THIRTY-THIRD SIR ALBERT CHARLES SEWARD MEMORIAL LECTURE

Analysis of some palaeogeographic and palaeoecologic problems of palaeobotany

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FOR a lecture dedicated to the memory of Sir Albert Charles Seward, and at the Institute of Palaeobotany bearing the name of his pupil and close friend, Birbal Sahni, it seems appropriate to consider a topic that was near the center of their scientific interests—the palaeogeography and palaeoecology of past floras. This is also appropriate since in the past two decades major advances in geology-geophysics have clarified our understanding that the Earth's crust is not stable. Continents, as well as parts of them, have moved long distances during geologic time, transporting fossil floras and faunas to positions distant from areas where they earlier lived.

Some of the most interesting and elusive problems of palaeobotany, and the field is filled with them, pertain to the vertical zonation of fossil floras, the juxtaposition of dissimilar floras, as well as the occurrence of similar floras in widely separated areas. We also find in the Neogene the association of fossil species whose close modern descendants (or the same species) are now in the same general region but are widely separated in altitude and distance from the fossil site. How are these to be explained when there is no evidence of high relief in the region during deposition? Such problems naturally involve an understanding of the geologic occurrence of the fossil flora, its topographic setting, the manner in which it may be interpreted in terms of its altitude and latitude, the responses of its taxa to changes in climate, and how local climate may account for the persistence of relict taxa, as well as the origin of new ones, for plants do change in time—some slowly—others more rapidly. It is these varied aspects of palaeobotany that I have chosen to review here.

PLATE TECTONICS AND DISPLACED FLORAS

Seward and Sahni were well aware of the present disjunct positions of the Glossopteris flora. In fact, Sahni (1935, 1936) believed that the position of the Glossopteris flora "cheek by jowl" with the *Gigantopteris* (and Angaran) flora in the Himalayas was indeed proof of continental displacement (Text-fig. 1). Although Seward and Sahni supported the notion of continental displacement, in those days a physical explanation of the displaced Glossopteris flora on the widely separated lands of Antarctica, Australia, South Africa, Brazil, and India was not certainly known.

One of the overlooked, yet impressive, examples of evidence that supports continental displacement occurs in the Pennsylvanian coalfields of the Appalachians and northwestern Europe. In this case we are dealing not only with numerous similar species in now-distant areas, but with a similar sequence of floral zones [(i.e., species) *in* Moore *et al.*, 1944; Read & Mamay, 1964)] in the coal beds (Text-fig. 2). Early investigators of these sequences were concerned chiefly with evidence of their age, not with explaining the sequential identity of numerous taxa in these now widely separated areas. Under present geographic relations, and regardless of the climate that might be postulated for these areas, it would be impossible to explain the similar succession of taxa by migration around the North Atlantic. Plate tectonic reconstructions of land areas in the Pennsylvanian now indicate that the Atlantic was closed and that the coal bed floras were geographically connected, or nearly so (Text-fig. 3; see Ferm, 1974). Progressively separated by ocean-floor spreading (see Smith *et al.*, 1981), they provide an

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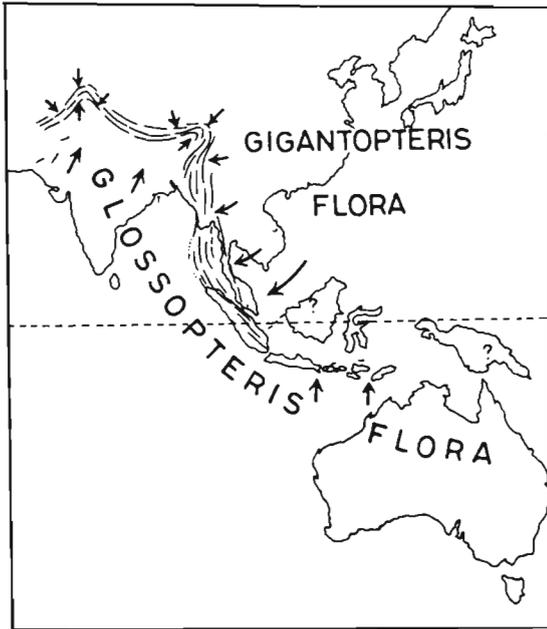
Text-fig. 1—The "cheek by jowl" occurrence of the *Glossopteris* with the *Gigantopteris* (and Angara) floras (from Sahni, 1963).

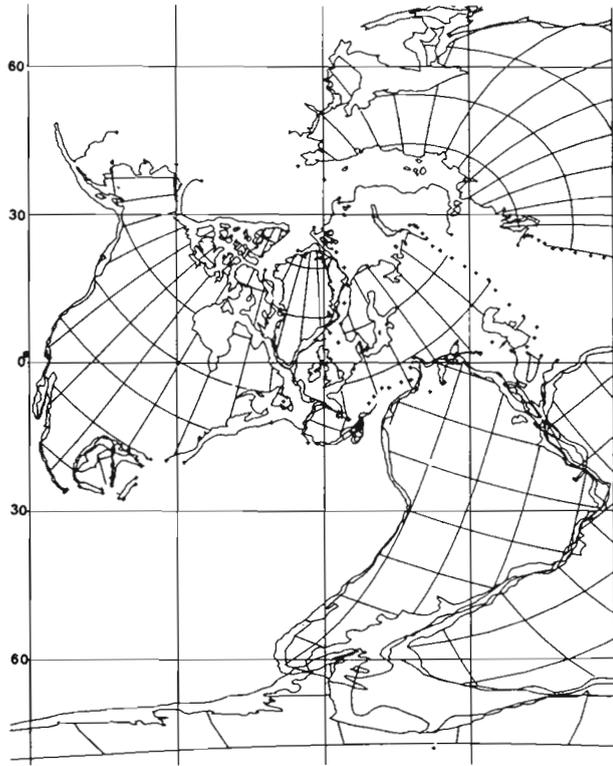example of displacement as significant as that of the Glossopteris flora.

There are also examples of displaced Tertiary floras.

1. Two Miocene floras in southern California that are close geographically differ greatly in composition and in the climate that they suggest (Text-fig. 4). The Puente flora of the Los Angeles basin includes broadleaved evergreens (e.g. *Annona, Magnolia, Ficus, Persea, Quercus, Sabal*) and a few rare sclerophylls with small leaves. By contrast, the Mint Canyon flora, situated only 65 km north, is composed chiefly of nanophyllous taxa that reflect semidesert climate. These include species of *Acacia, Bursera, Cardiospermum, Caesalpinia, Ceanothus, Celtis, Cercocarpus, Condalia, Fouquieria, Lysilona* and many others (*in* Axelrod, 1979a). Under present conditions, geologic evidence shows that there was no major topographic barrier between these floras, for the Mint Canyon Formation is overlain with slight unconformity by marine beds of essentially the same age, and these extend west. Detailed studies by Crowell and his associates (Crowell, 1962, 1982; Ramirez, 1983; Link, 1983) show that the Mint Canyon basin was in the area of the present Salton Sea, some 240 km south and in the interior when the Mint Canyon flora was living. At that time the Puente flora was in a marine basin situated near the Mexican border, in a mesic coastal position. It was separated from the Mint Canyon basin by low hills at the site of the present Peninsular Ranges, composed chiefly of granitic rocks. It is this that largely accounts for the contrast between these contemporaneous floras, and the climates that they suggest.

2. The Miocene Carmel flora near Monterey, California, is dominated by broadleaved evergreens, distributed in species of *Ficus, Nectandra, Ocotea, Persea, Quercus* and *Sabal* and others that indicate warm temperate, frostless climate. By contrast, the Temblor flora, situated 145 km southeast is dominated by deciduous hardwoods that lived along the shores of a marine embayment. It includes species of *Glyptostrobus, Pinus, Carya, Castanea, Cornus, Diospyros, Mahonia, Platanus, Nyssa, Quercus* (deciduous) as well as several broadleaved evergreens, notably *Magnolia, Persea* and *Quercus* (Renney, 1972). The Carmel flora is very similar to the Puente of southern California, then situated near the Mexican border, not to the Temblor which is much closer. In view of the position of the Puente much farther south it is expectable that several sclerophyllous taxa are in it, but not in the Carmel or Temblor. Whereas the

EUROPEAN CLASSIFICATION								AMERICAN CLASSIFICATION		
Series	Stage	Zone	U.S.S.R.	Germany	Holland Belgium	France	England	Floral Zones of England (Dix)	Eastern U.S.	Mid continent	Floral Zones of Appalachians (Read)
UPPER CORBONIFEROUS — Stephanian		D				Assise de St. Etienne		Zone of Odontopteris	Monongahela — Conemaugh Series	Virgil Series	Zone of Odontopteris and Danaeites
						Assise de Rive de Gier	Radstockian group	Zone of Pecopteris lamurensis			Zone of Lescuropteris
			Gjelian	Piesberg	Jabeek group	Assise de la Houve				Missouri Series	Zone of Pecopteris and Neuropteris flexuosa
		C₃		Flammkohle		Assise de Bruay		Zone of Neuropteris flexuosa			
	Westphalian	C	C₂	Gaskohle Gasflammkohle	Hendrik gr Maurits gr.	Assise d'Anzin	Stoffordian	Zone of Neuropteris rarinervis	Allegheny Series	Des Moines Series	Zone of Neuropteris rarinervis
		B	C₁				Yorkian	Zone of Neuropteris tenuifolia	Kanawha Series	Lamposos Series	Zone of Neuropteris tenuifolia
			Katharina					Zone of Lonchopteris			Zone of Cannophyllites

Text-fig. 2—Similar floral zones are represented in the Pennsylvanian coalfields of the Appalachians and England (from Moore *et al.*, 1944). For numerous species common to these zones, see Read and Mamay (1964).

