Diverse upland Eocene forests, western U.S.A.

Daniel I. Axelrod

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Mid-to Late Eocene floras in the western United States, preserved in thick piles of volcanic rocks, changed composition with increasing elevation. A deciduous hardwood forest above 455 m was replaced by conifer-deciduous hardwood forest near 1365 m, and it was supplanted by montane conifer forest at levels of about 1730 m. Whereas a normal lapse rate (5.5°C/1000 m, usually indicates elevation of modern upland stations within 100-2000 m, a lapse rate of 3.0°C/1000 m, introduced recently to estimate paleoelevation, yields levels for modern upland stations that are 1000-2000 m higher than actual elevations. Similar levels would be expected for Eocene-Oligocene floras and place treeline fully 1200 m higher than it is today. There is no geologic evidence for such high relief in this area in the Eocene. Furthermore, reasons for the decrease of treeline elevation fully 1000 m in the later Cenozoic—and in the face of increasing relief, are inexplicable.

Key-words—Palaeoecology, Vegetation, Middle-Late Eocene, U.S.A.

Daniel I. Axelrod, Section of Plant Biology, University of California, Davis, CA 95616, U.S.A.

सारॉंश

पश्चिमी अमेरिका में विभिन्न उपरिभूमि आदिनूतनकालीन वन

डेनियल आई. एक्सॅलरॉड

पश्चिमी संयुक्त राज्य अमेरिका में मध्य से अनंतिम आदिनूतन कालीन वनस्पतिजात, जो ज्वालामुखीय चट्टानों में सघन रूप मे परिरक्षित है, की संरचना ऊंचाई बढ़ने के साथ-साथ बदल गई। लगभग 455 मीटर के ऊपर पर्णपाती वन 1365 मीटर के पास कोनिफर-पर्णपाती वन में परिवर्तित हो गया तथा लगभग 1730 मीटर के आस-पास यह पर्वतीय कोनिफर में बदल गया। जबकि सामान्य ऊंचाई परिवर्तन दर (5.5/1000 मीटर)100 से 200 मीटर के मध्य वर्तमान उपरिभूमि का होना इंगित करती है। इसी प्रकार के स्तर आदिनूतन ओलिगोसीन वनस्पतिजातों के लिए भी हो सकते हैं। आदिनूतन काल में इस क्षेत्र में इतनी ऊंचाई पर वनस्पतिजात हेतु कोई भूवैज्ञानिक प्रमाण नहीं है। इसके अतिरिक्त, अनन्तिम नूतनजीवी कल्प में 1000 मीटर की ऊंचाई पर वृक्षों में ह्रास के आदि कारणों की व्याख्या नहीं की जा सकती ।

SOME 30 years ago, I described a montane flora of Eocene age (40 Ma), the Copper Basin flora of northeastern Nevada (Axelrod, 1966). In subsequent years, ten additional upland Eocene floras have been recovered from the present mountains of Nevada-Idaho (Text-figure 1). These vary in composition from deciduous hardwood forests, to conifer-deciduous hardwood forests, to those at higher levels that are (+90%) dominated by conifers such as *Abies, Chamaecyparis, Larix*, *Picea, Pinus,* and *Thuja*.

These floras differ greatly from those described previously from lower elevations in the bordering region to the east and west. The lower elevation floras represent, broadleaved evergreen forests. Over the years, palaeobotanists have tried to determine age of a flora by comparison with those of known age. The notion has been that if two floras have numerous species in common, they probably are of about the same age. The upland floras that I have collected are

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wholly unlike those at lower elevation in the region, yet they are of similar age as judged from mammalian and radiometric evidence.

The floras in the montane region represent different vegetation zones that those in the lowlands. Obviously, comparisons for age determination must made between floras of the same vegetation zone, otherwise there will be few species in common and little evidence for age. Another weakness of the species-similarity method is simply that it neglects the fact that plants migrate and in the long time involved there may be little significant change in the vegetation of two areas. The Arcto-Tertiary; conifer-deciduous hardwood forest that covered much of the general arctic region in the Eocene (ca. 45 Ma) had shifted into the lowlands of Oregon-Washington-Nevada by the Middle Miocene (18-15 Ma). Also, species of the Madro-Tertiary sclerophyll woodland vegetation, already present in southeastern California by 18-20 Ma, appeared 640 km (400 mi.) farther north in the San Francisco Bay region at 7-8 Ma.

Although species composition of vgetation changed as precipitation decreased, as the incidence of summer drought increased and as temperatures became more extreme (frost frequency, etc.), the principal composition of vegetation-deciduous hardwood forest, conifer-deciduous forests and sclerophyll woodland-persisted. Obviously, Eocene species were not present in younger floras, but their close descendants were and they contributed to similar vegetation in similar zones of Warmth (W).

GEOLOGIC OCCURRENCE

All the floras under consideration are associated with thick sections of volcanic rocks, the Challis Volcanics in Idaho, the Absaroka Volcanics in northwestern Wyoming-Montana, the Medicine Lodge Volcanics in southwestern Montana, and the Frost Creek Volcanics in northeastern Nevada. These volcanic piles are now some 1500-2000 m thick. As they accumulated, they were slowly subsiding in response to isostatic adjustment. This involved fully 4/5's of the volcanic load. Thus, it is understandable that the fossil floras were not living at very high elevation as some might assume from their association with the thick volcanic piles.

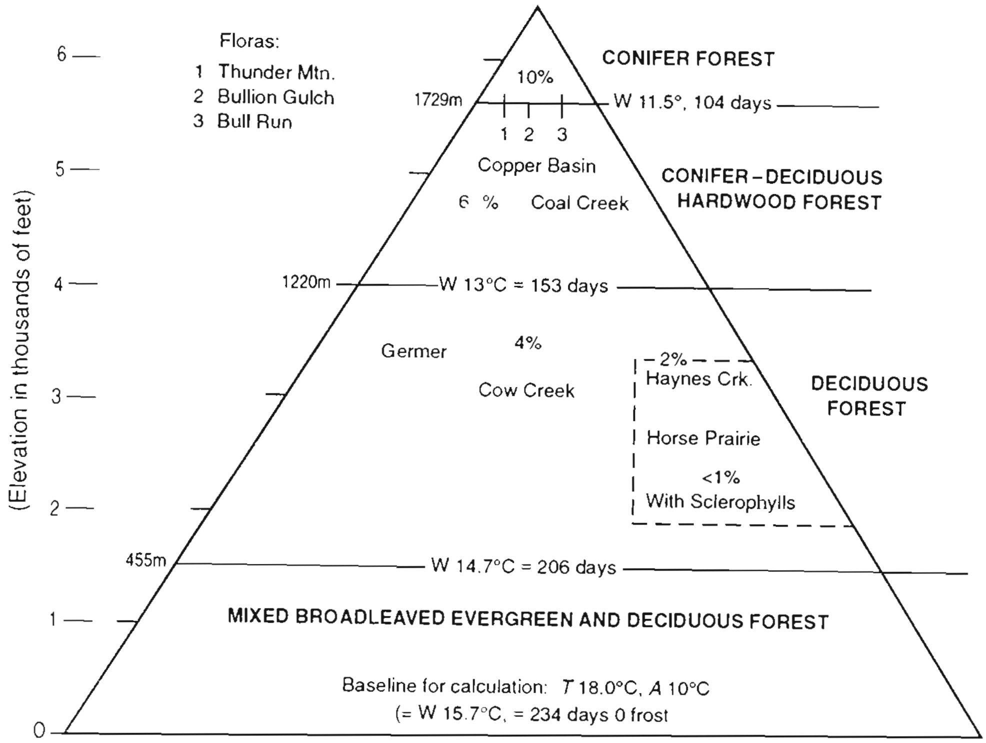
For example, the Thunder Mountain flora (Axelrod, 1990) of central Idaho was estimated to have been near 1547 m (5100 ft), whereas today it is at 2360 m (7500 ft). This suggests that the locality has been elevated on the order of 805 m (2640 ft) since it lived. This uplift may be attributed mainly to isostatic readjustment of the whole region whose chief components are the relatively less dense rocks of the Idaho batholith, the overlying Challis and other volcanics, and large Tertiary plutons. This evidently commenced in the Late Oligocene-Early Miocene as the Snake River basin gradually opened (Hamilton & Meyers, 1966) and has continued to the present with more rapid movement in the Late Miocene to Quaternary as judged from the volcanic and sedimentary record in the basin.

