EVOLUTION AND BIOGEOGRAPHY OF MADREAN-TETHYAN SCLEROPHYLL VEGETATION[1]

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ABSTRACT

Broadleaved evergreen sclerophyllous taxa occupied a subhumid belt across much of North America-Eurasia by the middle Eocene. They originated from alliances in older laurophyllous forests that adapted to spreading dry climate. Since the continued trend to aridity finally restricted sclerophyllous vegetation to subhumid areas separated by drier tracts, it now occurs in areas with summer rain as well as in summer-dry mediterranean climates. Taxa of chaparral and macchia habit are common undershrubs in sclerophyll woodlands, to which they are seral. Shrublands spread only recently, though the adaptive structural features of the taxa are ancient and probably not pyrogenic.

The history of Madrean-Tethyan sclerophyll vegetation illuminates three biogeographic problems. First, related taxa that link the Mediterranean-California areas are part of the larger problem of ties between these areas and those of summer rainfall, of taxa now in summer-rain areas that were in presently summer-dry areas into the early Pleistocene, and of the more numerous taxa that linked sclerophyllous vegetation of the Madrean-Tethyan regions during the Tertiary. The ties between summer-dry and summer-wet areas are relicts of the Neogene; taxa now in mediterranean-climate areas adapted functionally to these new climates during the Pleistocene; and most trans-Atlantic links owe to migration across a narrower ocean with more numerous islands, to a broader zone of subhumid climate, and to a more easterly trending Appalachian axis with numerous dry edaphic sites. Second, by the mid-Oligocene spreading dry climate had confined a formerly continuous temperate rainforest to southern Mexico, the West coast and the Appalachian area. Winter cold and summer drought exterminated it in the West, whereas in the East winter cold eliminated most evergreen dicots, leaving a dominantly deciduous hardwood forest there. The temperate "Appalachian disjuncts" in southern Mexico are therefore ancient, and did not migrate south to enter a forest previously without deciduous hardwoods, as others maintain. Third, the Canarian laurel forest derived its taxa from those in laurophyllous forests that covered northern Africa into the middle Miocene, not by southward migration from southern Europe in the Pliocene. Since many shrubs in the surviving laurel forest also contribute to macchia on bordering slopes, the ancient origin of their typical adaptive structural features is clearly implied.

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[1] Acknowledgments.—My current interest in this problem commenced in 1971, with my first glimpse of Mediterranean sclerophyllous vegetation, composed of Arbutus, Ilex, Laurus, Pistacia, Phillyrea, Pinus brutia, Quercus and Rhus. This was not a sunny, summer-dry Spain, but on the Black Sea coast near Inebolu, northern Turkey, where there is considerable rain during the summer months. There the sclerophyllous belt is replaced upslope at altitudes near 150 to 200m by a mixed deciduous hardwood forest composed of Acer, Carpinus, Castanea, Corylus, Cotinus, Fagus, Juglans, Pinus nigra, Quercus (deciduous), Rubus and Sorbus. The ecotone simulates the general composition of numerous late Tertiary floras of the Mediterranean region, as well as those in the western United States where members of sclerophyllous Madrean vegetation were also in ecotone with deciduous hardwood-conifer forests of Arcto-Tertiary alliance, though in each area the Neogene floras are far more diverse than the living.

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Sclerophyllous evergreen woodland and chaparral or macchia vegetation now inhabit discontinuous areas of subhumid climate across North America and Eurasia. They are remnants of an older sclerophyllous flora that appears to have originated from alliances in subtropical laurophyllous forests that evolved in response to the expansion of a new adaptive zone—dry climate. In North America, forerunners of modern sclerophyllous taxa appear in the middle Eocene, and their derivatives migrated widely as dry climate spread (Axelrod, 1958, 1967c, 1973) . This sclerophyllous vegetation was captioned the Madro-Tertiary Geoflora because remnants of it survive in the Sierra Madre of northern Mexico and related ranges to the north, and because its taxa appear to have originated over this region. It occupied a position between Tropical-Tertiary and Arcto-Tertiary forests throughout its history, and in the ecotones with them it regularly includes taxa from these dissimilar environments.

Evergreen sclerophyllous vegetation has had a similar history in Eurasia, to judge from the brief analyses presented by Andreánszky (1962a, 1962b) and Takhtajan (1969) . Its species were derived from alliances in older laurophyllous forests that adapted to dry climate that stretched across the Tethyan region of southern Eurasia by the later Eocene. As Andreánszky and Takhtajan note, it was situated between the Turgayan (Arcto-Tertiary) forests of mixed deciduous hardwoods and conifers that thrived under ample rainfall and mild temperate climate, and the Poltavian (Tropical-Tertiary) evergreen forests that were adapted to moist, subtropical and tropical conditions. Andreánszky felt the sclerophyllous flora had originated under dry climate in the Spain-Morocco region, and termed it a "Xero-Atlantic" element. However, Takhtajan (1969) noted that sclerophyllous vegetation was widespread across lands marginal to the Tethys Sea, and captioned it Tertiary-Tethyan vegetation.

The broadleaved sclerophyllous evergreen vegetation of the Madrean-Tethyan regions is similar in physiognomy and shares a number of related taxa. These relations have been considered by others, but chiefly in the context of affinities between the evergreen sclerophyllous floras of the Mediterranean basin and California which survive under mediterranean climate (Stebbins & Day, 1967; Walter, 1968; Raven, 1973) . Among the alliances in common are species of *Arbutus, Cercis, Cupressus, Juniperus, Pinus* (closed-cone) , *Platanus, Quercus* (evergreen), *Prunus (Laurocerasus, Emplectocladus), Rhus (Schmaltzia), Rhamnus, Staphylea* and *Styrax.* As to where and when the ties were established, some *(i.e.,* Engler, 1904, 1914) infer migration via subhumid climate around the north Atlantic; others (Stebbins & Day, 1967) suggest Miocene dry tracts in the lee of mountains along a Beringian route. Either route seems unlikely because (a) sclerophyllous taxa have not been recorded there, (b) moist temperate Arcto-Tertiary forests inhabited the region, (c) mountains of sufficient altitude to provide dry tracts were not yet elevated, and (d) xeric sclerophylls require short days, warm temperate to subtropical temperatures, and limited (subhumid) rainfall, a combination of conditions that can not occur at high latitudes. Engler (1904) also considered the possibility that ancient, now-sunken, Tertiary continental land bridges may account for the links between areas of mediterranean climate, and also between taxa of the desert and thorn scrub vegetation on opposite sides of the Atlantic. Not only is there no geologic or geophysical evidence of low density (2.8) sialic land bridges in the denser (3.2) simatic basement of the Atlantic basin, but mediterranean climate is much younger than the sclerophylls because it only appeared after the early glacials. Meusel (1969) suggested the present Mediterranean-Californian disjuncts are the result either of parallel differentiation of holarctic or amphitropical taxa under similar climate, or of long-distance dispersal from one center to the other.

The presence of related taxa in the now widely separated mediterranean climates of North America and Eurasia becomes understandable when we note that on each landmass species that contribute to broadleaved evergreen sclerophyllous vegetation are not confined to areas of summer-dry, mediterranean climate (Axelrod, 1973) . Many of them, or closely related ones, are also in subhumid regions of summer rainfall, as in Arizona-New Mexico or Nuevo Leon in southern North America, or in northern Turkey, Iran (Caspian shore) , and northwestern India-Baluchistan. The fossil record shows that by the middle Tertiary essentially continuous, sclerophyllous vegetation belts covered each continent at low—middle latitudes where they thrived under subhumid climates with mild temperature and moderate rainfall in the warm season. Late in the Tertiary, decreasing temperature and reduced rainfall restricted sclerophyllous vegetation at the expense of spreading grassland, steppe and desert climates. The present discontinuous areas of sclerophyllous vegetation are therefore relict, and one of them occupies a wholly new climate (mediterranean) that seems to have appeared after the first glacial (Axelrod, 1966, 1973) .

New evidence regarding the origin of sclerophyllous vegetation and the evolution of the adaptive characters of its taxa is considered here. A more complete explanation (Axelrod, 1971, 1972) of the present-day links between taxa now in the derived Madrean-Tethyan sclerophyllous zones is also presented. Furthermore, since spreading dry climate affected vegetation zones marginal to the expanding Madrean-Tethyan belt, two of them are considered. These are the history of the so-called "Appalachian" disjuncts in the Mexican-Central American temperate rain (cloud) forests, and the history of the sclerophyllous, evergreen Canary Island laurel forest that now inhabits the volcanic western Canaries, surrounded by ocean and desert.