Carmel flora has been displaced northward some 300 km by movement on the San Andreas rift system, the Temblor flora, situated 20 km east of the rift, represents the Miocene vegetation of its area (Text-fig. 4).

3. One might well ask: If the California coastal strip west of the San Andreas rift system has moved northward some 300 km (or more) since the early Miocene (Text-fig. 5) is modern floristic evidence consistent with this displacement? It is noteworthy that the flora of the present outer coastal area and that of the islands off southern California and 'adjacent Baja California (Cedros, Guadalupe Islands) includes a number of relict trees and shrubs whose closest allies are in the moist, equable uplands of Mexico where there is ample summer rainfall Among these may be noted:

Californian Taxa	Mexican Allies
Cupressus macrocarpa	*C. guadalupensis,* spp.
Pinus muricata	*Oocarpeae* (extinct)
Pinus radiata	*P. oocarpa*
Pinus remorata	*P. oocarpa*
Pinus torreyana	*P. oaxacana*
Arbutus menziesii	*A. xalapensis*
Ceanothus arboreus	*C. coeruleus*
Comarostaphylis diversifolia	*C.* spp.
Cercocarpus traskiae	*C. mojadensis*
Garrya elliptica	*G. ovata*
Gaultheria shallon	*C.* spp.
Laurocerasus (Prunus) lyonii	*L. (P.) prionophylla*
Myrica californica	*M. mexicana*
Vaccinium ovatum	*V. confertum*

Text-fig. 3—Reconstruction of land areas around the North Atlantic region in the Pennsylvanian (from Smith *et al.,* 1981).
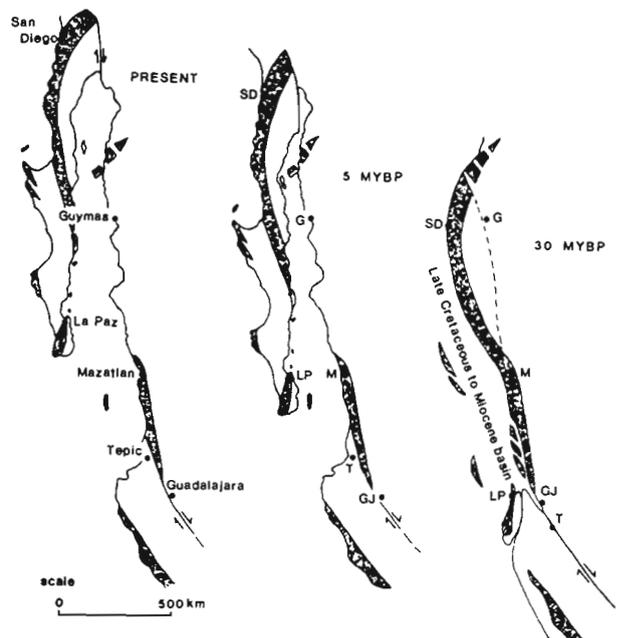

Text-fig. 4—Geographic relations of the Carmel, Temblor and Puente floras in the Miocene and today. Floras west of the San Andreas rift have been displaced on the order of 250-300 km.


Text-fig. 5—Displacement of the Peninsula of Baja, California, opening of the Gulf of California during the Miocene and later (from Gastil & Jensky, 1973).

The list becomes more impressive when we recall that during the Miocene and Pliocene, when there was ample summer rainfall, other taxa now in the oak-laurel-pine forests of the Mexican uplands also lived in coastal California. Among these were species of *Arbutus, Ilex, Myrica, Nectandra, Populus, Persea, Quercus* and *Sabal* (see Axelrod, 1977).

Apart from *Arbutus*, which also occurs at the lower margins of forest in the Sierra Nevada and Transverse Ranges, the listed taxa are typical members of the insular or maritime flora today. They are chiefly associated with the closed-cone pine forest dominated by *Pinus radiata* and *P. muricata*. In the past they were largely of insular or near-maritime occurrence, living under mild temperature without freezing (Axelrod, 1980a, 1983a). That they have been in the coastal area for some time is indicated by the distinctness of the coastal Puente flora as compared with the Mint Canyon and Tehachapi floras of interior southern California, a region where climate was too dry and temperatures too high for most of these coastal taxa. In brief, the taxa of the coastal region with present Mexican affinities were transported northward and have suvived in an equable climate with summer fogs that compensate for the dry summer climate (Text-fig. 6). These taxa occurred in coastal California prior to the expansion of the Sonoran Desert flora that now isolates them from their allies in Mexico (Axelrod, 1979a). This is shown by Neogene records of their occurrence in southern California, a time when the coastal area was joined to the Sonora-Sinaloa region of Mexico, prior to its northward displacement by movement on the San Andreas rift system during the Miocene and later (Text-fig. 5).

During the northward shift of the coastal strip, the fossil records of *Pinus radiata* (Monterey pine) show a trend to larger cones with larger seeds, primarily a response to the increasingly drier summer climate. The present pine groves are discontinuous, occurring at Monterey-Carmel, Año Nuevo, and Cambria in central California, and on Cedros and Guadalupe islands off northern Baja California. Proceeding northward from Cedros I., there is a gradual increase in cone size and seed size, but the trend is not clinal. In central California, the Monterey population with the smaller cones lies between the larger coned populations at Año Nuevo and Cambria (Text-fig. 7). Apparently the Monterey population is relict, for it survives in a very equable part of the coastal strip. Cold-water upwelling from Monterey submarine canyon provides the area with the coolest, foggiest climate in this part of the coastal strip (Axelrod, 1982). Fossil records of the forest show that it ranged nearly continuously along the coast into the Late Pleistocene (Text-fig. 8). It was confined to local areas as drought spread, and probably was most affected by the post-glacial warm dry Xerothermic period (8,000-4,000 B.P.) that restricted the forest to its present sites.