UPLAND EOCENE FOREST ZONES

The location of the floras representing the upland Eocene forests is shown in Text-figure 1. They are well sampled. Several have more than 2000 specimens, and one flora (Bull Run) involved 12,000 specimens counted in the field. As shown in Text-fig-

Text-figure 1—Location of Middle and Late Eocene floras in Idaho and Nevada discussed in this article.

As documented here, the Eocene vegetation zones in the western United States were far more diverse than palaeobotanists have previously realized. The relation, no doubt, holds for other areas where some relief was also present, as in central and southern Asia and elsewhere.



Text-figure 2—Estimated general elevation of Eocene uplanz vegetation zones and their fossil floras. Elevations are an average for the time period (45-35 Ma); % refers to annual hours with subfreezing temperatures (see Text-figure 6, descending lines).

ure 2, there was a major change in composition over the region. This involved (a) the Germer and Cow Creek floras that represent deciduous hardwood forest with few conifers, (b) at the southeast are the Haynes Creek and Horse Prairie floras with numerous deciduous hardwoods and some conifers as well as broadleaved sclerophylls that reflect warmer climate, (c) the Coal Creek, Copper Basin, and Bullion Gulch floras are primarily mixtures of montane conifers and deciduous hardwoods, with the latter close to montane conifer forest, and (d) the Bull Run (upper) and Thunder Mountain (lower) floras are wholly dominated by montane conifers and have only a few, rare dicots with very small (nanophyll) leaves. As Text-figure 2 illustrates, the major changes in composition of vegetation over the region reflect the shift into different climates, to *different growing seasons* defined by the duration of summer warmth (W) (Bailey, 1960, 1976; Axelrod & Bailey, 1976).

Other than *Metasequoia*, conifers are rare. Dicot leaves, usually microphyll in size. Age: 45 Ma.

Of special interest are two floras that show the transition from conifer-deciduous hardwood forest to pure montane forest. In the Bull Run basin, northeastern Nevada, 10 florules on the west flank of the anticline are distributed through some 1000 m of sedimentary rocks (Axelrod, MS). The lower three represent a mixture of deciduous hardwoods and conifers. They show that with a rise from Locality 1 to Loc. 2 and then to Loc. 3, conifers increase in abundance to fully 75 per cent of the sample. Some 20 m higher, Loc. 4 is wholly dominated (+95%) by montane conifers. By contrast, at Thunder Mountain a montane conifer forest reached down the walls of the caldera to the floor of the basin where it interfingered with conifer-deciduous hardwood forest. At that site two different vegetation zones were in contact (Axelrod, 1990, 1995).

Deciduous Hardwood Forest

This zone, dominated by broadleaved deciduous hardwood trees, includes some conifers but they were not important in the vegetation except locally along water-courses and in moist swales where *Metasequoia* and *Sequoia* were locally abundant. Broadleaved evergreen trees are essentially absent or very rare, and a few taxa may be present that reflect somewhat warmer conditions. The species in these floras are surprisingly modern in aspect, and most are allied to modern taxa, some distantly because they are extinct species.

COW CREEK FLORA, IDAHO

Ginkgoaceae
- *Ginkgo*

Cupresaceae
- *Calocedrus*
- *Chamaecyparis*
- *Pinacee*
- *Abies*
- *Picea* (2 sp.)
- *Pinus*
- *Pseudotsuga*

Taxaceae
- *Cephalotaxus*

Taxodiaceae
- *Metasequoia*
- *Sequoia*

Aceraceae
- *Acer* (2 sp.)
- *Dipteronia*

Anacardiaceae
- *Rhus* (2 sp.)

Berberidaceae
- *Berberis* (3sp.)
- *Mahonia* (2 sp.)

Betulaceae
- *Alnus* (2sp.)
- *Betula*
- *Fagopsis*

Cornaceae
- *Cornus*

Ericaceae
- *Ledum*
- *Rhododendron*
- *Vaccinium* (2 sp.)

Juglandaceae
- *Pterocarya*
- *Cruciptera*

Lauraceae
- *Lindera*
- *Sassafras*

Leguminosae
- *Cassia*
- 3 others

Myricaceae
- *Comptonia*

Rosaceae
- *Amelanchier*
- *Crataegus (2 sp.)*
- *Malus*
- *Physocarpus*
- *Prunus*
- *Rosa*
- *Salmonensea*
- *Sorbus*

Salicaceae
- *Populus* (2 sp.)
- *Salix* (2 sp.)

Saxifragaceae
- *Ribes*
- *Hydrangea*

Ulmaceae
- *Ulmus*
- *Zelkova*

Conifers are rare (most cones transported -few seeds). Only *Cunninghamia* is relatively common. Leaves of moderate size-chiefly microphyll.

GERMER FLORA, IDAHO (EDELMAN, 1975)

Polypodiaceae
- *Dennsteadtia*

Pinaceae
- *Abies*
- *Picea*
- *Pinus*
- *Pseudolarix*
- *Tsuga*

Taxodiaceae
- *Metasequoia*
- *Sequoia*

Cupressaceae
- *Chamaecyparis*

Liliaceae
- *Smilax*

Salicaceae
Salix
Myricaceae
Comptonia
Juglandaceae
Carya
Juglans
Betulaceae
Alnus (3 sp.)
Betula
Ostrya
Cercidiphyllaceae
Cercidiphyllum
Lauraceae
Sassafras
Saxifragaceae
Ribes
Eucommiaceae
Eucommia
Platanaceae
Platanus
Rosaceae
Rosa
Meliaceae
Cedrela
Rhamnaceae
Ceanothus
Hippocastanaceae
Aesculus

Specimens of *Metasequoia, Sequoia,* and *Pseudolarix* account for 65 per cent of the flora; all other conifers scarcely total 1 per cent of specimens. The flora is dominated by dicots, chiefly of microphyll size. Age: 47 Ma.

Two somewhat younger floras (35-34 Ma) dominated by deciduous hardwoods reflect a slightly different climate. They include more conifers (although not very abundant) and also have broad-leaved sclerophyllous trees and one (Horse Prairie) has woody legumes and others that suggest little frost in the area. These younger floras include the following:

HAYNES CREEK FLORA
(Axelrod, MS)

Osmundaceae
Osmunda
Ginkgoaceae
Ginkgo
Cupressaceae
Chamaecyparis
Thujopsis
Pinaceae
Abies
Larix
Picea (2 sp.)
Pinus (3 sp.)
Pseudotsuga
Taxodiaceae
Cunninghamia
Metasequoia
Sequoia
Taxodium
Aceraceae
Acer (5sp.)
Berberidaceae
Mahonia
Betulaceae
Alnus (2 sp.)
Betula (2 sp.)
Caprifoliaceae
Diplodipelta
Symphoricarpos
Cercidiphyllaceae
Cercidiphyllum
Celastraceae
Paxistima
Ericaceae
Ledum
Rhododendron
Eupteleaceae
Euptelea
Fagaceae
Chrysolepis
Lithocarpus
Quercus (5 sp.)
Gentianaceae
Nymphoides
Lauraceae
Sassafras
Leguminosae
Gleditsia
Oleaceae
Fraxinus

Platanaceae
Platanus
Rhamnaceae
Rhamnus
Rosaceae
Amelanchier
Cercocarpus
Crataegus (2 sp.)
Rosa
Sorbus (3 sp.)
Spiraea
Vauquelinia
Salicaceae
Populus (2 sp.)
Salix (3 sp.)
Tiliaceae
Craigia
Ulmaceae
Ulmus (2 sp.)
Zelkova

HORSE PRAIRIE FLORA, S.W. MONTANA (BECKER, 1967) (Representative listing)

Osmundaceae
Osmunda
Cupressaceae
Chamaecyparis
Juniperus
Pinaceae
Abies
Larix
Picea (3 sp.)
Pinus (2 sp.)
Pseudotsuga
Taxodiaceae
Metasequoia
Sequoia
Aceraceae
Acer (4-5 sp.)
Anacardiaceae
Astronium
Berberidaceae
Mahonia (2-3 sp.)