BROADLEAVED SCLEROPHYLL VEGETATION

My field studies in North America and southern Eurasia have been concerned with the sclerophyll zone, the relation between woodland and chaparral or macchia vegetation, and the nature of the ecotones to adjacent vegetation. The basic findings are summarized here in terms of the evidence they provide with respect to its origin. The literature is so extensive that only a few critical references are noted.

MADREAN PROVINCE

Evergreen sclerophyllous woodland and chaparral have been studied in the following areas.

California
  Closed-cone pine forest and chaparral
    Inverness at Tomales Bay; Monterey; Purisima Hills near Lompoc; Pecho Hills near San Luis Obispo; Santa Cruz Island.
  Pinyon pine-juniper woodland and chaparral
    Wrightwood, San Gabriel Mts.; Anza-Bautista Creek, San Jacinto Mts.; Rattlesnake Mt., San Bernardino Mts.; Frazier Mt. Park, Mt. Pinos; Rattlesnake Canyon, Cuyama Valley.
  Digger pine woodland and chaparral
    Throughout inner Coast Ranges and lower slopes, Sierra Nevada.
  Englemann oak woodland and chaparral
    Interior southern California, Pasadena to Campo.
  Walnut-oak woodland
    Coastal southern California, from Montecito south to Santa Ana River valley.
Baja California
  Live oak woodland and chaparral
    Sierra San Pedro Martir.
  Closed-cone pine forest
    W of San Vicente.
Arizona
  Pinyon-juniper woodland and chaparral
    Hualpai Mts., S of Kingman; Payson-Pine-Verde River; Highway 60 W of Miami; Highway 84 SW of Prescott; S slope, Catalina Mts.; Mescal Mts., S of Globe.
New Mexico
  Oak-juniper woodland and chaparral
    Highway 82 W of Cloudcroft; Highway 90 W of Kingston.
Eastern Mexico (Nuevo Leon to San Luis Potosi)
  Pinyon pine-juniper woodland
    Near Galaena, Nuevo Leon; near La Escondida, Nuevo Leon; W base of S Pena Nevada, Nuevo Leon.
  Oak woodland and chaparral
    Vic. Cerritos, San Luis Potosi; vic. Guadalcazar, San Luis Potosi.

It is amply clear that sclerophyllous vegetation inhabits regions other than the wet winter and dry summer climate that distinguishes the climate of California, and which is usually associated with its occurrence. Sclerophyllous vegetation is well developed across central Arizona and eastward into New Mexico and Texas, a region of subhumid climate with winter and summer precipitation. Chaparral and evergreen woodland also cover extensive areas on the western slopes of the Sierra Madre Oriental in eastern Mexico, from near Saltillo southward into San Luis Potosi, a region of summer rain and winter drought. Some species are common to two or three of these regions, or are represented there by paired-species (Table 1) . These include taxa that contribute to chaparral, as well as to the pine-oak woodland that borders chaparral or is mixed with it.

TABLE 1. Some identical and closely related taxa in sclerophyllous vegetation in subhumid Madrean North America (* = fossil occurrence).

Taxa	California	SW United States	Mexico
Arbutus	*menziesii*	—	*xalapensis*
Arctostaphylos	*pringlei*	*pringlei*	—
Arctostaphylos	*pungens* * (*prepungens*, Miocene)	*pungens*	*pungens*
Bumelia	* (*beaverana*, Miocene, Nevada)	*lanuginosa*	*lanuginosa*
Ceanothus	—	*fendleri*	*fendleri*
Ceanothus	*greggii*	*greggii*	*greggii*
Ceanothus	*insularis* * (Miocene)	—	*coeruleus*
Celtis	—	*iguanea*	*iguanea*
Celtis	* (Miocene)	*pallida*	*pallida*
Celtis	*reticulata* (very rare) * (Miocene & Pliocene)	*reticulate*	*reticulata*
Cercis	*occidentalis* * (*carsoniana*, Miocene, Nevada)	*occidentalis* (*very* rare)	—
Cercocarpus	*montanus* (= *betuloides*) * (*antiquus*, Miocene & Pliocene, California & Nevada)	*montanus*	
Cercocarpus	* (*holmesii*, Miocene, Nevada)	*paucidentatus*	*paucidentatus*
Cercocarpus	*traskiae*	—	*mojadensis*
Comarostaphylos	*diversifolia*	—	*many* species
Cupressus	*forbesii*; other species * (*preforbesii*, Miocene & Pliocene)	*arizonica*	*arizonica*
Dioon	* (undescribed, Miocene)	*purpusii* (NW Sonora-Sinaloa)	*edule*
Dodonaea	* (*californica*, Miocene & Pliocene)	*angustifolia*	*angustifolia*
Erythrina	—	*flabelliformis*	*flabelliformis*
Fraxinus	*dipetala*	*dipetala* (very rare)	—

TABLE 1. (continued)

Taxa	California	SW United States	Mexico
Fraxinus	velutina (S California only) *(*alcorni,* Miocene, Nevada)	velutina	berlandieriana
Fremontodendron	californicum * (Miocene, California)	californicum (very rare)	—
Garrya	elliptica * (mason, Pliocene)	—	ovata
Garrya	* (axelrodi, Miocene, Nevada)	—	ovata
Garrya	flavescens	flavescens	—
Garrya	wrightii	wrightii	wrightii
Gaultheria	shallon	—	hartwegiana; many species
Ilex	* (sonomensis, Pliocene)	brandegeei (S Baja California)	
Ilex	* (undescribed, Miocene)		rubra (W Mexico)
Juglans	* (Pliocene; Miocene, Nevada)	rupestris-major	mollis
Juniperus	californica	monosperma	deppeana; mexicana
Karwinskia	* (californica, Miocene & Pliocene)		humboldtiana
Mahonia	fremontii (rare)	fremontii	fremontii
Mahonia	* (Miocene, Nevada)		gracilens
Mahonia	—	trifoliata	trifoliata
Morus	—	microphylla	microphylla
Myrica	* (mohavensis, Miocene)		mexicana
Persea	* (coalingensis, Miocene & Pliocene)	—	borbonia; podadenia
Pinus	monophylla; quadrifolia	edulis	cembroides; nelsoni; pinceana
Platanus	racemosa	wrightii	—
Populus	fremontii	fremontii	arizonica

TABLE 1. (continued)

Taxa	California	SW United States	Mexico
Populus	* (*sonorensis*, Miocene & Pliocene, S California)	*brandegeei* (Baja California)	
Prunus	* (Miocene, S California)	*virens*	*virens*
Quercus	* (*mohavensis*, Miocene)	—	*brandegeei* (*Baja* California); *fusiformis* (*NE* Mexico).
Quercus	* (*undescribed*, Miocene, S California)	*emoryi*	*emoryi*
Quercus	*chrysolepis* * (*hannibali*, Miocene & Pliocene)	*chrysolepis*	
Quercus	*dunnii* (= *palmeri*) * (*pliopalmeri*, Miocene & Pliocene)	*dunnii*	
Quercus	*engelmannii* * (*Miocene* & Pliocene)	*oblongifolia*	
Quercus	* (*turneri*, Miocene)	*grisea*	*grisea* (*Zacatecas*)
Quercus	*turbinella* * (*dispersa*, Miocene, S California)	*turbinella*	
Quercus	* (*orindensis*)	*vaseyana* (*W* Texas)	
Quercus	* (*undescribed*, Miocene, S California)	—	*potosiana*
Quercus	* (*dayana*, Miocene, C & S California)	*fusiformis*	*virginiana* (on coastal plain)
Rhamnus	*californica* * (*precalifornica*, Miocene)	*californica*	species
Rhamnus	*ilicifolia* * (Miocene)	*ilicifolia*	
Rhus	* (*sonorensis*, Miocene)	*virens*	*virens*
Rhus	* (*tehachapiensis*, Miocene)	*chondroloma*	
Rhus	* (undescribed, Miocene)	*microphylla*	*microphylla*
Rhus	*trilobata*	*trilobata*	*trilobata*

TABLE 1. (continued)

Taxa	California	SW United States	E Mexico
Rhus (*Schmaltzia*)	*ovata* *(*preovata*, Miocene & Pliocene; Miocene, Nevada)	*ovata*	—
Ribes (Grossularia)	*quercetorum* *(*mehrtensis*, Pliocene)	*quercetorum*	
Robinia	*(*californica*, Miocene & Pliocene)	*neomexicana*	
Sabal	*(*miocenica*, Miocene & Pliocene, S California)		*mexicana*; *uresana*
Sageretia	*(Miocene, S California)	*wrightii*	*wrightii*
Salix	*lasiolepis*	*lasiolepis*	*lasiolepis*
Salix	*exigua*	*taxifolia*	*taxifolia*
Sapindus	*(*oklahomensis*, Pliocene)	*drummondii*	*drummondii*
Ungnadia	*(*clarkii*, Miocene)	*speciosa*	*speciosa*
Vauquelinia	(Oligocene, Nevada)	*californica*	*corymbosa*
Zizyphus	*(Miocene)	*obtusifolia*	*obtusifolia*