4. The history of the Canarian laurel forest is also clarified by plate movements (Axelrod, 1975). Many of the unique woody taxa of the present Canarian laurel forest are represented by the same (or very similar) species in the Miocene of southern Europe, from Portugal to eastward into Georgia, USSR. The notion that the laurel forest taxa (e.g. *Apollonias, Laurus, Ocotea, Persea,* and their associates) migrated from southern Europe to the islands pervades many discussions. But that does not explain the absence from the present Canarian flora of numerous taxa associated with Canarian plants in southern Europe during the Pliocene. These include: *a*) subtropicals now in the moister parts of Africa and southern Asia (e.g. *Buettneria, Cinnamomum, Myrsine*, etc.), *b*) temperate conifers and deciduous
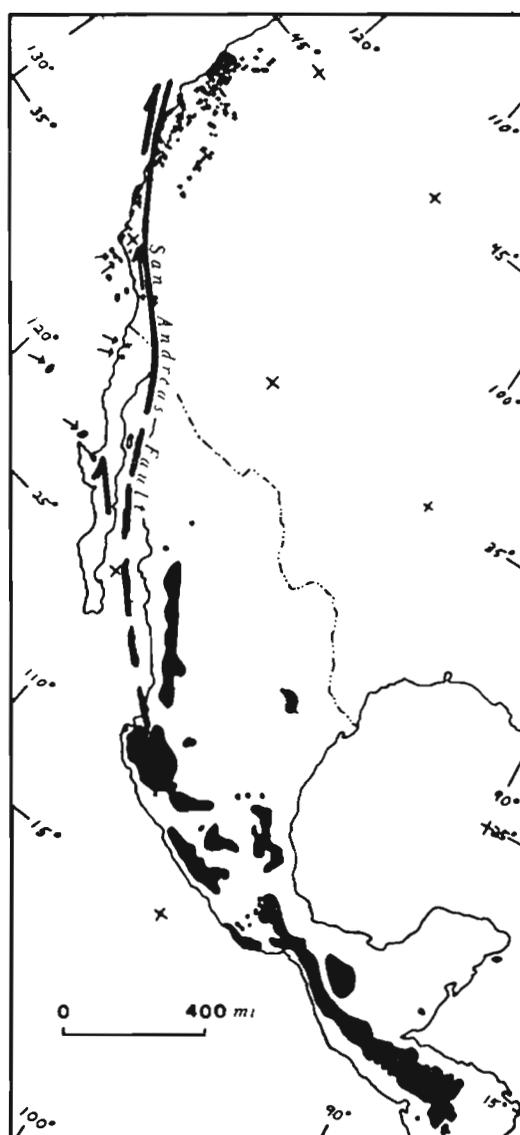
Text-fig. 6—Movement on the San Andreas rift system has displaced pines of the subsect. Oocarpeae, and their associates from Mexico to California.
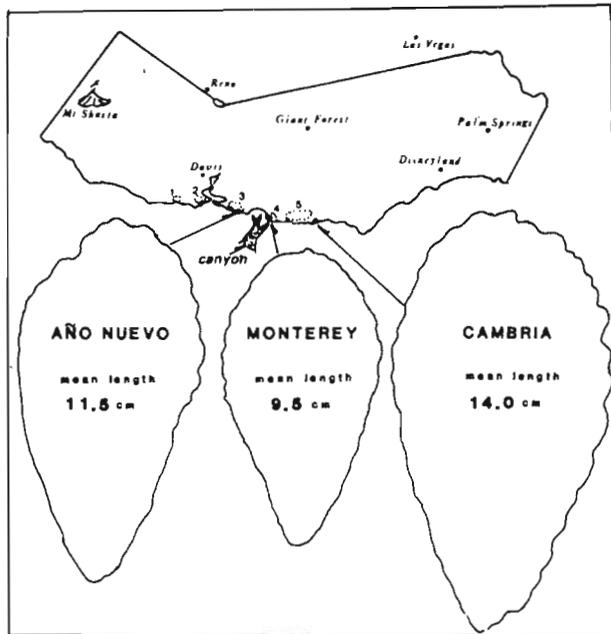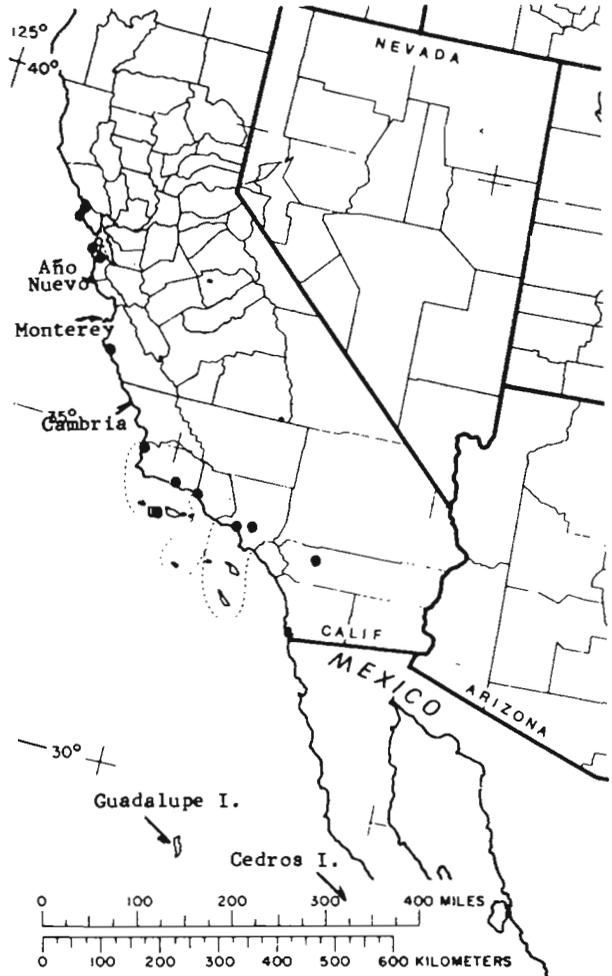
Text-fig. 7—Of the 3 populations of Monterey pine, *Pinus radiata*, on the central California coast, that at Monterey has the smallest cones. This reflects the cooler, highly equable climate resulting from cold-water upwelling from Monterey submarine canyon. Numerous other relict taxa also occur in this local area (Axelrod, 1982).

Text-fig. 8—*Pinus radiata* forms 5 small groves today (named), but in the Quaternary and earlier it was widely spread in coastal and near-coastal areas at sites marked (·).

hardwoods now in the eastern North America (e.g. *Acer, Carya, Liquidambar, Liriodendron, Robinia, Taxodium*), c) temperate alliances that are now chiefly in eastern Asia, with some in the Colchic region (e.g. *Albizzia, Carpinus, Cercidiphyllum, Ginkgo, Clyptostrobus, Parrotia*), d) taxa in temperate Europe (*Acer, Aesculus, Cornus, Crataegus, Populus, Quercus*), and e) broadleaved sclerophylls of the present Mediterranean region (e.g. *Ceratonia, Myrtus, Nerium, Quercus*).

During the Miocene and earlier, southern Europe was covered with subtropical to tropical evergreen forests that also blanketed the area of the present Saharan Desert. Their occurrence in southern Europe and north Africa during the Miocene and earlier reflects the position of the continents 10-12° Lat. lower than at present (Smith, Hurley & Briden, 1981). Further, geologic evidence shows that the Canary islands are composed of two groups. The low eastern islands (Lanzarote, Fuerteventura) are continental and were earlier connected with the mainland as shown by the remains of ratites there. The western islands (La Palma, Tenerife) are oceanic (volcanic) and Middle Miocene in age. The laurel forest taxa probably were in the eastern islands during the Paleogene, whereas they probably invaded the present western high islands only in the Middle Miocene and later.

This evidence, coupled with fossil records of mesic Tertiary rainforest and savanna in northern Africa into the Miocene, agrees with the distribution of a number of

Canarian taxa in the eastern paleotropics. Others have their allies in southern Africa, though not all are confined to the laurel forest community today. The present disjunctions (Text-fig. 9; also see Bramwell, 1976; Sunding, 1970, 1979) are the result of range restrictions as drier climates spread following the early Miocene. Northern Africa with its Canarian taxa was therefore transported north, out of the marginal tropics to meet the temperate forests at the north. The data suggest that the Arcto-Tertiary forests of Europe did not penetrate south into the Mediterranean region during the Miocene because climate there was too warm (tropical). Only as the European and African plates shifted north were temperate taxa able to invade southern Europe in the late Miocene and Pliocene. That is, as the African plate shifted north, the laurophyllous forests were carried into an ecotone with the temperate forests, the latter having been displaced southward by cooling climate as the continent moved north. The relict nature of the Canarian flora is consistent with its high percentage of diploids that reflect its antiquity (Bramwell, 1972), as does the
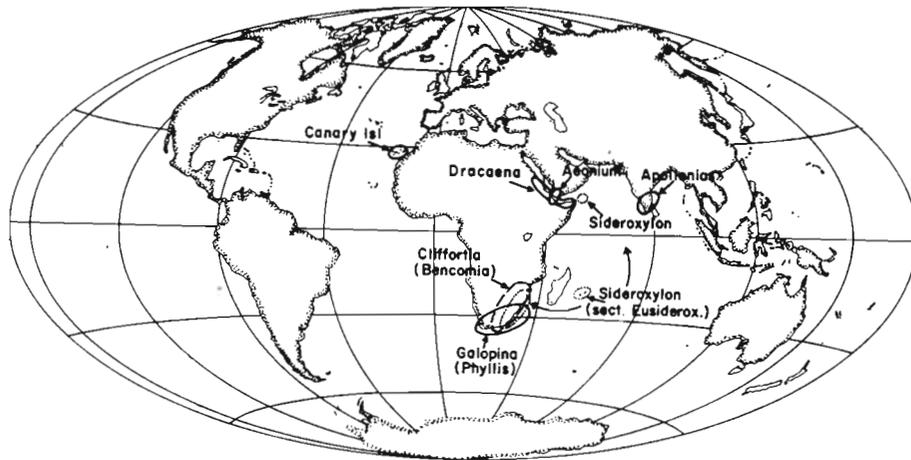
Text-fig. 9—Taxa of the Canarian laurel forest are related to alliances now widely spread across the Old World tropics, including paired genera between the Canaries and south Africa, e.g. *Cliffortia—Bencomia, Galopina-Phyllis*. For other examples, including those in the New World tropics, see Bramwell, 1976; Sunding, 1979; Humphries, 1979). These data, as well as plate tectonic evidence (see text), imply an origin for the Canarian laurel forest in the outer tropics during the Tertiary, not migration from southern Europe.

woody habit of much of the flora, the numerous ferns and lianas in it, and the widely disjunct occurrences of some of its unique taxa (see Bramwell, 1972, 1976; Humphries, 1979; Sunding, 1979). The sclerophyllous shrubs in it that contribute locally to macchia also support the idea they were derived early from alliances that contributed to laurophyllous forests then widely spread across low-middle latitudes of both Eurasia and North America (Axelrod, 1975). As for the more recent endemics, and the radiation of some genera (e.g. *Aeonium, Echium, Sonchus*) (Humphries, 1974), this probably was a late Miocene-Quaternary event. Invasion of the island region by the semiarid Saharan floral element that now dominates at low altitudes where rainfall is deficient probably was chiefly in the Quaternary.