+++ Numerous legumes reported but illustrations insufficient to identify genera. Those reported include species of *Cassia, Diphysa, Mimosites, Pithecolobium*, etc.

Betulaceae
Betula
Carpinus
Fagopsis
Ostrya
Celastraceae
Celastrus
Cercidiphyllaceae
Cercidiphyllum
Ebenaceae
Diospyros
Fagaceae
Castanea
Quercus (4-5 sp.)
Juglandaceae
Carya
Lauraceae
Sassafras
Leguminosae
Cercis
Robinia
Meliaceae
Cedrela
Oleaceae
Fraxinus
Platanaceae
Platanus
Rhamnaceae
Colubrina
Paliurus
Rhamnus
Rosaceae
Cercocarps
Crataegus
Rosa
Rutaceae
Ptelea
Salicaceae
Populus (2 sp.)
Sapindaceae
Cardiospermum
Sapindus
Simarubaceae
Ailanthus
Smilacaceae
Smilax
Tiliaceae

Tilia
Ulmaceae
Ulmus
Zelkova

CONIFER-DECIDUOUS HARDWOOD FOREST

Situated above the dominant deciduous hardwoods was a zone of deciduous hardwoods and abundant conifers. Broadleaved sclerophylls are rare or absent as are taxa such as woody legumes that reflect mild winter climate. This conifer-deciduous hardwood zone was regularly subject to freezing, probably on the order of +5% hours/year. The floras typical of this zone include the following.

COPPER BASIN FLORA
(Axelrod, 1966)

Conifers
Cephalotaxus
Abies (2 sp.)
Picea (3 sp.)
Larix
Pinus (3 sp.)
Pseudotsuga
Tsuga
Sequoia
Chamaecyparis
Salicaceae
Salix
Betulaceae
Alnus (2 sp.)
Fagaceae
Lithocarpus
Ulmaceae
Ulmus
Berberidaceae
Mahonia (3 sp.)
Lauraceae
Sassafras
Saxifragaceae
Ribes
Rosaceae
Amelanchier
Crataegus
Holodiscus
Prunus (3 sp.)
Rosa
Leguminosae
Amorpha
Celastraceae
Euonymus
Aceraceae
Acer (4 sp.)
Hippocastanaceae
Aesculus
Ericaceae
Rhododendron
Vaccinium

Leaves are chiefly <microphyllous in size. Conifers (apart from, *Sequoia*, 4%) make up scarcely 2 per cent of the specimans. Age: 40 Ma.

COAL CREEK, IDAHO

Cephalotaxaceae
Cephalotaxus
Pinaceae
Abies (2 sp.)
Larix
Picea (3 sp.)
Pinus (Strobi, Contortae, Balfourineae)
Taxodiaceae
Sequoiadendron
Sequoia
Salicaceae
Salix
Betuylaceae
Alnus
Betula
Juglandaceae
Carya
Berberidaceae
Mahonia
Lauraceae
Sassafras
Caprifoliaceae
Viburnum
Saxifragaceae
Ribes
Rosaceae
Crataegus (2 sp.)
Cercocarpus
Malus
Photinia
Rosa

Salmonensea
Sorbus
Aceraceae
Acer
Dipteronia
Ericaceae
Rhododendron

Conifers make up fully 75 per cent of all specimens. Dicot leaves include some of nanophy II, microphy II and a few ofr notophy II size. Age: 45 Ma.

LOWER BULL RUN FLORA, LOCS. 1-3

Pinaceae
Abies (3 sp.)
Picea (3 sp.)
Larix
Pseudotsuga
Tsuga
Cupresaceae
Chamaecyparis
Thuja
Salicaceae
Populus
Salix
Betulaceae
Alnus
Betula
Carpinus
Fagaceae
Quercus (2 sp.)
Ulmaceae
Ulmus
Zelkova
Berberidaceae
Mahonia
Berberis
Saxifragaceae
Ribes
Rosaceae
Amelanchier
Crategus (2 sp.)
Prunus
Sorbus (2 sp.)
Spiraea
Leguminosae
Robinia
Aquifoliaceae
Ilex
Aceraceae
Acer (5-6 sp.)
Rhamnaceae
Rhamnus
Tiliaceae
Tilia
Ericaceae
Rhododendron
Vacciniuum
Caprifoliaceae
Viburnum

Age: 42-40 Ma.

UPPER THUNDER MOUNTAIN FLORA (Axelrod, 1990, 1995)

Cephalotaxaceae
Cephalotaxus
Cupresaceae
Chamaecyparis
Thuja
Thujopsis
Taxodiaceae
Sequoia
Pinaceae
Abies
Larix
Picea (2 sp.)
Pinus (5 sp.)
Tsuga
Berberidaceae
Mahonia (2 sp.)
Betulaceae
Alnus
Caprifoliaceae
Viburnum
Celastraceae
Paxistima
Cornaceae
Cornus
Ericaceae
Arctostaphylos
Ledum
Rhododendron
Fagaceae
Lithocarpus
Quercus

Grossulariaceae
Ribes
Juglandaceae
Pterocarya
Myricaceae
Comptonia
Rhamnaceae
Rhamnus (2 sp.)
Rosaceae
Amelanchier
Malus
Prunus
Salicaceae
Populus
Salix
Vacciniaceae
Vaccinium

CONIFER FORESTS
(Axelrod, MS)

Two floras are presently known that are wholly dominated by conifers, notably the Upper Bull Run and Lower Thunder Mountain floras. In addition the Bullion Gulch flora, known from only a small collection, appears to have lived at the edge of the conifer forest zone. Freezing was a regular feature of the climate, probably on the order of at least 10% hours/year. All the dicots present in these floras have very small leaves that may be eigher serrate or entire (evergreen).

Representative taxa in these floras include the following:

Upper Bull Run Flora (Localities 4-10), Nevadas

Conifers make up fully 95 per cent of the flora

Pinaceae
Abies (3 sp.)
Larix (2 sp.)
Picea (3 sp.)
Pinus (3 sp.) (Strobi, Banksinae, Aristatae)
Pseudotsuga
Tsuga (2 sp.)
Betulaceae
Alnus
Betula
Ulmaceae
Zelkova
Saxifragaceae
Ribes
Cupressaceae
Chamaecyparis
Thuja
Thujopsis
Salicaceae
Populus
Salix (2 sp.)
Berberidaceae
Mahonia (2-3 sp.)
Rosaceae
Holodiscus
Prunus
Salmonensea
Aceraceae
Acer (3 sp.)
Oleaceae
Fraxinus
Ericaceae
Vaccinium
Caprifoliaceae
Viburnum
Age: 40-35 Ma.