In all these areas evergreen oaks and nut-pines form a rich woodland that has numerous sclerophyllous shrubs and typically borders chaparral or grades into it. At lower, drier levels from Arizona to eastern Mexico, both give way to grassland, or to desert where grassland has been overgrazed. In California, drier sites below chaparral are covered with oak savanna, or with sage or grassland. At higher, moister and cooler levels in eastern Mexico pinyon pine-juniper-oak woodland is replaced by a low montane forest dominated by oaks, or by a rich mesic cloud forest (Muller, 1939; Rzedowski, 1966). In Arizona-New Mexico, chaparral alternates with sclerophyllous oak-madrone woodland or with pinyon-oak woodland, and all are replaced at higher moister levels by mixed conifer forest. Similar relations exist in California, where its taxa additionally contribute to the understory of closed-cone pine forest in the coastal strip. This community closely parallels in physiognomy, and somewhat in composition, the *Pinus halepensis-brutia-Quercus* woodland vegetation of the Mediterranean coastal strip.

The sclerophyllous taxa in the woodlands and brushlands that stretch from California to eastern Mexico are interrupted now by more arid climates that support grassland and desert vegetation. As deduced by Clements (1936), a wider distribution at times of moister climate accounts for similar taxa in the chaparral and woodland on opposite sides of the Mohave and Sonoran desert regions in

California and Arizona, a conclusion supported now by additional fossil evidence (Axelrod, 1958, 1973). During the Miocene sclerophyllous woodland with a rich understory of sclerophyllous evergreen shrubs inhabited the present Mohave-Sonoran region. This implies 20-25 inches precipitation distributed in summer and winter, and mild temperature as judged from *Persea, Lyonothamnus, Myrica, Laurocerasus* and *Clethra.* Since most of the Miocene species appear indistinguishable from those now living, the identical species on opposite sides of the desert are no younger. As for the paired-species that provide links across the region, isolation may account for the differences, though this problem can only be settled by a more complete fossil record. In any event, a Neogene continuum that stretched from northeastern Mexico to California has been segregated into climatic subregions since the early Quaternary, following which dry climates rapidly expanded in each of the successive interglacial ages.

TETHYAN PROVINCE

Areas of sclerophyllous oak-pine-olive woodland and laurel woodland with a rich understory of shrubs that regularly contribute to macchia on bordering slopes have been examined in the following areas.

- Canary Islands
  - Laurel forest and matorral
    - La Palma; Tenerife; Gran Canary.
- Morocco
  - *Argania-Tetraclinis* woodland and macchia
    - Agadir to Imouzzer; NE of Taroudant.
- Spain
  - *Pinus halepensis-Quercus ilex-suber* woodland and macchia
    - Seacoast E of Barcelona; Malaga-Ronda-San Roque.
- France
  - *Pinus halepensis* woodland and macchia
    - Maritime Alps, vic. Nice.
- Turkey
  - *Pinus brutia* woodland and macchia
    - Alacam-Sinop-Inebolu, Black Sea Coast; Ismir-Mansia-Kusadasi; Marmaris-Fethiye-Mugla; Antalya-Akseki-Korkuteli-Dag.
- Iran
  - Sclerophyll woodland and macchia
    - Caspian seacoast.

In this region, macchia and sclerophyllous woodland thrive where precipitation is chiefly in winter and where there is a severe summer drought (Spain-Morocco-SE Turkey-Israel). Rainfall amounts and characteristics of summer drought of coastal California are most nearly matched in the eastern Mediterranean (Lebanon, Israel). Summer drought is not as pronounced along the shores of the Mediterranean as in California, and is replaced by summer-rain regimes in the mountains close to the sea, as in the Iberian, Italian, Balkan, and Anatolian peninsulas. The coastal fringe of summer-dry climate broadens in the African sector of the

TABLE 2. Some sclerophyllous links across the Tethyan region. Data from Meusel & Schubert (1971); Kitamura (1964); Meher-Homji (1973).

Taxa	Mediterranean * (& Canarian)	Mts. of Iran-Afghanistan	NW Himalayas to Baluchistan
Celtis	*australis*	*caucasica*	*caucasica;* *australis*
Cotinus	*coggygria*	*coggygria*	*coggygria*
Cupressus	*sempervirens*	*sempervirens*	*torulosa*
Daphne	*oleoides*	*oleoides*	*cashmirana*
Hedera	*helix* *(var. *canariensis)*	*himalayica*	*himalayica*
Ilex	*colchica; ?balaerica* ** (platyphylla;* *canariensis)*		
Juniperus	*phoenica*		—
Laurus	*nobilis* **(canariensis)*	*nobilis (to* Iran)	
Myrtus	*communis*	*communis*	*communis*
Nerium	**oleander*	*odorum; mascatine*	*odorum*
Olea	**europa*	*europa*	*ferrugina*
Persea	** (indica)*	—	*indica*
Pinus	** (canariensis)*		*roxburghii*
Pistacia	**lentiscus; mutica;* *terebinthus*	*mutica*	*integerrima;* *mutica;* *terebinthus*
Punica	*granatum*	*granatum*	*granatum*
Pyracantha	*coccinea*	*coccinea*	*crenulata*
Quercus	*ilex*	—	*baloot*
Rhamnus	*oleoides;* ** (glandulosa)* *catharticus;* other species	*catharticus;* other species	*catharticus;* other species
Rhus	**coriaria*	*coriaria*	*? (in* Turkestan)
Sageretia	*spinosa*	*spinosa; thea*	*brandethiana;* *thea*

Mediterranean, which is much drier than the European shore. It is also noteworthy that the severity of summer drought in the northern Mediterranean is alleviated by the regular occurrence of heavy rains into late spring (June) and they return suddenly in early autumn (October), thus reducing drought stress appreciably. On the north shore of Turkey, from near Zonguldak to Sansum, sclerophyll vegetation thrives under precipitation that is well distributed through the year, and with at least 1 to 2 inches during *each* summer month. Macchia and woodland extend discontinuously eastward, reappearing on the Caspian sea coast of northern Iran, and in the northwestern Himalayas (Meusel, 1971; Meusel & Schubert, 1969; Meher-Homji, 1973), where rainfall is chiefly in summer. The distribution of sclerophyllous vegetation across Eurasia clearly parallels that in North America at similar latitudes, with taxa extending from areas with protracted summer drought (California-Spain) to those with ample summer rainfall (Nuevo Leon, N Turkey, Caspian seacoast) . As in North America, some taxa range widely across southern Eurasia, though others are replaced by related species or varieties in regions of different subhumid climates. Representative taxa that are discontinuous across southern Eurasia are listed in Table 2.

The sclerophyllous shrubs that make up macchia commonly comingle with an evergreen (oak-laurel-olive) woodland that in many areas has been degraded by man's activities. At lower, drier levels or to the south in Africa, woodland-macchia gives way to desert grassland, or to steppe and desert in the drier colder interior of Turkey and Iran. At moister, cooler and higher levels in the Mediterranean basin, sclerophyll vegetation is replaced by a mixed conifer-hardwood forest of *Abies, Cedrus, Picea, Pinus, Acer, Betula, Carpinus, Castanea, Fagus, Quercus* (deciduous), *Tilia* and their common associates. In northern Turkey and Iran (Caspian shore) a narrow belt of sclerophyllous woodland quickly gives way to a mesophytic deciduous hardwood forest composed of Acer, *Alnus, Carpinus, Castanea, Diospyros, Fraxinus, Gleditsia, Juglans, Morus, Parrotia, Quercus, Litmus* and *Zelkova.* In India, sclerophyll woodland is bordered by thorn scrub at lower warmer levels, and by mesic mixed deciduous hardwood forests at cooler, moister altitudes (Meusel, 1971; Meusel & Schubert, 1969; Meher-Homji, 1973) .