5. The Lower Ravenian Eocene flora of the Gulf of Alaska region (Hollick, 1936; Wolfe, 1977) includes a number of broadleaved evergreen dicotyledons that indicate an outer tropical climate. Distributed in diverse families that are chiefly tropical in their adaptive relations, they include species of *Cyathea, Sabalites, Tetracentron, Diploclasia, Illicium, Cananga, Myristica, Litseaphyllum, Toona, Evodia, Melanorrhoea, Phytocrene, Allophyllus, Meliosma, Parashorea, Barringtonia, Kandelia, Alangium* and *Mastixia*. To explain their occurrence at Lat. 70°N it has been concluded that the Earth's axis was not tilted (Wolfe, 1977). Under this scenario, Earth would receive more warmth in polar areas in winter so that taxa could survive there without winter darkness and cold, yet have ample warmth in summer. However, if the axis had considerably less tilt than at present, the occurrence of mild temperate climate indicated by the Eocene floras of Spitzbergen, Ellesmere

Island, Greenland, Canada (mouth of Mackenzie River), and north-eastern Siberia, all of which are composed of deciduous hardwoods and conifers of temperate requirements, represent a major anomaly not considered by Wolfe. The asymmetric distribution of biota in the Gulf of Alaska region was charted earlier by Frakes and Kemp (1973, p. 547), though not explained. Geologic evidence shows that the Eocene floras of the coastal Alaska region have been displaced northward on the order of 1,000 km or more (e.g. Jones *et al*, 1970, 1972, 1977; Packer & Stone, 1974; Coney *et. al*, 1980; Jones & Silberling, 1982; Plumley *et al*., 1982; Helwig & Emmett, 1983; Saleeby, 1983; Bruns, 1983). This is supported by a recent study of the Eocene marine microfossil fauna which indicates considerable latitudinal displacement of the ocean floor off Alaska (Keller *et al*., 1985).

Since sections of the crust were transported long distances during the Tertiary, what significance does this have with respect to the proposed Tertiary Floral Stages of the Pacific coast (Wolfe, 1972, 1977, 1981). It means that their value is greatly diminished because the described Stages do not represent the sequence of taxa in their present geographic areas, but in distant sites. Furthermore, since the described Floral Stages are from the coastal strip they can not be applied outside that area because the composition of floras rapidly changed inland (Axelrod, 1965, figs 12, 13). As noted above, the dissimilar Puente and Mint Canyon floras of southern California represent coastal and interior environments; the few taxa in common (e.g. *Persea, Platanus*) are wide-ranging in time and occur in diverse environments. Furthermore, some fossil floras assigned by Wolfe (1981) to specific Stages do not have the taxa that define them. They lived well in the interior, at higher altitudes under

cool to cold temperate climate and hence supported wholly different floras. For example, the Eocene Bull Run and Copper Basin floras of northeastern Nevada are dominated by taxa of montane conifer forest and mixed conifer-deciduous hardwood forest. They can not represent the Ravenian Stage of Wolfe (1981) because taxa of that Stage are characterized by broadleaved evergreen species of the outer tropical zone, none of which occur in the Eocene floras of northeastern Nevada. Similarly, Wolfe (1981) assigns the Aldrich Station flora of west central Nevada to the Homerian Stage, the type of which is in the Cook Inlet region, Alaska. But there are no species and few genera common to the Aldrich Station and the Alaskan floras of the Homerian Stage. Wolfe also assigns the Stinking Water flora of eastern Oregon to the Homerian Stage, yet it has no species in common with the Alaskan floras. It is granted that these floras are of the same Age, but they do not represent the Stages assigned to them by Wolfe. Radiometric dating or magnetic-stratigraphy provide a more reliable basis for age assignment.
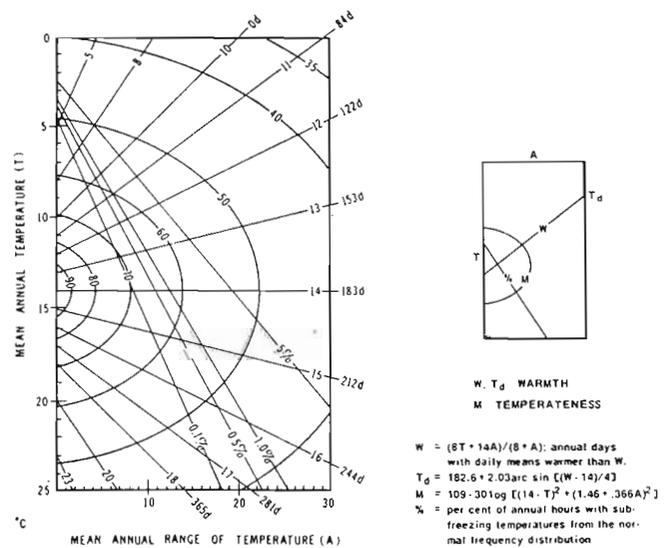
FORESTS OF POLAR REGIONS

Geologic evidence shows that land areas now in polar regions were also there in the Tertiary. In the north, fossil floras include those from Spitzbergen, Ellesmereland, Greenland, northern Canada (mouth of MacKenzie R.), Alaska, and northeast Siberia. They represent rich deciduous hardwood forest communities that reflect relatively mild temperate climate without severe winters. Regular seasonal variation in climate is attested by the marked growth rings of the fossil woods as well as the deciduous habit of the hardwood taxa.

The problem of survival there is clearly one of coping with the dark season. Recall that today numerous small trees and shrubs range north of the Arctic Circle, an occurrence that owes to post-glacial warming. Also, forest trees now range to lat. 60°N on the western sides of the northern continents, areas covered by ice as recently as 9,000-10,000 years ago. In addition, at Lat. 50°-59°N inner tropical plants flower and set seed today in greenhouses that are *not* illuminated in winter, but are kept warm (see data in Axelrod, 1983). This implies that under a longer photoperiod these taxa are confined not by light, but by temperature. Furthermore, experimental physiological evidence shows that evergreen conifers and dicotyledons, as well as deciduous hardwoods, undergo metabolic shutdown in winter season in temperate latitudes. They may be expected to have done so when they occurred at higher latitudes under the more equable climates of the Eocene and earlier. In addition, it was the equable climate that enabled "tropical" taxa (i.e. *Glyptostrobus*, cycads, palms, *Cedrela*) to inhabit climatic regions where they no longer occur (Axelrod, 1981b). As for the Eocene vertebrates from

high latitudes (i.e. Ellesmereland), reptiles (alligators, varanids, tortoises) probably hibernated during the low-light season when climate was mild temperate and freezing not severe. Mammals may well have been nocturnal as well as hibernating in habit, and some may have migrated into the area during the summer. The occurrence of dinosaurs in polar latitudes may also reflect seasonal migration during the poleward surge of high productivity as light and warmth increased following the polar night.

PALEOTEMPERATURE ANALYSIS

I have earlier presented a method for estimating thermal relations of a fossil flora (Axelrod, 1965) based on a method devised by Bailey (1960, 1964, 1966). It is also an effective means for estimating the altitude of a fossil flora. The method is based on estimating mean annual temperature (T) and the mean annual range of temperature (A). Together they provide a means for interpreting two very different aspects of climate, Warmth (W) and Equability (M). Warmth refers to the number of days warmer than a specified temperature. At W 10°C, 0 days are warmer than 10°C, at W 18°C, 365 days are warmer than that, and at 14°C, 183 days are equal to or warmer than 14°C (Text-fig. 10). The divisions of warmth (W) thus describe the duration of the *growing season.* W

W, T_d WARMTH
M TEMPERATENESS

$W = (8T + 14A)/(8 + A)$: annual days with daily means warmer than W.
$T_d = 182.6 + 2.03 \text{arc sin } [(W - 14)/4]$
$M = 109 - 30 \log [(14 - T)^2 + (1.46 + .366A)^2]$
% = per cent of annual hours with sub-freezing temperatures from the normal frequency distribution

