different environments. It is apparent that forests blanketing a volcanic cone rising 2,000-3,000 feet or more above the shore of a Tertiary lake will contribute microfossils to the sediments which represent a cooler zone of vegetation (and climate) than that at the lake shore which is adding leaves and other structures to the accumulating record. Similarly, rising air currents may carry microfossils from a warm temperate broadleafed evergreen forest of the coastal strip into the interior, to mingle there with a more temperate forest at moderately higher levels. If species of mega- and microfossil floras are combined for analysis, paleoecologic chaos may be expected to result. However, if they are evaluated separately, then the microfossils may provide valuable supplementary information with respect to the bordering upland or lowland forests which supplied the ecologically discordant microfossils to the record.

As for age, if lists of micro- and megafossil floras are combined, then a flora from a basin with nearby mountains will contain plants (microfossils) which lived in the cooler uplands, and which will impart to it a younger aspect. Similarly, an inland flora receiving palynomorphs from forests on the coastal slope will have species of warmer alliance, and will give it a somewhat older aspect. Since age must be known (see above) if altitude is to be determined accurately, it is evident that age analysis must be based on fossils which lived at the site of deposition, not on those transported to it from different forests in the bordering area.

ACKNOWLEDGEMENTS

This report is an outgrowth of problems of paleoclimate and altitude which have been raised by my studies of the Tertiary floras of Nevada, a research project supported by grants from the National Science Foundation. For their continued interest and generous financial aid, the writer is deeply grateful.

It is a pleasure to record here many fruitful discussions of paleoclimatic problems with Professor Harry P. Bailey, Department of Geography, University of California, Riverside. He has devoted much time to showing me how it is possible to apply the concepts of effective temperature and temperateness (Bailey, 1960, 1964) to paleoclimatic problems, and also has kindly permitted me to reproduce the nomograms which are included here, and which form the framework for the preceding discussion.

REFERENCES

Axelrod, D. I. (1950). The Anaverde flora of southern California. *Publ. Carneg. Instn.*, 590: 119-158.

Idem (1957). Late Tertiary floras and the Sierra Nevadan uplift. *Bull. geol. Soc. Amer.*, **68**: 19-45.

Idem (1958). Evolution of the Madro-Tertiary Geoflora. *Bot. Rev.*, **24**: 433-509.

Idem (1960). The evolution of flowering plants, *in* Evolution after Darwin, **1**: 227-305, *Univ. Chicago Press.*

Idem (1964). The Miocene Trapper Creek flora of southern Idaho. *Univ. Calif. Publ. Geol. Sci.*, **51**. 1-160.

Idem (1965). The Eocene Copper Basin flora of northeastern Nevada. *Ibid.*, **59**.

Bailey, H. P. (1960). A method of determining the warmth and temperateness of climate. *Geogr. Ann. Stock.*, **42**· 1-16.

Idem (1964). Toward a unified concept of the temperate climate. *Geogr. Rev.*, **54**· 516-545.

Berry, E. W. (1924). The middle and upper Eocene floras of southeastern North America. *Prof. Pap. U. S. geol. Surv.*, **92**: 1-206.

Idem (1930). Revision of the Lower Eocene Wilcox flora of the southeastern States. *Ibid.*, **156**: 1-196.

Idem (1934). Tertiary flora from the Rio Pichileufu, Argentina. *Spec. Pap. geol. Soc. Amer.*, **12**: 1-149.

Billings, W. D. (1949). The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. *Amer. Midl. nat.*, **42**: 87-109.

Brown, R. W. (1937). Additions to some fossil floras of the western United States. *Prof. Pap. U.S. geol. Surv.*, **186J** 163-186.

Idem (1940). New species and changes of name in some American fossil floras. *J. Wash. Acad. Sci.*, **30**: 344-356.

Idem (1944). Temperate species in the Eocene flora of the southeastern United States. *Ibid.*, **34**: 349-351.

Idem (1946). Alterations in some fossil and living floras. *Ibid.*, **36**: 344-355.

Idem (1960). Corkwood in the Eocene flora of the southeastern United States. *J. Paleont.*, **34**: 429-432.

CAIN, S. A. (1943). The Tertiary character of the cove hardwood forests of the Great Smoky Mountains National Park. *Bull. Torrey bot. Cl.*, **70**: 213-235.

CHANEY, R. W. (1936). The succession and distribution of Cenozoic floras around the northern Pacific basin. *in* Essays in Geobotany in honor of William A. Setchell. 1936: 55-85. T. H. Goodspeed, ed. *Univ. Calif. Press.*

Idem (1940). Tertiary forests and continental history. *Bull. geol. Soc. Amer.*, **51**: 469-488.

Idem (1959). Miocene floras of the Columbia Plateau. I. Composition and Interpretation. *Publ. Carneg. Instn.*, **617**: 1-134.

CHANEY, R. W. & HU, H. H. (1940). A Miocene flora from Shantung Province, China. II. Physical conditions and correlation. *Ibid.*, **507**: 85-147.

CHENG, W. C. (1939). Le forets du Se-tchouan et du Si-kiang Oriental. *Trav. Lab. for. Toulouse.*, 5, 1(2): 1-220.