As in North America, the areas of sclerophyllous woodland and macchia that stretch across southern Asia are isolated by more arid climates that support grassland, steppe or desert vegetation. During Neogene time, evergreen sclerophyllous vegetation covered southern Spain, France, Italy, Greece, Turkey, as well as areas farther east that are now too cold or dry for it. For example, the Sarmatian (16 m.y.) flora from Vale in Georgian USSR has 60-odd species (Chelidze, 1970), including a palm, *Ilex, Hedera, Laurus, Paliurus, Quercus, Sapindus* and *Zizyphus* that occupied warmer slopes bordering a mixed deciduous hardwood forest. Also, the early Pontian (~ 10-12 m.y.) Kodor River flora of 100-odd species from north of Kutaisi in Georgian USSR has numerous hemixerophytes, notably *Arbutus, Ceratonia, Chamerops, Cotinus, Hedera, Ilex, Laurocerasus, Laurus, Myrtus, Persea* and *Pistacia* that are similar to species in the Mediterranean woodland and macchia today (Kolakovskii, 1964). They inhabited warmer slopes bordering a rich deciduous-evergreen hardwood forest that had numerous taxa that now survive in eastern Asia *(Berchemia, Carya, Cinnamomum, Eucomia, Fortunearia, Magnolia* and *Sophora)* which indicate ample rainfall in summer.

Clearly, a broad ecotone existed at the general latitude of the northern Black-Mediterranean seas (~ Lat. 40°), with more numerous sclerophylls dominant to the south and with conifers and deciduous hardwoods of moist temperate requirements replacing them to the north (Szafer, 1946; Depape, 1928; Kutuzkina, 1974; Takhtajan, 1969) . This closely parallels the distribution of similar vegetation in the western United States at this time (Axelrod, 1967a: fig. 1; 1968: fig. 7) . The Tertiary sclerophyllous vegetation of the extended Mediterranean region, which may be captioned the Tethyan-Tertiary Geoflora, is clearly an eastern counterpart of the Madro-Tertiary Geoflora of southeastern North America, as noted earlier by Andreánszky (1962a, 1962b) , Takhtajan (1969), and Meusel (1969) .

Inasmuch as sclerophyllous vegetation was more widely spread in the Miocene and earlier times in both southern Eurasia (Tethyan) and North America (Madrean), and since there are taxa now common to these provinces, the questions naturally arise as to (1) the factors that account for the origin of the taxa that characterize the zones, (2) the paleogeographic setting that provided a means for interchange between these now widely separated areas, and (3) the impact the history of sclerophyllous vegetation had on adjacent vegetation zones.

ORIGIN

FLORISTIC SOURCES

Forests of tropical to subtropical requirements covered low—middle latitudes of North America and Eurasia during the late Cretaceous and Paleocene (Chaney, 1947; Krystofovich, 1929, 1935; Takhtajan, 1969) . They largely represent ancient oak-laurel-palm forests that lived under monsoonal climate, with precipitation concentrated in the warm season and with warm summers and frostless winters. In North America, they inhabited swampy (coal) basins and broad floodplains at or close to sea level, both in coastal regions (Alberhill and Goler floras, southern California; Ripley flora, Alabama; Midway-Indio floras, Texas-Alabama) and the interior (Vermejo-Raton floras, northeast New Mexico, Fruitland-Kirtland and Animas floras, northwest New Mexico; Coal Creek flora, central Arizona) .

At this time, taxa of relatively xeric requirements largely inhabited drier, exposed slopes on distant hills away from the floodplains and swampy basins of high water-table, sites from which they could have contributed but little to the accumulating record. This inference is consistent with the occurrence of a few taxa with small (microphyll to nanophyll) sclerophyllous leaves in the Fruitland-Kirtland and Ripley floras of late (Maastrichtian) Cretaceous age. Furthermore, some of the alliances in the late Cretaceous and Paleocene appear to be the forerunners of those in the succeeding laurel-oak-palm forests of the Eocene (Axelrod, 1958: 451-452) including species of *Bumelia, Clethra, Colubrina, Dodonaea, Karwinskia, Pithecolobium, Platanus, Ficus, Persea, Quercus, Sabal, Thouinia* and *Zanthoxylum.* In addition, the Eocene "Wilcox" flora includes *Bumelia, Clethra, Dodonaea, Karwinskia, Pithecolobium* and several other woody legumes, *Thouinia, Vauquelinia* and *Zanthoxylum.*

Dry climates had expanded over the interior by the middle Eocene, and ancestors of the present xerophyllous taxa were making their appearance (Axelrod, 1939, 1950; Leopold & MacGinitie, 1972). Among the small trees and shrubs that contributed to woodland vegetation in the Middle Eocene Green River flora of the central Rocky Mountain region are *Bursera, Cardiospermum, Celtis, Caesalpinia* (and other woody legumes) , *Mahonia, Ocotea, Persea, Pinus* (nut pine) , *Platanus, Populus, Quercus, Rhus, Sapindus, Styrax, Swartzia, Thouinia* and *Vauquelinia* (Axelrod, 1958: 448; MacGinitie, 1969) . By the Eo-Oligocene, as judged from the Florissant flora (Axelrod, 1958: 450; MacGinitie, 1953) more numerous taxa were present, notably species of *Bursera, Cardiospernium,* *Celtic, Cercis, Cercocarpus, Colubrina, Conzattia, Cotinus, Daphne, Dodonaea, Euphorbia, Ephedra, Mahonia, Morus, Platanus, Populus, Prosopis, Ptelea, Rhus, Rhamnus, Robinia, Sapindus, Stipa, Thouinia, Trichilia, Vauquelinia* and Zizyphus *(Condalia).* They lived under mild, frostless climate with precipitation concentrated in the warm season. This is implied by paleogeographic relations (warm oceans, no ice caps, no major cordilleras, low continents) and by the taxa and their associates that occur today only in areas with summer rainfall.

Descendants of these alliances make up xerophyllous woodland and chaparral vegetation today. Furthermore, the same species or allied ones regularly contribute to mesic oak-laurel-palm forest, or to oak-pine or oak forests that border the drier sclerophyllous woodland and chaparral in Mexico and the southwestern United States today. This implies many of these sclerophylls were derived from taxa in subtropical evergreen forests that had inhabited the region, including species of:

- Anacardiaceae
  - *Rhus*
  - *Schmaltzia*
- Aquifoliaceae
  - *Ilex*
- Berberidaceae
  - *Mahonia*
- Ericaceae
  - *Arbutus*
  - *Arctostaphylos*
  - *Comarostaphylos*
  - *Gaultheria*
  - *Vaccinium (evergreen)*
- Fagaceae
  - *Quercus*
- Leguminosae
  - *Bauhinia*
  - *Sophora*
- Myricaceae
  - *Myrica*
- Myrtaceae
  - *Eugenia*
  - *Psidium*
- Oleaceae
  - *Forestiera*
- Rhamnaceae
  - *Ceanothus*
  - *Condalia*
  - *Karwinskia*
  - *Rhamnus*
- Rosaceae
  - *Cercocarpus*
  - *Heteromeles*
  - *Laurocerasus*
  - *Prunus*
  - *Vauquelinia*
- Rutaceae
  - *Choisya*
  - *Helietta*
- Styracaceae
  - *Styrax*
- Sapindaceae
  - *Dodonaea*
- Verbenaceae
  - *Citharexylum*

Woodland with a rich understory of sclerophyllous shrubs had already occupied southeastern California by the Miocene, as shown by the composition of the Vasquez and Mint Canyon floras which have been displaced 150-175 miles northwest from their original areas in the Chocolate-Orocopia Mountains by movement along the San Andreas fault (Crowell, 1962; Ehlig & Ehlert, 1972). Included are members of a sclerophyllous woodland *(Arbutus, Lyonothamnus, Persea, Populus, Quercus*- 6 spp., palm, *Ilex* and *Thouinia)* and numerous shrubs *(Ceanothus, Cercocarpus, Fremontodendron, Prunus, Quercus, Rhus* and *Schmaltzia)* that may have formed local, seral brushlands on drier slopes with shallow soil. Annual rainfall was near 20-25 inches as compared with scarcely 3 inches today. Temperatures were relatively moderate as judged from the *Laurocerasus*, *Lyonothamnus*, *Malosma*, *Persea* and others that are found chiefly in mild climates today. The absence of frost is indicated by these taxa, as well as by the numerous woody legumes, *Bursera*, *Cardiospermum*, *Celtis*, *Euphorbia*, *Randia* and others that contribute to thorn scrub. Sclerophyllous oak-laurel woodland and thorn scrub had already covered the south end of the Sierra Nevada by the middle Miocene (17 m.y.) as shown by the Tehachapi flora (Axelrod, 1939) .