Text-fig. 10—Monogram showing warmth and equability (temperateness) of climate (Bailey, 1960, 1964, 1966). The radii express warmth of climate (W) in terms of a particular temperature and the number of days (d) in which mean temperature rises to or above that level. The radii measure the duration of the growing season, which decreases poleward and with altitude. The arcs nearly normal to the warmth lines depict equibility (M). They provide an index to thermal extremes, graded from an ideal of M 100 to lower values farther removed from the centrum T 14° and A 0°. The percentage lines indicate the percentage of all hours of the year below freezing.
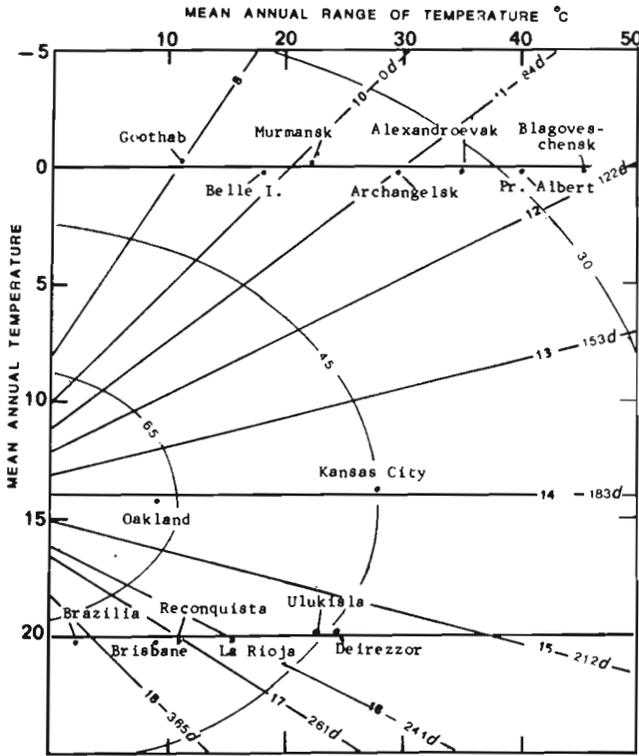
Text-fig. 11—Mean annual temperature can not provide an index to paleotemperature. Note that Oakland, California, with a low range of temperature rarely has frost whereas many days of freezing, snow and ice typify Kansas City, Missouri, which has a much greater range of temperature. Goothab, Greenland (T 0°) is near perpetual ice, Murmansk is close to the Tundra-boreal forest whereas Prince Albert is in a rich conifer forest. Similarly, Brasilia (T 20°C) is in the tropics, yet the other stations of similar mean temperature range well into warm tgemperate climates. The radiating lines of warmth show that in regions of cool climate increased range of temperature brings warmer conditions whereas in warm regions a rise in the range of temperature results in cooler conditions.

10°C represents treeline, whereas W 18°C is the margin of the tropics, and W 14°C lies in the middle of the temperate zone. By contrast, equability (M) provides a measure of thermal extremes. It is measured by a series of arcs that diverge from T 14° and A 0°C and range in value from M 100 (ideal, in the tropical uplands) to M 0 on Antarctica.

The relations shown in Text-fig. 11 reveal three major features. *First*, some stations with similar warmth (W) as Oakland, California, and Kansas City, Missouri, have very different equability values (M 67 vs. M 45, read the arcs). Whereas frost is rarely present in Oakland, many days at Kansas City have snow and subfreezing temperatures. *Second*, mean annual temperature (T) means very little in terms of paleoclimate or of vegetation. Note that stations with a mean annual temperature (T) of 0°C occur close to permanent ice (Goothab), are in Tundra (Belle, I.), in boreal forest

(Archangelsk), and in a rich conifer forest (Prince Albert). In the case of a mean temperature of 20°C, Brasilia is in the tropical belt but as the range or temperature increases the other stations are in more temperate climates. *Third*, it is evident that an increased range of temperature in temperate regions brings warmer climates, whereas in warm regions an increase in the range of temperature results in cooler conditions.

It is also apparent that as range of temperature increases, zones of warmth are separated by a greater distance vertically (altitudinally). Text-fig. 12 shows that with a 5° range of temperature, only 13° C separates W 10°C and W18°C; the tropics and treeline are only 13°C apart. But with a range of 20°C, these same zones are separated by 28°C. Clearly, with increased equability all vegetation zones—and their species—are closer in terms of altitude. Since temperature decreases with altitude (lapse rate), it is possible to determine approximately the altitude of a fossil flora. Today the normal terrestrial lapse rate varies across continents with orientation and the location of physical barriers. But in the Tertiary, climates were more equable, terrain was generally
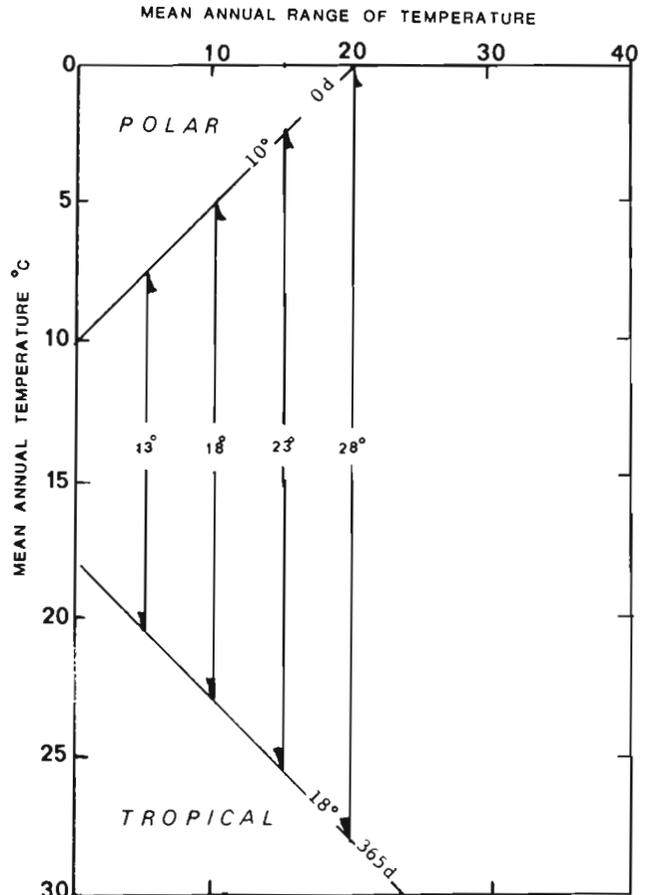

Text-fig. 12—Zones of warmth are closer in regions of more equable climate. The polar and tropical climate zones are progressively farther apart as range of temperature increases.

subdued, and oceans were warmer at middle and high latitudes. In general, the Tertiary had a normal terrestrial lapse rate of 0.55°C/100 m or 1°C/-183m (Axelrod & Bailey, 1976). An estimated warmth (W) and equability (M) of a flora in the coastal strip (sea level) or inland, thus provides a basis for inferring the probable altitude of a fossil flora in the interior.

For example, the Late Eocene Bull Run flora (40-35 m.y.), north-eastern Nevada, includes 10 florules distributed through 1,370 m (4,500 ft) of section. The lower 3 florules formed a conifer-deciduous hardwood forest, whereas the upper 7 are wholly dominated by montane conifers, notably *Abies, Larix, Picea, Pinus, Chamaecyparis* and include a few rare forest shrubs, as *Amelanchier, Berberis, Mahonia, Ribes, Sorbus* and *Vaccinium*. The coastal strip was then clothed with subtropical rainforest like that now in the cloud forest of southern Mexico. Average warmth there is W 16°-15°C and the range of temperature 5-7°C. Allowing for a somewhat greater range in the interior, say 9-10°C, then about 10.5°C separated the rain forest at sea level from the pure montane conifer forest in Bull run basin (Text-fig. 13). This implies an altitude near 1,958 m (10.5° × 183 m), or about 6.400 ft compared with 2,500 m (8,500 ft) for this zone today.

A Miocene flora from treeline in the summit region of the central Sierra Nevada south of Carson Pass is at 2.776 m (9,100 ft), and about 15 m above the granitic basement. Broadleaved evergreens (*Actinodaphne, Nectandra, Persea, Quercus*) and deciduous hardwoods (*Crataegus, Cyclocarya, Fagus, Liquidambar, Nyssa, Platanus, Populus, Quercus, Ulmus*) make up this well sampled flora. Conifers are not known from the assemblage. The flora suggests an environment like that now in the areas from northern Florida into south Carolina. Warmth of climate there ranges from W 15°-14°C. In view of the warmer ocean only 120 km west in the Middle Miocene, the absence of ice-caps, and the lack of major topographic barriers, climate was more equable than that now on the east coast. Hence warmth of climate probably was near W 14.5°, or lower. With a range of temperature near 12°C and a warmth of about 14.5°C, the distance to treeline is 12.5°C (Text-fig. 13), or approximately 2,288 m. Since the flora is now at 2766 m (9,100 ft), the data suggest an altitude near 478 m (i.e. 2,766-2,288 m), or about 1,570 ft in the Miocene. Hence, uplift in the area is on the order of 2,287 m (7,500 ft) since the Middle Miocene.