CHU, KWEI-LING & COOPER, W. S. (1950). An ecological reconnaissance in the native home of *Metasequoia glyptostroboides*. *Ecology*, **31**: 260-278.

CLAUSEN, J. (1963). Tree lines and germ plasm — a study in evolutionary limitations. *Proc. nat. Acad. Sci. Wash.*, **50**: 860-868.

DEPAPE, G. (1928). Les mondes des plantes a l'apparition de l'Homme en Europe occidentale. *Ann. Soc. sci. Brux.*, Ser. B. **48** (2): 39-101.

FERNALD, M. L. (1931). Specific segregations and identities in some floras of eastern North America and the Old World. *Rhodora*, **33**: 25-63.

GRAY, J. (1960). Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. *Science*, **132**: 808-810.

HARE, FREDRICK K. (1961). The restless atmosphere. *Hutchinson Univ. Library. London.*

HIBBARD, C. W. (1960). An interpretation of Pliocene and Pleistocene climate in North America. *Mich. Acad. Sci.*, **62**nd Ann. Rept.: 5-30.

HOPKINS, D. M. (1959). Some characteristics of the climate in forest and taiga regions in Alaska. *Arctic*, **12**: 215-220.

JONES, E. L. (1961). Environmental significance of palynomorphs from lower Eocene sediments of Arkansas. *Science*, **134**: 1366.

LEOPOLD, A. S. (1950). Vegetation zones of Mexico. *Ecology*, **31**: 507-518.

MACGINITIE, H. D. (1941). A middle Eocene flora from the central Sierra Nevada. *Publ. Carneg. Instn.*, 534: 1-178.

Idem (1953). Fossil plants of the Florissant beds, Colorado. *Ibid.*, 599: 1-188.

Idem (1962). The Kilgore flora: a late Miocene flora from northern Nebraska. *Univ. Calif. Publ. Geol. Sci.*, **35**: 67-158.

MIRANDA, F. & SHARP, A. J. (1950). Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology*, **31**: 313-333.

NICHOL, A. A. (1937). The natural vegetation of Arizona. *Univ. Ariz. Tech. Bull.*, **68**: 181-222.

SHARP, A. J. (1951). The relation between the Eocene Wilcox flora to some modern floras. *Evolution*, **5**: 1-5.

SHREVE, F. (1942). The desert vegetation of North America. *Bot. Rev.*, **8**: 195-246.

TAKEDA, H. (1913). Vegetation of Japan. *New Phytol.*, **12**: 37-59, 1913.

WANG, CHI-WU (1961). The forests of China with a survey of grassland and desert vegetation. *Maria Moors Cabot Fdn. Publ.* **5**: *Harvard Univ. Bot. Mus.*

APPENDIX

List of Meteorological Stations Used to Determine *ET-M* Requirements of Vegetation Shown in Text-figs. 3-9

Text-fig. 3. Stations in Forests of California

Closed-cone pine forest — Del Monte, Monterey, Pt. Arena.

Redwood forest — Crescent City, Eureka, Santa Cruz, Scotia.

Yellow pine forest — Blue Canyon, Calaveras Bigtrees, Burney, Camptonville, Covelo, Deer Creek, Downieville, Fall River Mills, Gold Run, Happy Camp, Idyllwild, Inskip, Lake Arrowhead, McCloud, Mt. Wilson, Neilie, Nevada City, Placerville, Quincy, Seven Oaks, Wawona, Weaverville, Yosemite.

Fir forest — Fordyce Dam, Gem Lake, Huntington Lake, LaPorte, Lake Sabrina, Lundy Lake, Marlette Lake, Norden, Soda Springs.

Subalpine forest — Ellery Lake, South Lake, Tamarack, Twin Lakes.

Oak-madrone — Kentfield, Los Gatos, Petaluma, Orinda, St. Helena, San Rafeal, Santa Rosa.

Digger pine woodland — Auberry, California Hot Springs, Camp Pardee, East Park, Grass Valley, Hullville, Idria, Ione, Jenny Lind, Oakdale, Oroville, Paso Robles, Redding, Rocklin, Santa Margarita, Shasta Dam.

Text-Fig. 4. Stations in Forests of Southwestern Washington and Adjacent Coastal Oregon

Cedar-Hemlock forest — Aberdeen, Astoria, Tillamok, Willipa Hbr.

Lowland Douglas fir forest — Centralia, Kosmos, Long View, Oakville, Olympia, Vancouver.

Upland Douglas fir forest — Greenwater, White Salmon, Wind River.

Fir-Hemlock forest — Lake Kechess, Ranier Longmire, Rimrock T. Dam.

Subalpine forest — Bumping Lake, Ranier Paradise, Snoqualmie Pass, Spirit Lake, R. S.

Yellow pine forest (east side) — Goldendale, Lake Cle Elum, Mt. Adams R. S., Tieton Lake.

Text-Fig. 5. Station in Forests of New England

Oak pine forest — Massachusetts: Edgartown, North Truro, Sandwich.