BULLION GULCH, IDAHO

Pinaceae
Abies
Picea
Pinus (Contortae, Strobi, Aristatae)
Larix
Pseudotsuga
Salicaceae
Salix
Betulaceae
Alnus
Carpinus
Rosaceae
Rosa
Salmonensea
Ericaceae
Vaccinium
Rhamnaceae
Ceanothus

Remains of conifers are much more abundant than leaves of dicots that are small, chiefly of nanophy II size. Occurs in the Upper Challis Volcanics west of Hailey. Age: ca 35 Ma.

LOWER THUNDER MOUNTAIN FLORA, IDAHO

This flora, dominated by conifers, covered slopes of the Thunder Mountain caldera and adjacent uplands and reached the floor of the caldera where it interfingered with a conifer-deciduous hardwood forest represented by the Upper (Road locality) flora (Axelrod, 1990, 1995).

LOWER THUNDER MOUNTAIN FLORA

Pinaceae
Abies
Larix
Picea
Pinus (2 sp.)
Pseudotsuga
Taxodiaceae
Saquoia
Betulaceae
Alnus
Myricaceae
Comptonia
Rosaceae
Rosa
Spiraea
Sorbus
Salicaceae
Populus
Salix
Ericaceae
Vaccinium

Conifers make up 90 per cent of the florule. Age: 45 Ma.

VEGETATION ZONES AND THEIR ELEVATIONS

Text-figure 1 shows the area where these upland floras occur and Text-figure 2 indicates the major vegetation zones, their Warmth (W), and the elevation at which they probably lived. The temperature (Warmth) of vegetation boundaries used here is based on the data for North America (Greller, 1989; Axelrod, 1966, figs 3-5). They differ by 1-2 ^{o}C(2-4^{o}F) from those charted by Wolfe (1979, 1980, 1985) and others, i.e., Wing & Greenwood, 1993). Those boundaries are based on present climatic data for eastern Asia.

The temperature boundaries of the major vegetation zones charted by Wolfe (1979, plate 2, 1980, 1985) have no significance in terms of Warmth (W)—the growing season represented by the vegetation zones (see Axelrod, 1986, fig. 10). Text-figure 3 (from Wolfe, 1985) shows that mean annual temperature (T) and the mean annual range of temperature (A=amplitude) only mark the major thermal boundaries of a vegetation zone. These data are so broad they can only provide a general indication of temperature conditions under which a fossil flora (or vegetation) may have lived. By contrast, Text-figure 4 plots the temperature data charted byWolfe (1979,pl. 2) and shows that the vegetation boundaries have very different degrees of Warmth (W=growing season) to which the species of the zone are adapted. As illustrated in Text-figures 4 and 6, the growing season (Warmth, temperature (T) is lowered and as the range of temperature (A=amplitude) increases; Table 1 indicates the duration of ?Warmth for different temperatures. In addition to Warmth (W) Text-figure 6 also shows (a) the temperateness of climate (M=moderation) rated from an ideal of M 100 to MO; (b) the frequency (% hours) of subfreezing temperatures; and (c) the Water Need (N) of vegetation (Table 2) under stipulated temperature conditions, all features not determinable from the figures presented by Wolfe (1979, 1980, 1985).

Table 1—Warmth (W) and duration of summer (d=days) in British units and metric units. Warmth (W) and Duration (Td) of Summer (British units)

W(^{o}F)	T_d (days)	W(^{o}F)	T_d (days)
50.0	0.0	57.0	179.4
50.1	19.4	57.1	181.0
50.2	27.4	57.2	182.6
50.3	33.6	57.3	184.3
50.4	38.9	57.4	185.9
50.5	43.6	57.5	187.5
50.6	47.8	57.6	189.1
50.7	51.7	57.7	190.7
50.8	55.3	57.8	192.4
50.9	58.7	57.9	194.0
51.0	62.0	58.0	195.6
51.1	65.1	58.1	197.2
51.2	68.2	58.2	198.8
51.3	70.9	58.3	200.4
51.4	73.7	58.4	202.1
51.5	76.4	58.5	203.8
51.6	79.0	58.6	205.4
51.7	81.5	58.7	207.1

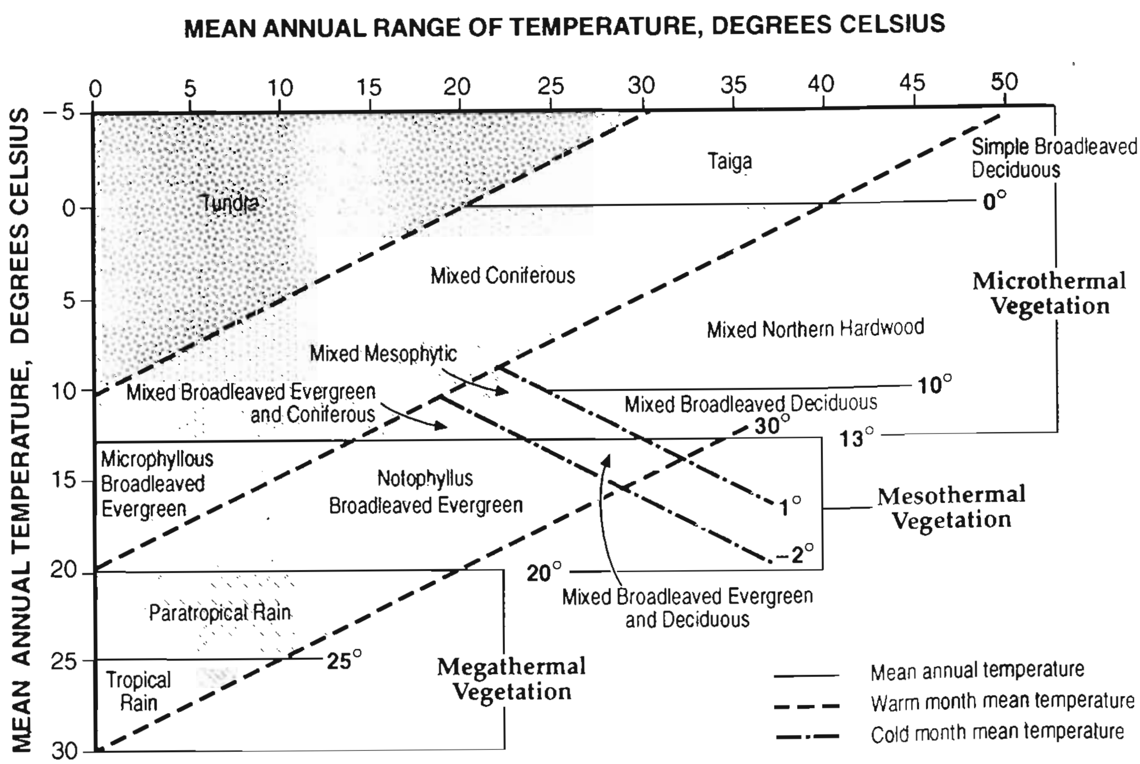
W(°F)	Td (days)	W(°F)	Td (days)
51.8	84.0	58.8	208.7
51.9	86.4	58.9	210.4
52.0	88.8	59.0	212.0
52.1	91.1	59.1	213.7
52.2	93.4	59.2	215.4
52.3	95.6	59.3	217.1
52.4	97.8	59.4	218.8
52.5	99.9	59.5	220.5
52.6	102.0	59.6	222.2
52.7	104.1	59.7	223.9
52.8	106.2	59.8	225.6
52.9	108.2	59.9	227.4
53.0	110.2	60.0	229.1
53.1	112.2	60.1	230.9
53.2	114.1	60.2	232.6
53.3	116.1	60.3	234.4
53.4	118.0	60.4	236.2
53.5	119.9	60.5	238.0
53.6	121.7	60.6	239.9
53.7	123.6	60.7	241.7
53.8	125.4	60.8	243.5
53.9	127.3	60.9	245.4
54.0	129.1	61.0	247.3
54.1	130.9	61.1	249.2
54.2	132.7	61.2	251.2
54.3	134.4	61.3	253.1
54.4	136.2	61.4	255.1
54.5	137.9	61.5	257.1
54.6	139.7	61.6	259.1
54.7	141.4	61.7	261.2
54.8	143.1	61.8	263.3
54.9	144.8	61.9	265.4
55.0	146.5	62.0	267.5
55.1	148.2	62.1	269.7
55.2	149.9	62.2	271.9
55.3	151.6	62.3	274.2
55.4	153.3	62.4	276.5
55.5	154.9	62.5	278.9
55.6	156.6	62.6	281.3
55.7	158.2	62.7	283.8
55.8	159.9	62.8	286.3
55.9	161.5	62.9	288.9
56.0	163.2	63.0	291.6
56.1	164.8	63.1	294.4
56.2	166.4	63.2	297.2
56.3	168.1	63.3	300.2
56.4	169.7	63.4	303.3
56.5	171.3	63.5	306.6
56.6	172.9	63.6	310.0
56.7	174.6	63.7	313.6
56.8	176.2	63.8	317.5
56.9	177.8	63.9	321.7
		64.0	326.4
		64.1	331.7
		64.2	337.9
		64.3	345.9
10.0	0.0	16.0	243.5
10.1	26.0	16.1	246.9