This estimate is comparable to that indicated by the Mt. Reba flora (6-7 m.y.) situated 20 km south at an altitude of 2,620 m (8,600 ft) and about 30 m above the granodiorite basement (Axelrod, 1980b). The flora is dominated by evergreen oak (*Quercus*), tan-oak (*Lithocarpus*, Douglas fir (*Pseudotsuga*), and cypress that represent broadleaved sclerophyll forest. Mixed conifer forest taxa (*Abies, Pinus, Sequoiadendron*) are
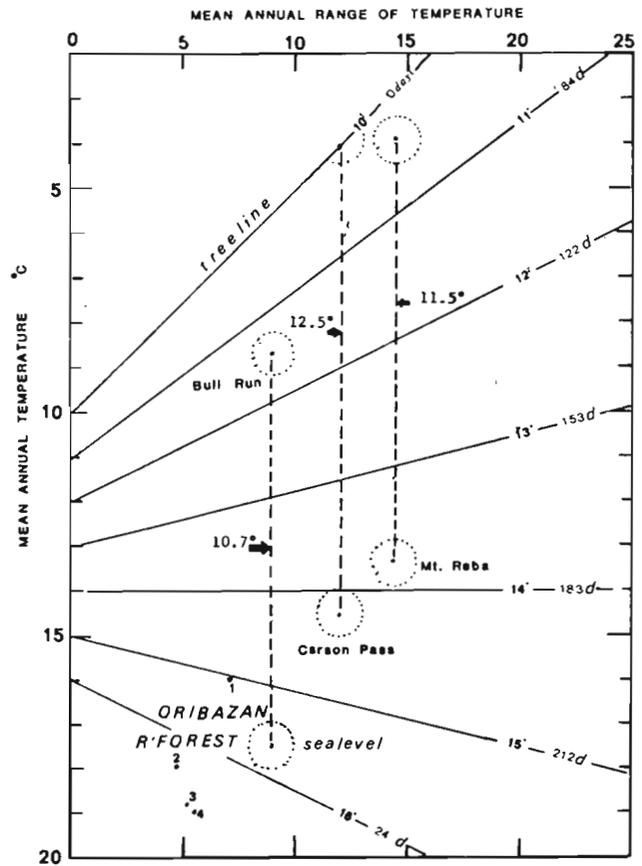
Text-fig. 13—Estimated altitudes of an Eocene flora, Nevada, and of two Miocene floras in the central Sierra Nevada based on pale-otemperature, and its indication of the amount of uplift in the range. Stations in the Orizaban rainforest are: 1. Huachianago, 2. Jalapa, 3. Huatusco, 4. Orizaba.

exceedingly rare. A few deciduous taxa, notably *Salix* and *Ulmus*, are also present. The relations imply a position at the upper margin of sclerophyll forest with mixed conifer forest on the bordering slopes. Allied vegetation is now in the Sierra Nevada to the northwest near 760 m (2,500 ft). The flora suggests mean annual temperature was near 13.4°C and the range was about 14.5°C, with warmth of W 13.7°C, or 174 days warmer than that (Text-fig. 13). This implies that the distance to the upper subalpine zone (W 10.5°C) was about 11.5°C or 2,105 m (7,100 ft). This is approximately the amount of uplift in the area since the close of the Miocene. The flora is overlain conformably by a thick, giant-boulder conglomerate at this site which is perched on a ridge crest overlooking Mokelumne River gorge where the river is now 1,360 m (4,500 ft) below the flora. This represents the amount of erosion that has occurred since 5-6 m.y. ago, and probably less.

As to the possible utility of the method, reference is made to the Middle Miocene Namling flora from the Tibetan Plateau west of Lhasa, and now at an altitude of 3,800 m. Represented by deciduous hardwoods chiefly,
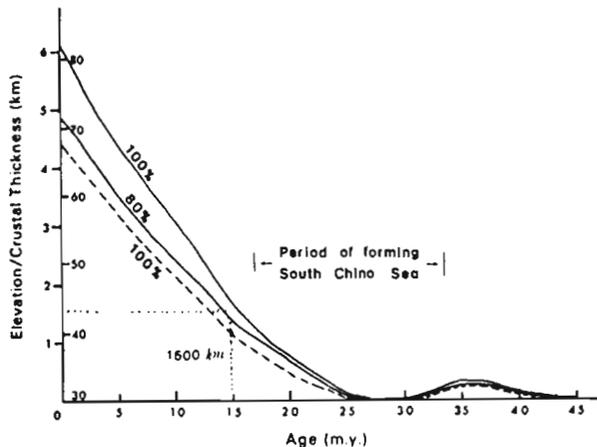
Text-fig. 14—Paleotemperature analysis of the Middle Miocene Namling flora, Tibet, suggested an altitude near 1,500 m (Axeirod, 1981a). This agrees with tectonic estimates of uplift of Tibet since the Middle Miocene (from Zhao & Morgan, 1985).

the flora certainly lived at a much lower altitude. Its thermal relations suggest an altitude of about 1,500 m (Axelrod, 1981a). This agrees closely with that estimated from plate tectonic history in south-east Asia (Text-fig. 14), including the opening of the South China Sea (Zhao & Morgan, 1985).

CENTERS OF ORIGIN

The local areas where taxa may have originated can rarely be determined apart from those of comparatively recent origin by hybridization, introgression, and other means from allied taxa in the nearby region. The problem of recognizing centres of origin is that taxa shift in area (altitude, latitude), as climate changes and taxa also change in time. This is the fallacy of pinpointing southeast Asia (eastern Himalayan region) as the center of angiosperm origin (Takhtajan, 1969). That area is a center of survival, one where climate is highly equable and with ample precipitation. The fossil record shows that a number of Magnolian taxa in that area have been recorded in regions distant from the east Himalayan region. Also, the Himalayan axis is very young, having been uplifted largely following the later Eocene. Prior to that the area was covered by ocean (see Smith et al, 1981), an environment scarcely conducive to the origin of angiosperms. The group originated in the tropics in pre-Cretaceous time and then migrated poleward (Axelrod, 1952, 1959). More recent evidence suggests that West Gondwanaland was the general region of early angiosperm evolution (Raven & Axelrod, 1974), and that this most probably took place on its drier margins and in drier sites (Stebbins, 1952, 1974; Axelrod, 1967).

The principal regions of Tertiary evolution were the areas of the major Gefloras, situated in tropical, temperate and subhumid-semiarid climates. Allied

species now occur in the disjunct areas of the eastern and western hemispheres, indicating migration and diversification from a common boreal or austral source. However, the species commonly represent different tribes or sections, implying evolution following spread from a common center. In each region there have been local areas of diversification, as seen for the oaks and pines, with few taxa common to the eastern and western hemispheres (Axelrod, 1983b, 1986). In each hemisphere a number of taxa are restricted to the dry or temperate regions and have apparently been there throughout their history as judged from the known fossil record, for example, of the 250-odd species of oak only 10-12 species of the allied Subsects. Diversipilosae and Prionoide link America and Eurasia, a link that was already established by the Paleocene. Of the 90-odd species of Pinus, only species of the Strobi and Cembrae of Subg. Strobus are common to the northern continents,
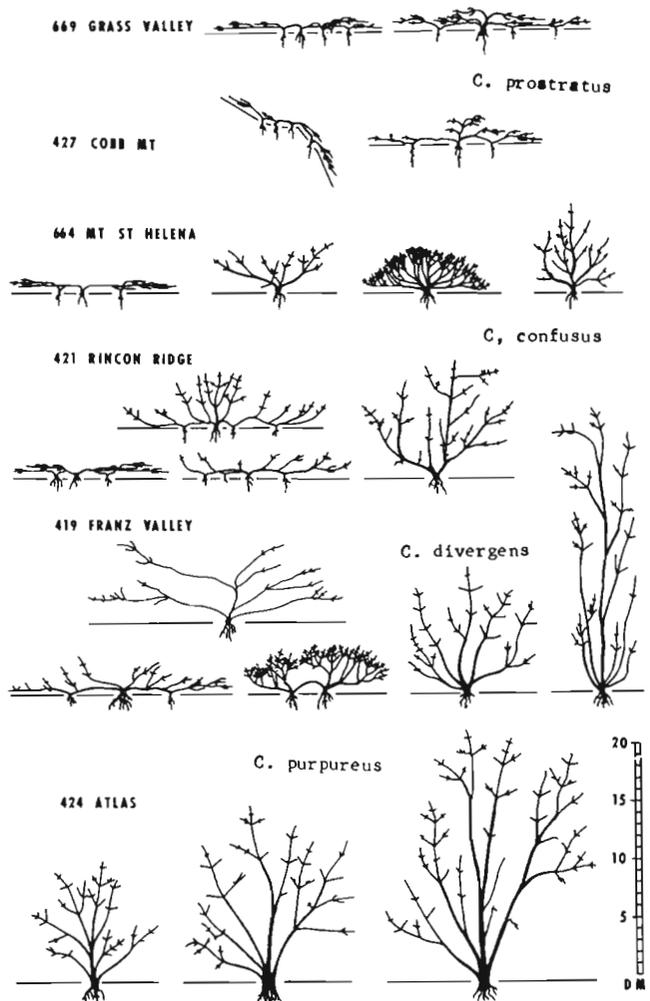
Text-fig. 15—Rapid evolution is indicated for the Ceanothus purpureus—C. prostratus series in the north Coast Ranges, California. With a rise in altitude into the young volcanic mountains there is a comparable response in plant form, branching, leaf size, etc. (from Nobs, 1963).
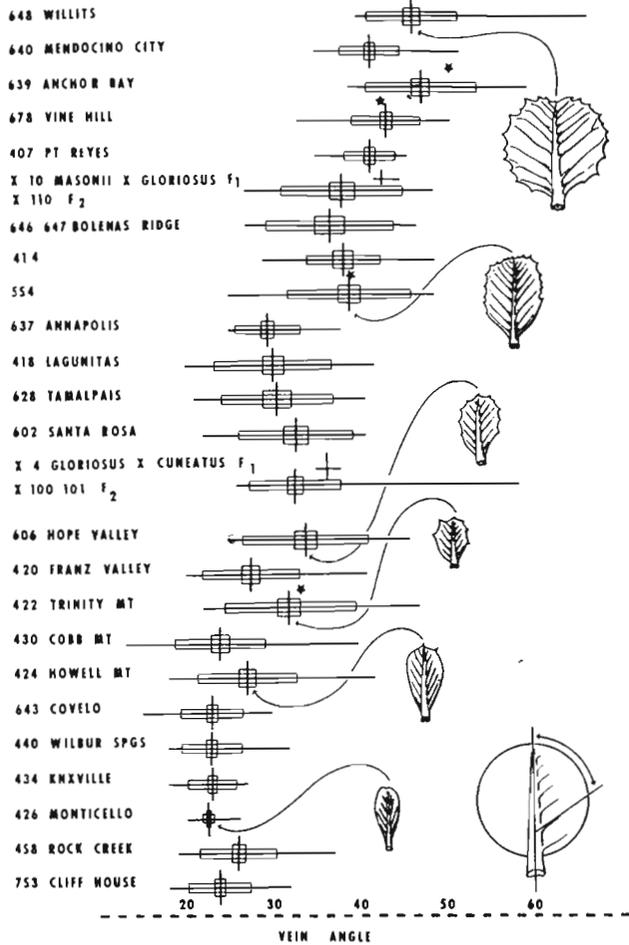
Text-fig. 16—Evolutionary change is also seen in moving from the inner Coast Ranges to the coastal strip in the series *C. cuneatus-gloriosus.* Not only is there a shift in leaf size, angle of departure of veins, teeth, etc. but in habit as well (from Nobs, 1963). In this case the older species (*cuneatus*) appears first in the interior.