Oak-(chestnut)-tulip — *Rhode Island:* Greenville, Kingston. *Connecticut:* Danbury, Norfolk, Putnam, Waterbury, Westbrook. *Massachusetts:* Haverhill, Springfield, Swampcott, Taunton.

Mixed Conifer-Hardwood forest — *Massachusetts:* Fitchburg, Stockbridge, Turners Falls, Worcester. *Maine:* Farmington, Lewiston, Orono, North Bridgton, Rockland, Winslow. *New Hampshire:* Bethelem, Durham, Keene, Wolfboro Falls, Woodstock. *Vermont:* Bennington, Cavendish, Dorset, Montpellier, Newport, Rutland, St. Albans.

Spruce forest — *Maine:* Eastport, Fort Kent, Greenville, Houlton, Millinocket, Presque I. *New Hampshire:* First Connecticut Lake. *Vermont:* Somerset.

Text-Fig. 6. Stations in Southeastern Deserts of California and Adjacent Nevada

Great Basin Desert — Beatty, Bishop, Goldfield, Independence, Lone Pine, Mina, Rattlesnake, Sarcobatus, Tonopah.

Mohave Desert — Barstow, Daggett, Mohave, Trona, Twenty-nine Palms.

Sonoran Desert — Amos, Bagdad, Blythe, Borrego, Brawley, Calexico, El Centro, Hayfield Reservoir, Imperial, Indio, Iron Mt., Mecca, Needles, Palm Springs, Parker Reservoir, Silver Lake.

Text-Fig. 7. Stations in Deserts of Western Nevada and Southwestern Arizona

Western Nevada — Shadscale desert. Coaldale, Hawthorne, Lahonton Dam, Mina, Rye Patch, Sand Pass, Schurz, Smith, Thorne, Yerington.

Sagebrush desert. Basalt, Goldfield, Imlay, Tonopah.

Southwestern Arizona — Succulent desert. Ajo, Organ Pipe Cactus Nat'l Mon., Pisinemo, Sells.

Larrea-Franseria desert. Casa Grande, Gila Bend, Mohawk, Wellton, Yuma Citrus Sta.

Text-Fig. 8. Stations in Alaska

Sitka spruce-hemlock forest — Coastal. Angoon, Annette, Annex Creek, Baranof, Cape Decision, Cape St. Elias, Cape Spencer, Cordova, Gustavus, Haines, Homer, Juneau, Ketchikan, Kodiak, Little Pt. Walter, Petersburg, Seward, Sitka Magnetic, Tree Point, Wrangell, Yakataga, Yakatut.

Interior & Northern. Kaislof, Moose Valley, Valdez.

White spruce-birch forest — Coastal. Anchorage, Bethel, Illimana, Kenai, King Salmon, Matanuska, Palmer, Skwentna, Talkeetna.

Interior. Aniak, Beetles, Big Delta, Circle Hot Spr., Crooked Cr., Eagle, Fairbanks, Farewell, Flat, Ft. Yukon, Gulkana, Holy Cross, Hughes, Manley Hot. Spr., McGrath, McKinley Park, Moses Pt., Nenana, Shungnak, Tanana, Unalakleet, Wiseman.

Tundra — Aleutian I. Area. Adak, Dutch Harbor, Cold Bay, Middleton I., St. Paul, Shemya.

Bering Sea Is. & SE. Coast. Dillingham, Gambell, Nunivak, Platinum.

West Coast. Candle, Kotzebue, Nome, Puntilla, Sheep Mt., Shishmaref, Summit, Teller.

Arctic Coast. Barrow, Wainwright.

Text-Fig. 9. Stations of high temperateness in some extratropical areas with relict Tertiary vegetation

WARM TEMPERATE FORESTS

I. Broad-leafed Evergreen Forest.
Mexico. 1 Jalapa, 2 Huauchinango, 3 Orizaba. *Yunnan.* 4 Tengchung, 5 Kunming. *Juan Fernandez.* 6 Masatierra. *New Zealand.* 7 Auckland.

II. Broad-leafed Sclerophyll Woodland & Scrub.
Canary I. 8 La Laguna. *California.* 9 Avalon, 10 Los Gatos, *Chile.* 11 Valpariso. *Baja California.* 12 La Laguna. *South Africa.* 13 Pt. Elizabeth, 14 Capetown. *Spain.* 15 Lisbon.

TEMPERATE FORESTS

I. Coast Redwood Forest.
California. 16 Eureka, 17 Crescent City, 18 Santa Cruz.

II. Cedar-hemlock Forest.
Oregon. 19 Tillamok. *Washington.* 20 Aberdeen

III. Closed-cone Pine Forest.
California. 21 Monterey, 22 Pt. Arena, 23 Lompoc.

IV. Subantarctic Beech Forest.
Chile. 24 Valdivia. *Tasmania.* 25 Hobart. *New Zealand.* 26 Westport, 27 Nelson.

V. Deciduous Hardwood Forest.
Eastern United States. 28 Highlands, N.C., 29 Logan, W. Va. *Central China.* Station data are not available for the most temperate parts of Szechuan-western Hupeh. All atlases and reports indicate frost rare to absent, *ie.* less than 1% hours of year with freezing (see frost-lines in Fig. 9).