W(°F)	Td (days)	W(°F)	Td (days)
10.2	36.9	16.2	250.4
10.3	45.3	16.3	253.9
10.4	52.4	16.4	257.5
10.5	58.7	16.5	261.2
10.6	64.5	16.6	264.9
10.7	69.8	16.7	268.8
10.8	74.8	16.8	272.8
10.9	79.5	16.9	277.0
11.0	84.0	17.0	281.3
11.1	88.3	17.1	285.8
11.2	92.5	17.2	290.5
11.3	96.5	17.3	295.5
11.4	100.4	17.4	300.8
11.5	104.1	17.5	306.6
11.6	107.8	17.6	312.9
11.7	111.4	17.7	320.0
11.8	114.9	17.8	328.4
11.9	118.4	17.9	339.4
12.0	121.7	18.0	365.1
12.1	125.1		
12.2	128.4		
12.3	131.6		
12.4	134.8		
12.5	137.9		
12.6	141.1		
12.7	144.1		
12.8	147.2		
12.9	150.2		
13.0	153.3		
13.1	156.3		
13.2	159.2		
13.3	162.2		
13.4	165.1		
13.5	168.1		
13.6	171.0		
13.7	173.9		
13.8	176.8		
13.9	179.7		
14.0	182.6		
14.1	195.6		
14.2	188.5		
14.3	191.4		
14.4	194.3		
14.5	197.2		
14.6	200.2		
14.7	203.1		
14.8	206.1		
14.9	219.0		
15.0	212.0		
15.1	215.1		
15.2	218.1		
15.3	221.1		
15.4	224.2		
15.5	227.4		
15.6	230.5		
15.7	233.5		
15.8	236.9		
15.9	240.2		

Table 2—**Translation of lines of relative water need (N) into isohyets of mean annual precipitation (P) according to specified vegetation/moisture (V) categories, where P = N x V.**

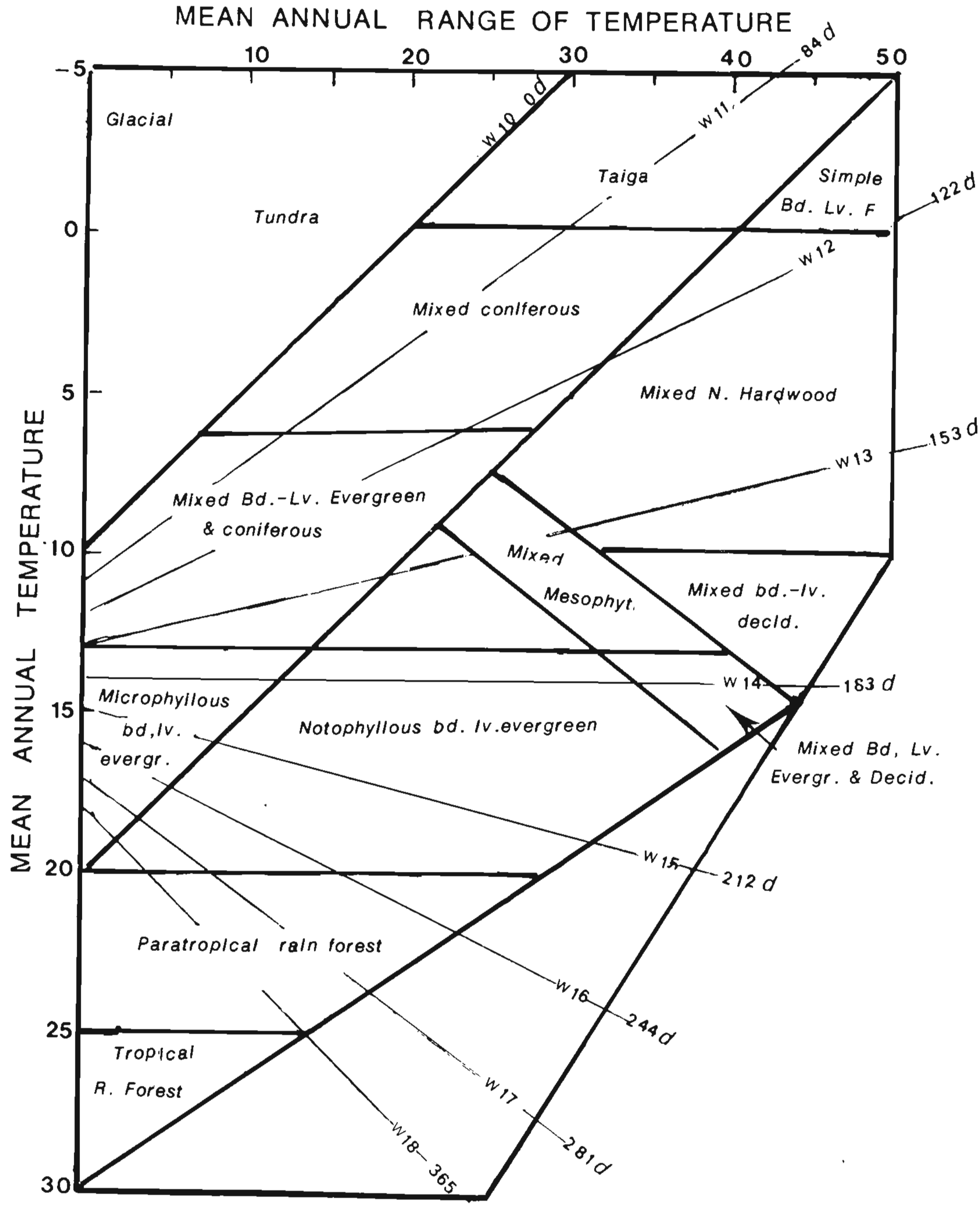
Moisture/ Veget. V	Arid	Semi-Arid	Subhumid		Humid		Perhumid
	2.5	4.7	6.4	8.7	10.7	13.2	16.2
Water Need N	Mean annual precipitation (inches)						
1	2.5	4.7	6.4	8.7	10.7	13.2	16.2
2	5.0	9.4	12.8	17.4	21.4	26.4	32.4
3	7.5	14.1	19.2	26.1	32.1	39.6	48.6
4	10.0	18.8	25.6	34.8	42.8	52.8	64.8
5	12.5	23.5	32.0	43.5	53.5	66.0	81.0
6	15.0	28.2	38.4	52.2	64.2	79.2	97.2
7	17.5	32.9	44.8	60.9	74.9	92.4	113.4
8	20.0	37.6	51.2	69.6	85.6	105.6	129.6
9	22.5	42.3	57.6	78.3	96.3	118.8	145.8

To determine elevation, the methodology used here relies on the present association of diverse taxa allied to those in a fossil flora. Granted, their physiological responses have changed some what since the Eocene, i.e., greater adaptability of freezing, and the loss of ability of withstand summer drought so that taxa are now exotic to the region. But the significant fact is that associations of species allied to the fossils can still be found in areas of similar Warmth-in areas with similar duration of the growing season-as in the Pacific States, the eastern United States, and eastern Asia. Floristic associations provide



Text-figure 3—Temperature boundaries of major vegetation zones of eastern Asia charted by Wolfe (1979). They only indicate *boundaries* of vegetation in terms of T and A. No other climatic conditions are indicated and can not be determined.