and in the Subg. *Pinus,* only members of Subsect. *Sylvestres* now link the northern continents. The remainder may well be of local origin. For example, the 8 species of Subsect. Cembroides evidently originated in areas of drier climate in southwestern United States and Mexico. The 12 species of Subsect. Ponderosae are chiefly Mexican today, though some ranged more widely to the north in the Miocene. The species of Subsect. Balfourianae are largely Rocky Mountain and Great Basin in origin, as judged from the fossil record. In Eurasia, Subsect. Canarienses, with *P. canarienses* and *P. roxburghii,* link the Canary Islands with the western Himalayas today, implying more widespread occurrences in the past. This is demonstrated by fossil pines allied to them in southwest Asia.

As the moist temperate and tropical floras retreated during the Tertiary, vegetation on their cold (Taiga, Tundra) and dry (savanna, thorn scrub, grassland and semidesert) margins gradually expanded. Hence,

younger genera and species are often found in the more stressful areas when considered in terms of the world flora. But this is not to imply that there has been no change in the moist, more equable temperate or tropical regions; many new species originated there during the Tertiary.

There have been some very local centers of origin, areas where new opportunities have "suddenly" appeared. This is exemplified by the 8 species of *Ceanothus* (Subgenus *Cerastes*) in the Coast Ranges north of San Francisco Bay (Nobs, 1963). They apparently originated in this area following the accumulation of the Pliocene Sonoma Volcanics. The *C. purpureus-prostratus* series of several taxa shows a trend toward smaller size, less branching, and smaller leaves with fewer teeth to the north and at higher levels in the Coast Ranges (Text-fig. 15). The *C. gloriousus-cuneatus* series shows a shift to smaller size, less branching, and smaller leaves with few or no teeth from the coast toward the interior (Nobs, 1963) (Text-fig. 16). The genus *Arctostaphylos* in California includes some 40-odd species, most of which occur in the Coast Ranges that were elevated to their present heights at the close of the Pliocene and during the Quaternary. The rapid appearance of varied substrates and microclimates in the Coast Ranges facilitated the proliferation of numerous minor taxa in the major species groups. In Eurasia, the flora of the extended Tethyan region, situated in dry climate between the tropical and temperate geofloras has been a broad regional center of origin that extends from Portugal into the western Himalayas. There are a number of links with the Madrean vegetation of southwestern North America. These reflect migration across islands in the Atlantic before it was very wide (Text-fig. 17), chiefly during the Paleogene (Axelrod, 1975). The links were favored by the more nearly east-west orientation of the Atlantic coast of North America (prior to its counter-
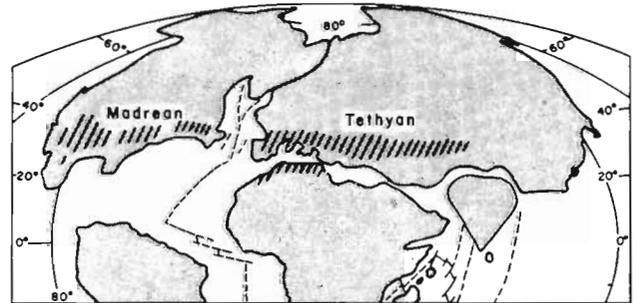
Text-fig. 17—There are numerous floristic links between the Tethyan and Madrean regions. They apparently reflect Paleogene connections across the Atlantic when it was narrower, populated with now-sunken islands, and before North America was rotated counter-clockwise. Its former position provided more numerous south-facing warmer and drier sites on basement rocks suitable for sclerophyllous taxa of warm temperate requirements (from Axelrod, 1975).
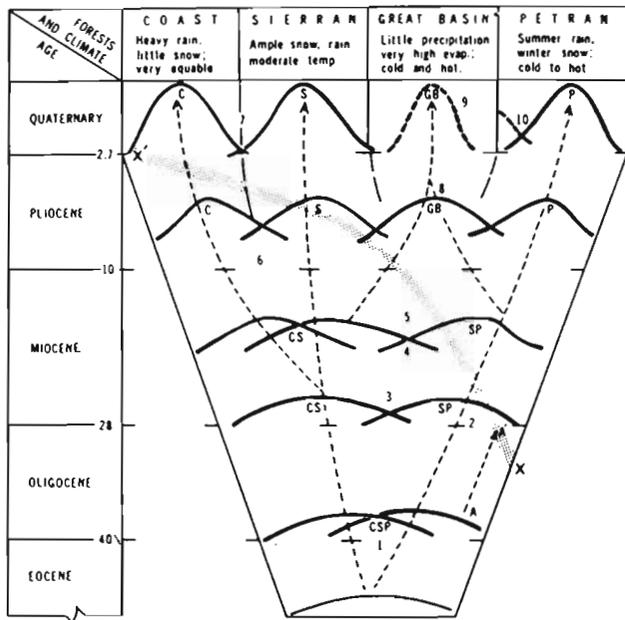
Text-fig. 18—Modernization of forests in western North America commenced in the central to southern Rocky Mountain region and thence spread coastward. Fossil· species allied to modern taxa that were associated in the past now largely contribute to forests of different composition in these more recently emerged climatic regions (from Axelrod, 1976).

clockwise rotation) that provided more numerous drier, warmer sites on south- and west-facing slopes. Links could not have been around the north Atlantic, as some have suggested, because that area was under cool temperate climate, as shown by the records of deciduous hardwoods and conifers there, not sclerophyllous taxa. The longer photoperiod there may also have been a factor in their restriction to middle latitudes.

VEGETATION CHANGES

Plants respond to changes in temperature and/or precipitation regimes which select some, segregate others to narrower relict areas, and eliminate some from areas they formerly occupied. During the Miocene, the present dry region east of the Cascade-Sierra Nevada axis, from British Columbia to south-central Nevada had ample rainfall and moderate temperature that supported a rich forest flora. It included species of *Acer, Betula, Castanea, Diospyros, Fagus, Ilex, Juglans, Liquidambar, Magnolia, Nyssa, Ostrya, Quercus, Sassafras, Taxodium* and *Ulmus* allied to species in the eastern United States. In addition, they were associated with species now represented by allied taxa in eastern Asia, distributed in *Acer, Alnus, Betula, Cercidiphyllum, Cinnamomum, Ginkgo, Metasequoia* and others. Further, a number of trees and shrubs that are now in the forests of the western United States are also recorded with them. These are distributed in *Abies, Picea, Pinus, Chamecyparis,*

Sequoia, Sequoiadendron, Alnus, Amelanchier, Betula, Crataegus, Fraxinus, Mahonia, Quercus, Sorbus, Rosa, and many others. As mountains were elevated and rainshadows appeared, a more seasonal climate developed and rainfall over the interior gradually decreased. At the same time, progressively colder water was spreading into the middle latitudes, resulting in decreased summer precipitation. Both factors appear to account for the elimination of numerous forest taxa during the later Miocene and Pliocene that occur now in eastern North America and eastern Asia. Their associates, however, adapted to the present forest climates of the western United States, notably those of the Rocky Mountain axis, the Sierra-Cascade Range and the Coast Ranges (Text-fig. 18). Further environmental diversification resulted in the spread of new forest subzones, notably those of the Rocky Mountain axis, the Sierra-Cascade Range and the Coast Ranges (Text-fig. 18). Further environmental diversification resulted in the spread of new forest subzones, notably those of the lower, drier margins of forest, as well as those of the drier slopes where different local communities have been segregated from the richer forest of the Miocene and earlier times.