Although large Neogene floras are not now known from the area farther east, the continuity of sclerophyllous vegetation across the subhumid part of North America may be inferred from the present distribution of similar taxa in sclerophyllous oak woodland and chaparral in Arizona, New Mexico, west Texas and eastern Mexico. Hint of a former continuous zone is implied by a small early Pliocene pollen flora from west-central Arizona (Gray, 1960a) which resembles conifer-oak woodland and associated chaparral like that in central Arizona today, with *Quercus*, *Pinus*, *Juniperus*-*Cupressus*, *Juglans*, *Celtis*, *Agave* and others that imply continuity since then. The early Pliocene Clarendon flora of northern Texas includes seeds of manzanita and *Sabal* palm (Chaney & Elias, 1936: 12) . Further, there are xerophyllous taxa in the Miocene of Nebraska (MacGinitie, 1962), implying they were more dominant in areas to the south. The transitional Oligo-Miocene Creede flora (27-28 m.y.) of Colorado has a rich juniper woodland and chaparral (*Cercocarpus* and *Peraphyllum*) which is consistent with the inference of widespread sclerophyllous woodland to the south. The continuity of sclerophyllous woodland was disrupted by spreading dry climates which enabled grassland, steppe and desert vegetation to displace it. Sclerophyllous vegetation was segregated into three major subhumid regions (California, Arizona to west Texas, northeast Mexico) following the Tertiary, and it is this that accounts for the east-west discontinuous distribution of the taxa today (Table 1) . That these restrictions in range are very recent is apparent from the record in California which shows that taxa (*Persea*, *Magnolia* and *Sapindus*) that are now found far to the southeast in summer rain areas were in California into the early Pleistocene (Soboba flora; San Joaquin flora).

In southern Eurasia, taxa of sclerophyllous woodland-macchia alliances were also preceded by more mesic laurophyllous forests. In the late Cretaceous, the Tethyan region was characterized by evergreen trees and shrubs, representing numerous Lauraceae, evergreen Fagaceae and palms that thrived under warm temperate to more tropical climate southward. The Tethyan-Cretaceous subtropical flora inhabited the shores of the Tethys and its islands, reaching across southern Europe and into southwestern Asia. It no doubt extended farther east into southwestern China, for the entire region from North Africa to southwestern China was a dry belt, as shown by the occurrence there of saline (gypsum, salt) deposits and red beds (Strakhov, 1967: vol. 1, chap. 5) .

As in North America, there was a rapid modernization of generic composition during the Paleogene. Whereas the affinities of many genera of the late Cretaceous are doubtful, numerous Eocene plants can be referred to modern genera, and Oligocene floras are made up primarily of living genera whose species show some affinity with living ones. In the early Paleogene, the Tethyan region of North Africa was situated at lower latitudes (Phillips & Forsyth, 1972) , dominated by tropical forest and savanna. Numerous fossil woods indicate evergreen alliances chiefly, as implied by records of Annonaceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Euphorbiaceae, Fagaceae, Lauraceae, Leguminosae, Moraceae, Myrtaceae, Rutaceae, Sapindaceae, Sterculiaceae and Tamaricaceae (Aubréville, 1970) . As noted by Takhtajan (1969: 18.3), the Tethyan-Tertiary region was characterized by subtropical forests composed of evergreen trees and shrubs. Leaf floras have taxa referred to *Cinnamomum, Laurus, Litsea, Neolitsea, Persea,* and with *Quercus, Lithocarpus* and *Castanopsis* in the Fagaceae. There were also numerous palms, notably the genera *Chamerops, Livistonia, Sabal* and *Trachycarpus* (Takhtajan, 1958) . To the north, generally commencing at the latitude of Kazakhstan, subtropical forests graded into the Arcto-Tertiary forests composed of temperate deciduous hardwoods, conifers, and some broad-leaved evergreens (Makulbekov, 1972) .

Markedly xerophyllous floras had appeared by the later Eocene and early Oligocene. The transitional Eo-Oligocene flora from Er Olian Duz, close to the Afghanistan border in southern Turkmenia, is markedly xerophytic (Korovin, 1932; Vasilevskaya, 1957), composed of various laurels, and taxa referred to *Rhus,* Zizyphus and others. As emphasized by Takhtajan (1969: 200), the floras in southern Kazakhstan are also xerophyllous, as shown by the narrow leaves and their coriaceous texture (Budantsev, 1957) . The floras of the southern Urals are similar, with dicots represented by small, narrow, and revolute leaves with mostly a coriaceous texture, and referred to *Myrica, Quercus* and other evergreens (Uznadze-Dgebudze, 1948) . Clearly, environmental conditions in the broad region from Spain eastward to central Asia were favorable for the origination of mediterranean-type taxa, some of which appear to be foreshadowed in these and other floras, as noted by Andreánszky (1962*a*). Among the taxa he lists are *Arbutus, Laurus, Persea, Tetraclinis, Quercus, Myrsine, Myrica, Rhamnus* and Zizyphus, all represented in the early Tertiary floras of central Europe (which was then situated further south), and in the Neogene of the Mediterranean region. They are microphyllous or stenophyllous with hard leaves and other xeric features. Captioned the "Xero-Atlantic" element by Andreánszky (1962b), he inferred it originated at low middle latitudes, probably in the area of Spain-Morocco. Their origin in response to spreading dry climate over southern Eurasia now seems demonstrated.

By Oligocene and early Miocene times, the lowlands of the Mediterranean region were clothed with a broad sclerophyll woodland composed of oaks, laurels, palms, olives and numerous sclerophyllous shrubs, as shown by the floras from eastern Spain (Cervera flora: Bataller & Depape, 1950; Depape & Brice, 1965), the Balearic Islands (Arenes & Depape, 1956) , and central Italy (Sinigaglia flora: Massalongo & Scarabelli, 1859). As emphasized by Depape & Brice (1965), these floras are xerophyllous, and show scarcely any relation to the temperate deciduous hardwood forests that thrived to the north. Sclerophyllous vegetation extended far to the east, as demonstrated by the nature of the flora in the Caucasus region, in the ecotone with the Arcto-Tertiary Geoflora. Also, the distribution of modern taxa *(Punica, Nerium, Olea,* etc.) discontinuously eastward into the northwestern Himalayas and southwest China parallels the discontinuous distribution of the xerophyllous vegetation in the western United States-northern Mexico and, like it, implies a Neogene connection via subhumid climate across regions that are presently too dry or too cold for them.

Floristic relations in relict areas of Eurasia, as well as North America, provide critical evidence for appraising the origin of the sclerophyllous mediterranean-type vegetation. The Canary Island laurel forest, clearly of tropical derivation (see below), includes numerous shrubs that contribute to the bordering matorral. Most of them inhabited the mainland into the late Pliocene, associated with numerous taxa (*Quercus, Punica, Arbutus* and *Olea)* that are now confined to mediterranean lands (Depape, 1922, 1928) .

There are outposts of mediterranean-type sclerophyllous vegetation in the lower montane belt of the northwest Himalayas in India (Meusel & Schubert, 1971; Mani, 1974; Kitamura, 1964), and also in the north-trending ranges of west Pakistan (Meher-Homji, 1973) . In the Pir-Panjal range (alt. 4,500 m), centered about 70 miles east of Rawalpindi in India, the lower southwest-facing flank of the range is covered with thorn scrub composed of *Acacia, Carissa,* Zizyphus, and their usual associates (Meusel & Schubert, 1971) . At slightly higher levels is the evergreen vegetation with species of *Cercis, Cotinus, Dodonaea, Olea, Paliurus, Pistacia, Nerium, Quercus, Rhus, Rhamnus* and others, some of which are deciduous. This community inhabits drier sites, chiefly the deep rainshadow-valleys as near Bhadawar (alt. 1,690 m) and Hardwara (alt. 1,700 m) where there is a reduced rain (Bhadawar) or a long dry summer (Hardwara) because the mountain ridges intercept much of the monsoonal rain. However, Meher-Homji (1973) has noted that in some areas there is (up to 50%) summer rain, notably to the west. The evergreens are replaced above by a *Pinus roxburghii* forest, a pine very closely related to *P. canariensis.* It lies above the laurel forest dominated by evergreens, many of which also contribute to the flora in the Mediterranean region. The *P. roxburghii* forest gives way at higher levels to a mixed conifer forest of *Abies, Cedrus* and *Picea,* associated with several oaks, *Aesculus, Acer, Fraxinus, Juglans, Populus* and other temperate taxa. This closely parallels the general composition and mode of occurrence of forests in the Mediterranean where the conifers and dicots are represented by very similar species. As noted by Meusel (1971: 70), in the western Himalayas some 40% of the semiarid taxa show relationship to species in the Mediterranean region, though some *(Cercis, Cotinus, Punica, Pistacia, Myrsine* and Zizyphus) range into subhumid southwestern China and are not restricted Mediterranean taxa.