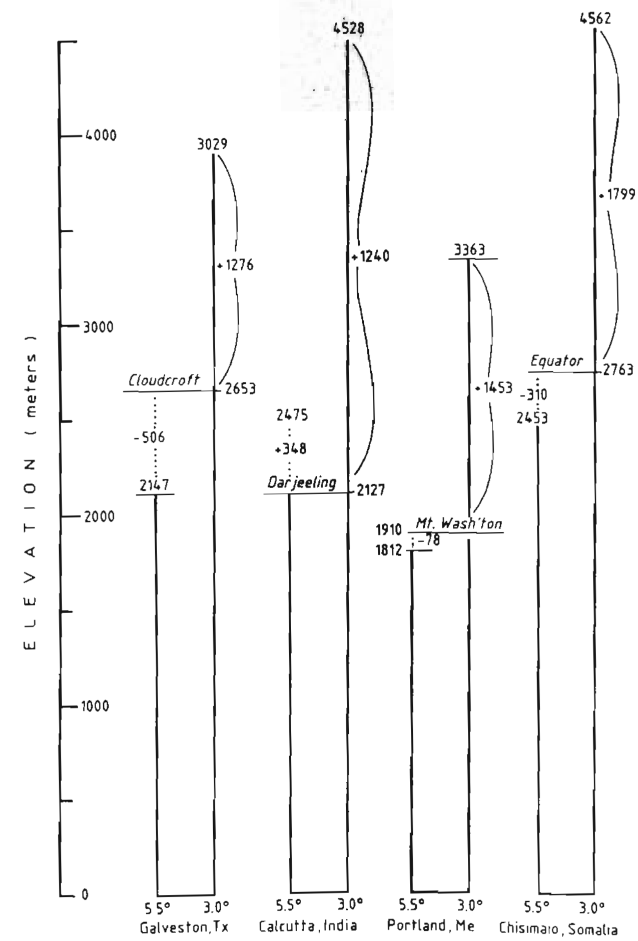
a closer approximation of paleoclimate and of elevation than resort to data based on leaf morphology (size, tip, evergreen or deciduous, margin, entire-serrate lobed, etc.) championed by Wolfe (1993). Among the weaknesses of that method are: (a) it does not consider the climatic significance of conifers that may make up well over 50 per cent of a Tertiary flora, (b) it does not take into account riparian taxa that may dominate vegetation well outside their normal area of forest-riparian occurrence, as on the the Great



Text-figure 4—By contrast, this charts the temperature data for the vegetation zones of eastern Asia plotted by Wolfe (1979, pl 2). They have very different Warmth (W) or growing seasons, are very different in terms of temperateness, and also of subfreezing conditions, as detailed in Text-figure 6.

plains, in the Kirghis, the Chad, the Ramu Valley or Kenya: (c) the method does not account for the gradual change in climate that occurs in any vegetation zone as it ranges across temperature zones (Warmth) as the oak-hickory forest, the Coast conifer forest, etc. and in which species composition does not change significantly; and (d) large leaf size need not indicate a relatively warm climate. Dicots in the Paleocene-Eocene floras of Spitzbergen are composed of serrate leaves, many of notophy II and mesophy II in size. Their large size need only indicate a response to the long day-length at the area, then near 68-70° N. The effect of a long light period is seen in the gigantic size of lettuce and cabbage leaves at Matanuska, Alaska (lat. 60° N) with only 4.6 months with mean temperature of 10°C and only 2 months with mean temperature of 12.8°C (55°F). In this regard note that the Middle Miocene Seldovia point flora, Alaska (Wolfe, 1980, then near Lat. 63° N (Smith, Hurley & Briden, 1981, has leaves that a group average larger than the Mascall flora, eastern Oregon(Chaney & Axelrod, 1959), situated some 2900 km farther south at Lat. 44° N. One may argue that the Mascall flora had moderate elevation (ca. 300-400 m) and was under a cooler climate and therefore has somewhat smaller leaves than the Kenai from near sea level. However, the Latah flora (Knowlton, 1924; also in Brown, 1937) in eastern Washington, and of similar age as the Mascall and Kenai (ca. 15.5 Ma), and then close to sea level, also has foliage than on average is smaller than the Kenai. The larger leaves of the Kenai flora need not indicate a climate warmer than that at Mascall or Latah, but a longer summer light period for their growth.

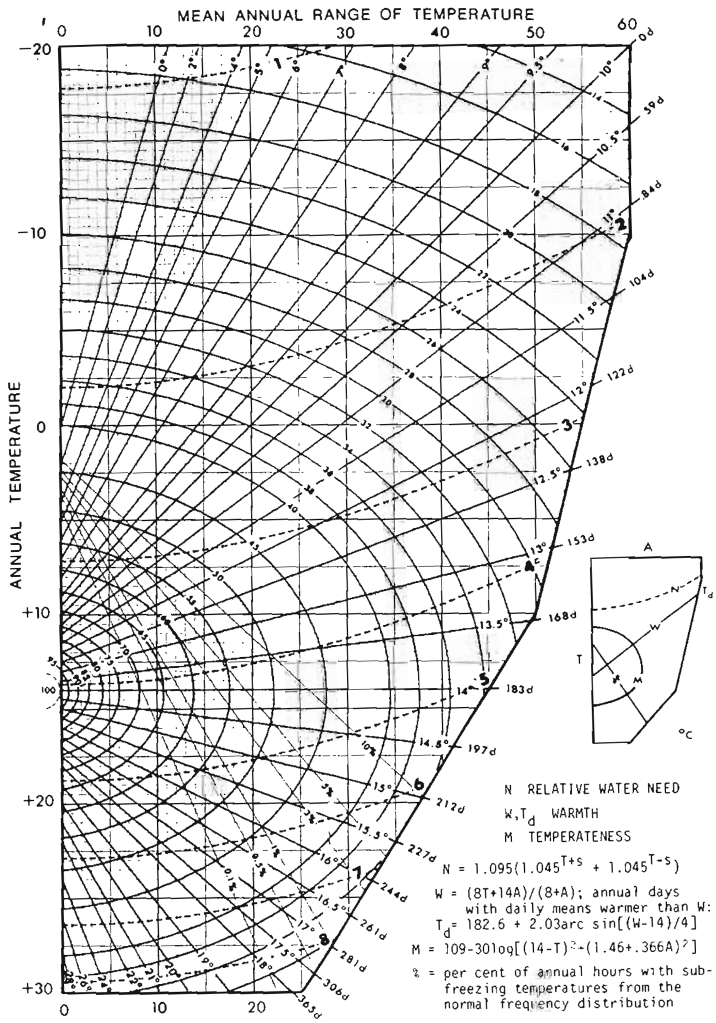
Application of the method, captioned CLAMP by Wolfe, to estimate the paleotemperature and elevation of a fossil flora, leads to questionable results. For example, Wolfe and Schorn (1994) state that the mesic forest at Fingerrock lived under a mean annual temperature (T) of 5° C (-5°C in abstract is a printers' error). No estimate was given as to the range of temperature (A=amplitude). As emphasized previously (Axelrod, 1981, fig. 11; 1986, fig. 11; 1992, fig. 2), T alone can not provide an indication of temperature of a modern or of a fossil flora of the Warmth (W) or growing season under which it lived. If the Fingerrock flora had a range of 0-10°C, it was in a zone of Tundra (Text-figures 4, 6; Greller, 1988, 1989; fig. 2) if the range was from 10-20°C, the flora was in conifer forest zone. A range of 20-40°C places it in a conifer- deciduous hardwood forest zone, and a range of 40-60° C indicates the area of deciduous hardwood forest. Such a range (A) is unlikely because the flora also includes not only deciduous hardwoods but broadleaved evergreen trees and a few conifers. As illustrated earlier (Axelrod, 1985, fig. 3; 1991, fig. 3), very similar modern associations thrive today under a range of 10- 12°C, and Warmth (W) of 12.5°C (136 days) to 13.3°C (162 days) as listed in Table 1.