Sclerophyllous vegetation of the Madrean province dominated south of the forests of Arcto-Tertiary alliance. The transition between these dissimilar floras occurred in central and southern Nevada during the Miocene (Text-fig. 19). The ecotone included forest taxa that interfingered with sclerophyllous oaks, *Pinus* (aff. *monophylla-edulis*), *Juniperus, Lyonothamnus,* and many semiarid shrubs distributed in *Arctostaphylos, Ceanothus, Cercocarpus, Heteromeles, Peraphyllum, Schmaltzia* and others. Farther south woody legumes become abundant as do more numerous sclerophyllous oaks, thorn taxa, palm and many others indicative of generally frostless
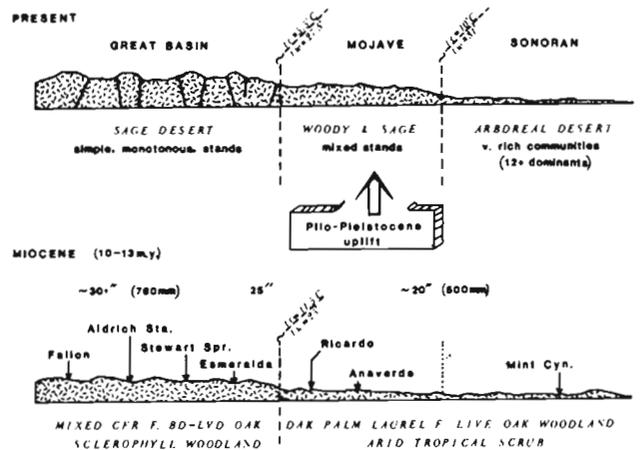

Text-fig. 19—Comparison of a north-south transect from the central Great Basin, western Nevada, into the Sonoran region, southern California, during the Miocene with that of today. The Mohave region represents an uplifted block with a flora transitional between the Sonoran and Great Basin desert floras.

climate. With decreasing summer rain and increasing cold sclerophyllous woodland taxa gradually retreated farther south. The surviving piñon-juniper woodland is relatively impoverished today, and occurs in a zone above the desert and sage-scrub belts. The preceding changes in woodland vegetation in the western United States are summarized in Text-fig. 20 and reviewed in detail elsewhere (Axelrod, 1977). It is amply clear that segregation of the rich Tertiary woodland in response to environmental changes during the middle and late Cenozoic shaped the present associations.

An additional vegetation change in the late Cenozoic has been the spread of wholly new zonal (regional) vegetation types. These notably include the grassland and desert environments, both of which are of post-glacial age in their present contexts (Axelrod, 1950, 1979a, 1979b, 1985). With respect to the tropical deserts, such as the Sonoran Desert of western North America, it has been the diversity of adaptive types of "peculiar" life form that has led to the notion that deserts are ancient earth features. Paleobotanical evidence shows that these diverse adaptive types represent taxa that persisted in the face of increasing dessication over the region. Earlier, they were members of woodland, thorn forest (scrub), and dry tropical forest and/or savanna vegetation. Some of them still enter these vegetation zones. These taxa were adapted to dry climate in the Eocene, and have further adapted to increased drought and heat more recently. This is certainly true of such unique taxa as *Fouquieria* (Fouquieriaceae), *Carnegiea* (Cactaceae), *Beaucarnea* (Liliaceae), and the leafless *Pedilanthus* (Euphorbiaceae). The occurrence of endemic families in the Sonoran area and on its borders is also consistent with gradual adaptation to drier climate later in the Tertiary and probably to their origin under subhumid climates in the Eocene and probably earlier.

Finally, mention must be made of the occurrence in Neogene floras of taxa whose modern derivatives are in the same region today, but are separated by fully 1,370-1,575 m (4,500-5,000 ft) in altitude. For example, *Populus* (cf. *tremuloides*) and *Picea* (cf. *breweriana*) occur in the Sonoma flora at sea level near Santa Rosa, California (Axelrod, 1944b). Their fossil associates were species of *Abies* (*grandis*), *Chamaecyparis* (*lawsoniana*), and *Sequoia* (*sempervirens*), as well as sclerophylls (*Lithocarpus, Heteromeles, Persea, Quercus, Umbellularia*), all of which indicate a lowland, mild climate with little frost. There is no evidence of nearby high mountains in the Sonoma region from which the upland species of aspen and spruce might have been derived. A comparable occurrence is seen in the presence of aspen with sclerophyllous oaks (cf. *Q. wislizenii, Q. douglasii*) and chaparral taxa (*Arctostaphylos, Heteromeles, Ribes*) in the low Sierran foot-hills in the early Pliocene (Axelrod, 1944a), yet these taxa are separated now from aspen by fully 1,575 m
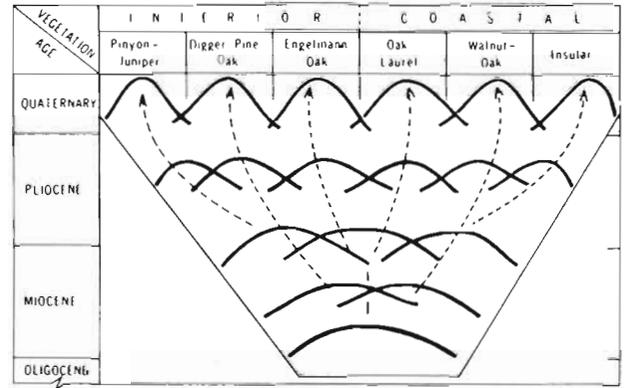
Text-fig. 20—Coastal and interior woodland associations were gradually segregated from the richer Madro-Tertiary woodland as summer rains decreased in the Neogene, and as areas of high equability were restricted coastward (from Axelrod, 1977).

(5,000 ft) in the Sierra Nevada some 80 km to the east. Another example is provided by the presence of *Picea* (cf. *breweriana*) and *Abies (cf. magnifica)* in the Late Miocene (13 m.y.) Purple Mountain flora of western nevada together with sclerophyllous taxa, notably species of *Cercocarpus* (cf. *betuloides*) *Quercus* (cf. *chrysolepis*), *Heteromeles* (cf. *arbutifolia*) and others. The conifers are now at altitudes 1,200 —1,520 (4,000-5,000 ft) higher, well removed from the sclerophylls. Geological evidence certainly provides no evidence that the spruce and fir may have been derived from high mountains near at hand.

These and other comparable occurrences seem to reflect the nature of Neogene climates. They were equable so that forest and woodland belts were closer in terms of altitude (see Text-figs 10, 12). Under these conditions, taxa were able to transgress their present
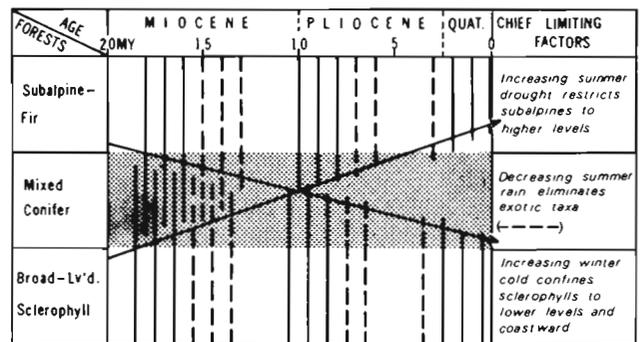
Text-fig. 21—Shifting associations of forest taxa in the Miocene and later. Vertical lines that shorten represent taxa whose ranges of tolerance were narrowed as climate changed. Increasing summer drought confined fir-subalpine taxa to higher, cooler levels, whereas increased winter cold restricted broadleaved evergreens to lower, warmer altitudes. It was this that gave rise to the modern, more distinct, less diverse associations than those of the Neogene. For clarity, taxa in the area of the mixed conifer forest (stippled) are now shown.

ecologic boundaries. In addition, there was summer rainfall, and it also provided conditions favorable for montane taxa at lower altitudes. This is seen today in the occurrence of aspen all through the forest belt in the eastern Great Basin and Rocky Mountains where it descends to meet the conifer woodland of *Pinus edulis* and *Juniperus* spp. together with its sclerophyllous chaparral taxa. It appears that as summer rains decreased in the west, montane taxa were confined to higher altitudes where lower evaporation rate compensated for the decrease (or absence) of summer precipitation. And as winters became more severe and snow frequency increased, taxa of the sclerophyll belt were gradually confined to lower altitudes (Text-fig. 21).

Some investigators have attempted to explain these and comparable occurrences by erecting high mountains in the nearby region from which the fossil remains might be carried to the lake basins or lowland floodplains. As noted, there is no geological evidence of high mountains in these areas. Those that may have been present were situated some 20-25 km (12-15 mi) south of the fossil sites (e.g. Mascall), areas from which it seems highly improbable that the abundant delicate winged seeds of spruce, fir and other taxa might have withstood transport without destruction.

The preceding review of some palaeobotanical problems certainly suggests that the present is not always the key to the past.

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