Nearly a century ago, Hooker (in Hooker & Ball, 1878) suggested that the different races or subspecies of *Cedrus* in the Atlas, Taurus and Himalayan ranges resulted from isolation and extinction of transitional forms in intermediate areas of what may once have been a continuous forest. It is now clear that isolation of *Cotoneaster, Olea, Punica, Quercus* and others along the alpine axis as orogeny and aridity spread during the later Cenozoic has broken up formerly more continuous populations and has resulted in the emergence of closely related taxa (Axelrod & Raven, 1972: 227) . In this regard, Meusel (1971) illustrates the

TABLE 3. Some Madrean-Tethyan links, past (*) and present.

Taxa	California	SW US or Mexico	E US	Mediterranean
Arbutus	menziesii	xalapensis		andrachne
Buxus		lancifolia; mexicana		sempervirens
Cercis	occidentalis	occidentalis		siliquastrum
Clethra	* (petiolaris)	lanata		arborea
Cupressus	forbesii	arizonica		sempervirens
Helianthemum	species		species	species
Ilex	* (sonomensis)	brandegeei; rubra		balaerica; canariensis; platyphylla
Juniperus	californica	deppeana; monosperma; species	virginiana	phoenica; species
Laurocerasus	lyonii		caroliniana	lusitanica
Myrica	californica	mexicana	caroliniana	faya (Canarian & Portugal?)
Ocotea	* (Miocene)	ovoidea	(nectandra; Florida)	foetans (Canarian)
Persea	* (Miocene & Pliocene)	hartwegii; podadenia	borbonia	indica
Pinus "closed-cone pines" (see text)	muricata; radiata; remorata	oocarpa; pringlei	pungens	halepensis; brutia
Pistacia	* (Miocene)	mexicana	—	atlantica; lentiscus; terebinthus
Platanus	racemosa	racemosa; wrightii	—	orientalis
Populus	fremontii	arizonica; fremontii	sargentii	nigra
Quercus "sect. Ilex" (see text)	chrysolepis	chrysolepis; fusiformis; virginiana	virginiana	ilex
Rhamnus	californica; species	species	species	species
Sageretia	* (Miocene)	wrightii	minutiflora (very rare)	spinosa
Sapindus	* (Pliocene)	drummon	drummondii (to Arkansas & Louisiana)	* (Pliocene & Miocene)
Styrax	californica officinalis var.	faliscanus	americana	officinalis
Zizyphus	* (Miocene)	obtusifolia	—	lotus

distribution of a number of these across subhumid Eurasia, some of which reach eastward into the drier parts of southwestern China (Table 3). Apart from the sclerophylls, Chatterjee (1947) has also noted that there is a strong influence of east Mediterranean plants in northwest India, where much of the flora from the Middle East is concentrated, especially members of the Cruciferae and Caryophyllaceae.

The time of appearance of taxa of mediterranean affinities (Table 3) in this region poses a problem because none of the taxa are now known as fossils in the area east of the Caspian. They may have entered northwest India-West Pakistan during the late Miocene or Pliocene. Prior to this, the region evidently was too humid for sclerophyllous plants because the area was then dominated by heavy monsoonal rains. This is indicated by the rich flora in the Karewa Formation at Liddarmarg (alt. 10,500 ft, ~ 3,100 m) on the drier, colder northeast (lee) slope of the Pir Panjal range which rises to 15,000 ft (~ 4,500 m) . The flora inhabited the upper Kashmir valley during the late Pliocene (Gansser, 1964: 45-53)—in pre-glacial time—when the valley was bounded on the northeast by the main Himalayan range, while a low ridge—now represented by the lofty Pir Panjal- was on the south (see Puri, 1960: vol. 2: 510) . As demonstrated by Puri (1960: vol. 1: 75-80), the flora represents a moist warm temperate to subtropical forest like that now in the outer Himalayas near Murree, on the Simla Hills, and at Mussorrie, which receive heavy monsoonal rain. From paleobotanical evidence, Puri (1946) estimated minimum uplift at Liddarmarg was at least 6,000 ft (~ 1,800 m), though he cited structural evidence (faulting, with displaced Karewa beds now at 13,000 ft) that indicates uplift may have been 8,000-10,000 ft (~ 2,400-3,000 m) since the flora lived.

The outer flanks of the northwestern Himalaya as well as West Pakistan were too moist in the Miocene for mediterranean-type sclerophyllous taxa, as judged from the record now known. As noted elsewhere (Lakhanpal, 1970; Prakash, 1972; Axelrod, 1974), the trend to aridity accounts for major modifications in the distribution of Indian plants since the Miocene. Forests withdrew to the east from the west which is now desert to semidesert, and also from the middle monsoonal area to regions farther east that are ever-wet. As aridity increased, savannas spread at the expense of rain forest, and thorn scrub displaced areas of savanna. India probably was invaded during the late Miocene and Pliocene by taxa of drier requirements from the region farther west, where aridity had appeared earlier. This agrees with evidence noted by Lakhanpal (1970) that the floras from the lower and upper Siwalik beds show a change to a drier climate, as judged from the shift to a flora with much smaller leaves. Pollen evidence (Banarjee, 1968; Lukose, 1969) from the lower and middle Siwalik rocks in Bihar and Punjab shows increasing grains of gymnosperms, notably those of *Pinus* (up to 25%), indicating that during middle Siwalik deposition the Himalayan range had sufficient altitude to support conifer forests. That longitudinal valleys with drier lee slopes were present at this time is consistent with the structural evidence. Thus, sclerophyllous taxa may have been present by the Pliocene, and shifted to the outer northeast-trending valleys as the inner, main Himalayan range was elevated to higher, colder levels in the Quaternary.

The record in southern Eurasia, which is much more complete than that in North America at low-middle latitudes, gives us a reasonably accurate picture of the early history of the sclerophyllous vegetation. As noted by Krystofovich (1954) and Takhtajan (1969), forerunners of sclerophyllous taxa appeared at low—middle latitudes in the late Cretaceous, when they lived under warm temperate to subtropical climate. Sclerophyllous trees and shrubs had originated there by the early Paleogene, by the close of the Oligocene many species resemble modern ones, and by the middle Miocene most species can scarcely be separated from those now living. This analysis agrees fully with the sequence of events inferred for the history of similar vegetation in western North America (Axelrod, 1958), a region where the record is not so complete.

In summary, the relations suggest that in the Tethyan and Madrean regions semihumid sclerophyllous vegetation (1) has formed an ecotone between tropical and temperate forests throughout its history, (2) that it derived taxa from both sources, though chiefly the former, (3) that it had a wider distribution in the past, covering areas presently too dry for it, and (4) that the present restricted distributions reflect selection and segregation in response to the development of new dry climates during the Quaternary.

EVOLUTION OF ADAPTATIONS

Structure.—Sclerophyllous woody taxa in regions of mediterranean climate have small, thick, sclerophyllous evergreen leaves, often with a villous covering, and frequently with a thick cuticle and sunken stomata, all of which enable them to conserve moisture during the long period of drought. In addition, they have hard wood ("hard chaparral" of Jepson, 1925: 6), and deep root systems that provide a means to tap water at deep levels during the period of drought. Furthermore, many of the shrubs and small trees regularly sprout following fire, so that the slopes are quickly covered again with a dense cover.

These structural adaptations are not unique to plants of mediterranean-type climates. Many of the same species range into regions with summer rainfall (Table 1), a condition like that under which they lived in Neogene time. The origin of these structural adaptations becomes apparent when we realize that taxa with xeromorphic structures now occupy diverse environments. These include ever-wet tropical rainforests, montane rainforest, and evergreen microphyllous scrub at timberline. They also inhabit subhumid to semiarid landscapes where they contribute to sclerophyllous woodland and scrub (chaparral, macchia, fynbos) that grade into more mesic laurophyllous forests in which sclerophyllous taxa are also common. Such diverse occurrences by taxa that belong to numerous wholly unrelated families implies that the sclerophyllous habit must be ancient and recurrent. This agrees with the occurrence of many sclerophyllous taxa in diverse environments of Cretaceous and Tertiary times. Some of the oldest fossil leaves that have been attributed to angiosperm s are sclerophyllous nanophylls from the Shasta series (Hauterivian-Barremian transition: — 127-128 m.y.) of northern California. Since the basic adaptive structural features—sclerophylly, deep root systems, stump sprouting, thick epidermis—occur repeatedly in diverse taxa in numerous dissimilar environments, of which Mediterranean-type habitats are only one, broadleaved evergreen xeromorphic plants can scarcely be considered "specialists." Contrary to most ecologists, I believe they may best be regarded as "generalists."