Text-figure 5—Illustrating the marked difference in estimated elevation of modern upland stations using a normal laps rate of 5.5°C/1000 m; the line at the right is calulated from a lapse rate of 3°C/1000m. Temperature data (T = mean annual temperature) from Wenstgedt, 1972 are as follows; Galveston 21.1°C and Cloudcroft 9.3°; Calcutta 26.9°C and Darjeeling 13.3°C; Portland 7.4°C and Mt. Washington -2.7°C; Chisimaio 26.9°C and Equator 13.1°C.

Likewise the pyramid flora, dominated by deciduous hardwoods is stated by Wolfe and Schorn (1994) to represent a mean annual temperature (T) of 7.5°C. Again, no indication is presented as to the range of temperature (A amplitude). If it was 0-5 °C the flora was in Tundra zone, with A 5-13°c, it would be in a conifer forest zone, from 13-25°C the flora would represent a conifer-deciduous hardwood forest, and from 25- 50°C the flora was in a deciduous forest. But temperatures of amplitude 40-50°C were not present until the Quaternary. Wolfe and Schorn used a lapse rate of 3°C/1000m to estimate elevation of these floras which places the Fingerrock at 4 km and the Pyramid flora at 3 km. There is no geologic evidence that such relief was in the region (Durrell, 1986). And at such levels subfreezing temperatures would occur on fully 30% hrs/yr and eliminate many of the species.

The method developed by Wolfe to use leaf morphology to estimate paleotemperature has also been used to determine elevation of the Florissant flora, Colorado (Gregory & Chase, 1992; Wolfe, 1992; Gregory, 1994). They infer a T of 11-12°C, but do not indicate the range of temperature (A). With only a



Text-figure 6—Nomogram (Bailey, 1976) showing T (mean annual temperature) and A (=amplitude, mean annual range of temperature); descending lines indicate % annual hours with subfreezing temperatures; arcs centering at T 14°C and AO°C designate a perfectly temperate climate, with lower temperateness indicated by lower values of M (=moderation); heavy dashed lines rising upward designate Water Need (N) as presented in Table 2.

moderate range, say 20°C, at least 10% hrs/year would be subfreezing and eliminate all the subtropicals and broadleaved evergreens from the area. And with a lapse rate of 3°C/1000m, The flora would have an elevation of 2500-3000 m. In such areas today, as in the uplands of Brazil, India, Nepal, or Guatemala, there is only a very low range of temperature (A 5-10°C), they are frost-free, and support broadleaved evergreen forests *Wholly unlike* that represented at Florissant. The estimate of high elevation for the eaea is not supported by geologic evidence which suggests only low relief for the area if the later Eocene are Early Oligocene (King, 1977; Epis & Chapin, 1985). In my opinion, all evidence suggests that the Florissant flora probably had an elevation near 640 m, a T of ca. 15.5°C and an A of 13°C. This represents a Warmth of W 14.5°C (197 days) and would support all; the frost-sensitive subtropicals, the associated deciduous hardwoods, as well as the conifers and chaparral species.

To estimate elevation, I use a normal lapse rate (Oliver & Fairbridge, 1987) of 5.5°C/1000 m/=182 m/°C. The procedure involves estimating the mean annual temperature (T) and Warmth (W) at sea level, or at the margin of a known floristic vegetation) level defined with Warmth (W) (Bailey, 1960). The difference in T or W between it and that of an upland flora at about the same latitude provides an indication of its elevation. For example, if the difference is 10°C, then the interior upland flora is at 10°x182m or 1829 m (5979 ft.). The method was refined by the climatologist H.P. Bailey (in Axelrod & Bailey, 1976) and gives consistent results for areas with normal lapse rate as well as for areas where lapse rate is lower-as along the Pacific Coast from Washington State southward, as demonstrated earlier by Axelrod 1966, Tables 2-9).

That a normal lapse rate in areas with ample summer rainfall gives a fair estrimate of elevation can readily be tested by calculating elevation of modern upland stations, one at sea level, the other in mountains (Text-figure 5 left vertial line). A recent proposal is that lapse rate 3°C/1000 m (33 m/-°C) gives a close approximation of elecation (Wofe, 1992). However, if used the above example (10°C x 333 m) elevation would be 3996 m (13,108 ft). As illustrated in figure 5 m (right vertical line) elevations determined from lapse rate 3° C/1000 are regularly 1000-2000 m higher than those of known upland stations. Comparable differences are to be expected if used to estimate elevation of a Tertiary flora.

With respect to the elevation of the Copper Basin flora (Axalrod, 1966), 30 years ago I estimated that it was near 1089-1220 m (3600-4000 ft). This is now revised on the basis of a better understanding of the significance of Warmth (W), the growing season of vegetation zone as developed by Bailey (1960) and illustrated for diverse associations by Axelrod (1956, figs 3-8; 1964, fig. 5; 1980, fig. 5; 1991, fig. 3; 1992, fig; 3); Axelrod and Raven (1985, figs 5,6); and Greller (1988, 1989). The Copper Basin flora was situated in the middle-upper part of the conifer- deciduous hardwood forest of the warm temperate rainforest represented by the Goshen and allied floras noted earlier (Axelrod, 1966, p. 48-49). With a mean annual temperature (T) of 18°C and a mean annual range of A 10°C (A-amplitude), Warmth was W 15.7°C (234 days warmer), as shown in Text- figure 6. With a normal lapse rate, elevation was near 182 x 9.0°C, or at 1635 m (5395 ft.). Because the fossils site is now at 2164 m (7,100 ft), uplift has been on the order of 530 m (1730 ft.). Treeline, situated 13°C above T 18°C and W 15.7°C was then near 2366 m (8710 ft). Which is 395 m (1290 ft.) *lower* than it is today. This is expectable for with greater equability (temperateness) all Warmth lines coverage (Text-figure 6).

By Contrast, if we use a lapse rate of 3°C/1000 m (Wolfe, 1992), then the Coppwe Basin site would be at 9° x 333 m or at 2995 m (9830 ft). This is 830 m (2730 ft) *higher* than the locality today. Treeline, situated 13°C above T 18°C, W 15.7°C and A 10°C, would then be at 4330 m (14,200 ft.). This is 1220 m (4000 ft.) *higher* than treeline today. The factors that might account for such a major decrease in treeline since the Eocene, and in the fae of the onsiderable geologic evidence that there has been muh regional uplift, are not explainable.

CONCLUSION

The species in these montane floas show that each vegatation zone has an impressive number of modern genera that have survived from the Eocene. Further, the species show relationship to modern speccies-groups, i.e., setionss, series. This is apparent in *Pinus* Sect. Strobi, Ponderosae, Contortae; in *Populus* Sect. Tacamahaca, Leuce; in *Querus* Sects. Phellos, llex, Rubrae, Albae; in *Acer* Seccts. Negundo, Integrifoliae, Spicata; in *Betula* Series Acuminate, Excelse and many other genera. Further, the associations of thses species allied to the fossils occupy areas of similar Warmth (W=growing season, the duration of summer). It is this that provides a sound basis for climatic interpretation and also estimating the elevation at which they probably lived.

As charted in an early study (Axelrod, 1955, fig. 12), Miocene floras were arranged with respect to several vegetation zones that represent progressively cooler climate (shorter summers) with increasing elevation. This is also true of the upland Eocene foras. At elevations above mixed evergreen temperate rainforest a rich broadleaved deciduous hardwood forest dominated at elevations from 455-365 m (1195-4180 ft). It gave way to a mixed conifer-deciduous hardwood forest that covered areas at elevations from 1365-1730 m. Above the general level of 1730 m pure conifer forest sumed normal lapse rate of 5.5°C/1000 m, provide a closer estimate of elevation than a lapse rate of 3°C/1000 m which raises serious tectonic, ecologic and climatic problems.

REFERENCES

Axelrod D1 1964. The Miocene Trapper Creek flora of Southern Idaho. *Univ. Calif. Publ. Geol. Sci.* **51**, 180 pp.

Axelrod D1 1966. A method of determining the altitudes of Tertiary floras. *Palaeobotanist* **14**(1-3): 144-171.

Axelrod D1 1980. Contributions to the Neogene Paleobotany of Central California. *Univ. Calif. Publ. Geol. Sci* **121**. (The Mt. Reba flora, pp 13-60).

Axelrod D1 1981. Altitudes of Tertiary forests estimated from paleotemperature, pp. 131-137. *Prof. Sympos. Quinghai-xizang (Tibet) Plateau, Beijing. China. Scci. Press Gordon & Breacch, Sciene Publ. In.* N.Y.

Axelrod D1 1986. Analysis of some palaeogeographic and palaeoecologic problems of palaeobotany. *Palaeobotanist* **35**: 115-129.

Axelrod D1 1990. Environment of Middle Eocene (45 Ma) Thunder Mountain flora, Central Idaho. *Natn. geogra. Res.* **6**(3): 355-361.

Axelrod D1 1991. The Early Miocene Buffalo Canyon flora of Western Nevada. *Univ. Calif. Publ. Geol. Sci.* **135**, 76 pp.

Axelrod D1 1992. What is an equable climate? *Palaeogeogr. Palaeoclim. Pataeoecology* **91**: 1-12.

Axeelrod D1 1992. The Middle. Miocene Pyramid flora of Western Nevada. *Univ. CAlif. Pub. Geol. Sci.* **137**.50pp.

Axelrod D1 1995. The Eocene Thunder Mountain flora of Central Idaho. *Univ. Calif. Publ. Geol. Sci.* (submitted Dec. 1994). 77p.

Axelrod D1 1976. Tertiary vegetation, climate and altitude of the Rio Grande depression, New Mexico-Colorado. *Paleobiology* **2**(3): 235-254.

Axelrod D1 & Raven PH 1985. Origins of the Cordilleran flora. *J. Biogeography* **12**:21-47.

Bailey HP 1958. A simple moisture index based upon a primary law of evaporation. *Geografisker-Annaler* **50**(3-4): 196- 215.

Bailey HP 1960. A method of determining the Warnth and Temperateness of climate. *Geografisker Annaler* **42**: 1-16.

Bailey HP 1964. Toward a unified concept of the temperate climate. *Geografisker Rev.* **54**:516-545.

Bailey HP 1966. The mean annual range and standard deviation as measures of dispersion of temperature around the annual mean. *GEografisker Annaler* **48**-A: 183-194.

Bailey HP 1976. Monogram showing Warmth (W). *Temperateness (M) and Water Need(N) and frost frequency. Univ. California, Riverside, Geography Department.*

Brown RW. 1937. Additions to some fossil floras of the western United States. *U.S. Geol. Surv. Prof. Paper* 186.

Chaney RW & Axelrod D1 1859. *Miocene floras of the olumbia Plateau.* Carnegie Inst. Wash. Publ.

Durrell C 1987. *Geologi history of the Feather River country, California.* Univ. Calif. Press. Berkeley.

Epis RC & Chapin CE 1975. Geomorphic and tectonic implications of the post Laramide, Late Eocene erosion surface in the southern Rocky Mountains. *Geol. Soc. Am. Mem.* **144**: 45-74.

Gregory KM 1994. Paleoclimate and paleoelevation of the 35 Ma Florissant flora, Front Range, Colorado. *Palaeoclimates* **1**: 23-57.

Gregory KM & Chase CG. 1992. Tectonic significance of paleobotanically estimated climate of the late Eocene erosion surface, Colorado. *Geology* **20**: 581-585.

Greller AM 1988. Vegetational composition, leaf size and climatic warmth in an altitudinal sequence of evergreen forests in Sri Lanka. *Trop. Ecol.* **29**: 121-145.

Grellwe A.M. 1989. Correlation of Warmth and temperateness with the distributional limits of zonal forests in estern North Ameria. *Bull. Torrey. bot. Club* **116**(2): 145-163.

Hamilton W & Myers WR 1966. Cenozoic tectonics of the western United States. *Rev. Geophys* **4**: 509-549.

King PB 1977. *The evolution of North America.* Princeton Univ. Press. Princeton, N.J. 197 pp.

Knowlton FH 1926. *Flora of the Latch Formation of Spokane, Washington. and Coeur d Alene. Idaho. U.S. Geol. Surv. Prof. Paper* 140-A.

Oliver IE & Fairbridge RW 1987. *The Encyclopedia of Climatology.* Van Nostrand Reinhold Co., New York.

Smith AG, Hurley AM & Briden JC 1981. *Phanerozoic Paleocontinental world maps.* Cambridge Univ. Press.

Wernstedt FL 1972. *World Climatic Data.* Climatic Data Press, Lemont, P.A. 16851.

Wing. SL & Greenwood DR. 1983. Fossils and fossil climate, the case for equable continental interiors in the Eocene. *Phil. Trans. R. Soc. London* **B 141**: 243-252.

Wolfe JA 1979. Temperature parameters of humid and mesic forests of eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. *U.S. Geol. Surv. Prof. Paper* **1106**. 37 pp.

Wolfa JA 1980a. Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. *Paleogeogr. Palaeoclim. Paleoecol.* **30**: 313-323.

Wolfe JA 1980b. The Miocene Seldovia point flora from the Kenal Group, Alaska. *U.S. Geol. Surv. Prof. Paper* 1105.

Wolfe JA 1985. Distribution of major vegetational types during the Tertiary *In* Sundquist ET & Broeker WDC (Editors)—The carbon cycle and atmospheric CO_2: National variations Archean to Present: 357-375. *Am. Geophys Union Monogr.* **32**: 627 pp.

Wolfe JA 1992. An analysis of present day terrestrial lapse rates in the western Contimerous United States and their significance in palaeoaltitudinal estimates. *U.S. Geol. Surv. Bull.* **1964**.

Wolfe JA 1993. A method of obtaining climatic parameters from leaf assemblages. *U.S. Geol. Surv. Bull.* **2040:** 71 pp.

Wolfe JA & Schorn H 1994. Fossil floras indicate high altitude for west-central Nevada at 16 MA and collapse to about present altitudes by 12 MA. *Geol. Soc. Am. Abstra. Programs. Ann. Meeting. Seattle,* WA. pg. A 521.