The structural features of evergreenness, sclerophylly, deep root system, etc.

appear to have originated under relatively warm, moderately mesic conditions at least, and appear to have preadapted taxa to climates of lower rainfall, a shorter rainfall period, and greater ranges of temperature. Sclerophyllous evergreen leaves are not only ancient, they may well be a primitive feature of angiosperms. The basic modifications in terms of adaptation to different climates have been minor changes in structure, such as reduction in size, formation of deep internal crypts, and thickened cuticle or waxy covering, to reduce water loss in areas of restricted precipitation and high evaporation. Such modifications are ancient, as judged from the presence of essentially modern evergreen chaparral and woodland taxa in Miocene and Oligocene floras which lived under ample summer rain. Clearly, these features are not an evolutionary response to an ancient, persistent mediterranean-type climate, as many have implied.

The outstanding Australian geologist-naturalist, E. C. Andrews (1913, 1914, 1916) was one of the first to perceive the general evolutionary relations of xeromorphic plants. He noted that in Australia xeromorphs are confined to drier areas characterized by coarse, mineral-poor sandstones. These are now known to be the result of sedimentation on stable shelves in which the unstable minerals (with necessary elements for plant growth) are gradually eliminated, leaving rocks like quartz sandstone, quartz-glauconite sandstone, quartz muscovite sandstone, clay shale, and siltstone with quartz. These sites are largely inhabited by the unique Australian taxa, including *Banksia, Callistemon, Candollea, Darwinia, Epacris, Leptospermum, Melaleuca, Persoonia* and a host of others. The mineral-deficient areas are surrounded by rich, sheltered, well-watered valleys in which the taxa are not peculiarly Australian, but are wide-spread, such as *Elaeocarpus, Eugenia, Ficus, Livistonia, Myrtus* and many others. He inferred adaptive radiation in Australia involved the perfection of structural adaptations of the unique xeromorphic taxa to the sandy, extremely siliceous, mineral-poor ("hungry soils") substrate, and that this adaptation has been proceeding in many groups since the middle Cretaceous at least.

Beadle (1966) presented further evidence that adaptation to low-fertility soils, and particularly those low in phosphate, has resulted in the evolution of new taxa by accentuating xeromorphic characters *(contra* Loveless, 1961, 1962). This may involve reduction of leaf size and structure, or a reduction in aerial parts, or increased proportion of non-living to living tissue, or seasonal growth and dormancy by underground perennating root tubers. He also suggested lineages with lower nutrient requirements probably adapted to areas of lower fertility early in angiosperm history, so that the relationship between taxa in sites of low fertility and those living on more normal substrates is now remote in many cases. The xeromorphs on low-fertility soils are adapted in most cases to a limited phosphate supply, which also determines levels of soil nitrogen. Thus, the low fertility of Andrews's "hungry soils" excludes plants with higher nutrition requirements, and enables the xeromorphs to exploit them. This exclusion principle applies also to other substrates, notably limestone, serpentine, and other rock types.

The habit of stump-sprouting has been assumed to be of pyrogenic origin (Jepson, 1925: 6; Hanes, 1971; Sampson, 1944). Actually, many of the woody plants in laurophyllous forests that survive under moist, warm temperate climate, have this character as do species in these forests that have related taxa in chaparral-macchia. Crown sprouting probably is an ancient trait among angiosperms to judge from the fact that most woody plants do stump-sprout, and the habit is found in all climatic areas that support woody taxa of diverse origins. From an evolutionary standpoint, Wells (1969) has shown that over 75% of the species of Arctostaphylos (59 of 75 species) and Ceanothus (46 of 58 species) in California have lost the habit of stump sprouting. He suggests the change in mode of reproduction to one by seeds has resulted in a greater frequency and intensity of selection, and has quickened the tempo of evolution in major sections of these genera. The increased diversity of non-sprouting species, most of which are narrow endemics and separated by only minor characters, probably commenced late in the Tertiary as judged from topographic-climatic relations.

The evolution of plant form that allows a relatively large proportion of the limited rainfall to reach the soil surface in the form of stem flow (reviewed in Mooney & Dunn, 1970), also appears to be an ancient character. Plants with stiff, upright branches and smooth bark obviously have greatest stem flow, which yields a slow and steady supply of moisture at the base of the shrubs. This character could not have originated under mediterranean climate inasmuch as many of the taxa are known from the Miocene. The adaptation may have originated in response to monsoonal climate in the understory of laurophyllous forests—where the same adaptations occur today. To judge from the fossil record, the adaptive shift in terms of evolution of structural characters had already taken place in many alliances by the middle Eocene. This presumably occurred in local, exposed sites in a terrain of more mesic aspect (Stebbins, 1952; Axelrod, 1967c), as well as in dry edaphic sites wherever these were present (Axelrod, 1972) .

The origin of taxa of lower stature (small tree to shrub) and with smaller leaves (microphyll-nanophyll-leptophyll-aphyllous) from those in mesic evergreen forest and woodland scarcely poses an evolutionary problem. Adaptations of this nature are well established by sequences that can be observed today. In taxa that have a wide range, size decreases from small trees in moist equable areas, to shrubs in the drier interior or in more exposed and rocky situations, as shown by Garrya ovata, Cercocarpus *mojadensis* and Mahonia fremontii in Nuevo Leon; by Rhus ovata, Cercocarpus montanus, and Quercus *turbinella* in central Arizona; or by Heteromeles arbutifolia, Prunus *ilicifolia* and Quercus dumosa in coastal California.

Not only is there a decrease in stature, adaptation to drier areas has involved other structural features, notably a trend to smaller leaves, more sunken stomata, thicker cuticle, denser villous covering, etc. Such modifications occur today in taxa that range from mesic coastal or insular sites to drier, more extreme interior regions. They are well illustrated by geologically new phylads, as exemplified by species of Ceanothus (Nobs, 1963) in the north Coast Ranges of California that have originated since the late Pliocene (3.5 m.y.) ; by species and varieties of Cercocarpus in California (Mortenson, 1973) ; by species of Quercus that are typical trees of woodland and savanna (Quercus *agrifolia, wislizenii*) or woodland (chrysolepis) vegetation, but occur as shrub varieties in chaparral. These scrub oaks are found chiefly on edaphically drier sites with poor thin soil, or on notably rocky sites, but occasionally on markedly different substrate, as in *Q. durata* on serpentine.

Current studies of California chaparral in terms of morphological changes within the vegetation type provide information in terns of adaptive responses (Mooney & Dunn, 1970; Mooney & Harrison, 1972; Mooney *et al.,* 1974) . In the Sierra San Pedro Martir, northern Baja California, morphological features vary systematically with increasing moisture and decreasing temperature as altitude increases. Evergreen species become more important with increased altitude, leaf size increases, vertically-oriented leaves become more frequent, and leaves become more sclerophytic. Sclerophylls also increase as water stress decreases with altitude since photosynthesis can occur all year and it is "advantageous" not to replace the entire leaf crop each year. The leaves become larger and more sclerous at higher altitudes because water availability and lower temperatures reduce the likelihood of leaf overtemperature. At lower altitudes where there is less moisture and where leaf temperature may exceed that of the air, leaves are typically smaller, species of drought deciduous coastal sage increase, and so do succulents. These features closely parallel a gradient from the Canarian laurel forest down to the drier and hotter desert which also has numerous sage species, as well as succulents.

Function.—Functionally, adaptation to mediterranean climate represents a fine attunement with respect to the ability to reproduce (flower, set seed, germinate, establish) within a relatively brief period of moist climate during the cooler part of the year. In this regard, it is recalled that the coincidence of cool wet winters and hot dry summers is the distinguishing feature of mediterranean climate. Winter is not the chief period of rest, nor is summer the principal time of activity for vegetation as in areas farther north (Oregon, central Europe) . Drought in summer is the main limiting factor to plant activity, not winter cold. As emphasized recently by Bailey (1972), frost and snow are rare to absent in areas with mediterranean climate, and winter rain is adequate for sclerophyllous vegetation. Thus, flowering and growth occur chiefly in winter and spring, and only a few species and rare individuals of typical mediterranean vegetation flower and grow in summer. This occurs notably in the, milder coastal strips—often fog-bound-where the stress of high evaporation is reduced.

A clue to the evolution of functional relations of chaparral taxa is provided by the occurrence of the same species in areas of summer rain (eastern Mexico) , or summer and winter rain (Arizona to New Mexico) , as well as in a region of prolonged summer drought (California) . As listed in Table 1, numerous species (and varieties) are common to the chaparral of southern California and central Arizona, and some of them *(Arctostaphylos pungens, Ceanothus greggii, Mahonia fremontii* and *Rhus trilobata)* range to Nuevo Leon in eastern Mexico where rainfall is in summer, not winter. Climate in areas with summer rain parallels that indicated for the Miocene and Pliocene of California where summer drought now prevails, though temperature was not so extreme in the Neogene in California. Ample summer precipitation in the Miocene of southern California is indicated by the occurrence there of *Bursera, Clethra, Persea, Pithecolobium, Quercus* (some spp.), *Robinia, Sabal* and others that live today only in areas with warm-season precipitation. They disappeared as summer rainfall decreased during the Pliocene and early Pleistocene as the ocean chilled, and as the thermal contrasts between land and sea increased.

A similar pattern occurs in the Mediterranean region. Numerous sclerophyllous species of the macchia and woodland extend from Spain to northern Turkey where there is summer rain, and some (or their varieties) range discontinuously farther east into the Himalayan region where rainfall is chiefly in summer (Meusel & Schubert, 1971; Meusel, 1971; see below) . Apart from Spain-northwest Africa-southern Turkey-Israel, the period of summer drought in the Mediterranean area is not so prolonged as that in California. As noted earlier, relatively heavy rain continues into June and commences abruptly again in October, whereas in California precipitation gradually tapers off to the long dry season and then increases gradually in autumn.

The present distribution of sclerophyllous taxa that range from areas of summer rain into those with summer drought provides a basis for understanding functional responses in the latter area. Obviously, the taxa that occur in both regions have adapted to summer-dry climate more recently. This could be accomplished by shifting the time of seedling germination and establishment from late spring—early summer to the late winter—early spring, coupled with appropriate physiologic adjustments for the times required for growth, flowering and seed maturation. It is known (Hanes, 1965; Mooney & Parsons, 1973) that as moisture supply becomes restricted and limited in early summer (June) , chaparral taxa become dormant or nearly so, and by August—September plants are operating at only 4-5% of their wet season maxima. At the same time in Arizona, 12 of the same species that also make up the chaparral there must be operating at peak efficiency under high rainfall and temperature, much as they are presumed to have done during the Neogene in California.

In this regard, Walter (1973: 121) points out that the significance of sclerophylly is that the taxa can conduct gaseous exchange in the presence of adequate water supply, but can also cut it down radically by closing the stomates when water is scarce; measurements of transpiration show that water losses in summer are 3 to 6 times greater in wet than in dry habitats. This control enables sclerophylls to survive periods of drought with neither alteration of plasma hydrature, nor reduction of leaf area, so that when rains recommence in autumn, the plants resume production immediately. Hence, they compete successfully in winter-rain regions with non-sclerophyllous evergreen species that are sensitive to drought, as well as with deciduous trees. This implies again that a dormant summer period due to drought was not a feature of the ancestral taxa, a view consistent with the paleoclimatic record. Thus, it seems that sclerophylly (or near-sclerophylly) is a fundamental adaptation of great antiquity, and that it can (and has) developed various functional means for coping with limited moisture as well as with other environmental needs. The same sclerophyllous species that live under summer drought (California) as well as winter drought (Nuevo Leon) , clearly indicate the potential for functional adaptation. This suggests again that broadleaved sclerophyllous taxa are "generalists", having basic structures that have been functionally adaptable to diverse environments.

In the Madrean-Tethyan region, the shift in functional adaptation may have been originating in the Pliocene as summer rains commenced to decrease, or it may have developed gradually and intermittently during the warm-dry phases of the interglacial ages, or it could be younger, with the taxa representing very new ecotypes that originated in response to the recent extreme drought. Comparative physiologic studies of the responses of different populations of taxa that occur in California-Arizona, or Spain-northern Turkey, may provide insight into the functional differences between the living populations, and hence an understanding of their origin.

In this regard, comparison of the mediterranean-type climates of California, Spain and Chile with those in Australia and South Africa reveals significant differences (Emberger, 1930, 1933; Walter, 1968; Aschmann, 1973a; Raven, 1973) . In Australia, seasonal flowering in the sclerophyll vegetation is chiefly in spring, but vegetative growth of shrubs continues through the drought period, whereas it is largely confined to spring in California, Chile and the western Mediterranean (Specht, 1969; Mooney & Dunn, 1970) . However, in South Africa rainfall is distributed more evenly through the years, there is at least 0.7 inches rain in each summer month, there is no severe summer drought, and flowering in the fynbos is rather continuous through the year in this highly equable climate. This finds a parallel in the mildest parts of the coastal strip of California (Inverness at Tomales Bay) or Turkey (Inebolu to Sansum) where flowering of evergreen sclerophyllous shrubs continues sporadically through summer and into autumn. There is an implied gradient in these areas of mediterranean-type climate, from a transitional condition with no significant drought (South Africa; N. Turkey) to one in which it is moderate (Australia) , to one that is severe (Spain, California) . In terms of functional responses, these are precisely the stages through which taxa that make up sclerophyllous vegetation passed during the late Pliocene and Quaternary, as the mediterranean condition gradually developed.

A current article by Seddon (1974) presents a valuable review of the problems raised by terminology of sclerophyllous taxa and vegetation, and the role of soil nutrients and other factors controlling the distribution of sclerophyllous forest and rainforest in Australia. The review mentions additional data consistent with the thesis that sclerophylly is an ancient character, and not one that is attributable to evolution under mediterranean climate. Thus, Specht & Rayson (1957) note that in South Australia and West Australia many taxa have a growth phase out of rhythm with the present mediterranean-type climate, making their major growth during the driest summer months. Further, Burbidge (1960) has suggested that these growth rhythms appear to belong to climates of earlier *(i.e.,* Tertiary) , more humid times, and similar observations have been made with respect to the sclerophyllous Cape flora of South Africa, elements of which also extend into summer rain regions (Levyns, 1964) . Further, in a current manscript Johnson *Sr* Briggs (1975) also emphasize that sclerophyllous vegetation is not restricted to areas of mediterranean climate in Australia or South Africa, but may range into summer rainfall regions as well. Their review of the available evidence leads them to speak of the "mediterranean myth" so far as the restriction of sclerophyllous taxa to mediterranean climate is concerned, a view that most ecologists have held since the days of Schimper. These data further support the notion that sclerophylly is one of several linked characters (deep roots, crown sprouting, etc.) common to many angiosperm families, and probably of ancient (Cretaceous) age, that tend to endow an alliance with the characteristics of "generalist"—enabling it to adapt readily to diverse environmental conditions, of which the mediterranean-type climate is evidently the most recent.

In summary, the adaptations of diverse taxa of sclerophyllous evergreen shrubland (chaparral, macchia, matorral, fynbos) represent ancient structural features inherited from ancestors in laurophyllous forests. The functional adaptations in response to mediterranean climate have evolved more recently. Some taxa have ecotypes that live in both summer-wet and summer-dry areas, but the endemics now in mediterranean-climate areas may easily have adapted to this condition by shifting the period of flowering and growth into the early part of the year.

RISE OF CHAPARRAL-MACCHIA

The remains of many sclerophyllous shrubs that characterize chaparral vegetation in California *(i.e., Arctostaphylos, Ceanothus, Cercocarpus, Garrya, Quercus, Rhamnus* and *Rhus)* and the similar macchia of the Mediterranean region *(Arbutus, Ilex, Myrtus, Phillyrea, Pistacia, Quercus* and *Rhus)* are now known from the fossil record. According to accepted principles of paleoecology (Clements, 1916, 1936; Chaney, 1938; Cain, 1944: Chaps. 5,6), which are based on the adage "The present is the key to the past," the occurrence of several sclerophyllous shrubs in a fossil flora implies chaparral (or macchia) probably was a well-developed climax on nearby slopes. Although this principle forms the basis for the opinion that chaparral formed climax vegetation during much of Tertiary time *(i.e.,* Clements, 1936; Dorf, **1930;** Axelrod, 1937, 1958, 1973; Becker, 1961; MacGinitie, 1953), several lines of evidence now cast doubt on its validity. In the first place, the fossil floras that are presumed to have had prominent chaparral come from areas where topographic diversity was insufficient to support it as well as thorn scrub, oak savanna-woodland, and bigcone forests *(i.e.,* Mount Eden flora, Axelrod, 1937), or thorn forest, oak woodland, mixed conifer forest and subalpine forest *(i.e.,* Ruby flora, Becker, **1961;** Florissant flora, McGinitie, 1953), or laurel forest, sclerophyll woodland, and mixed deciduous forest (Theziers flora, Boulay, 1890), and still enable plants from all these vegetation-climatic belts to contribute importantly to the record. Secondly, sclerophyllous shrubs that make up chaparral (and macchia) regularly form the understory of adjacent oak, or oak-pine-laurel woodland with which it typically alternates on adjacent slopes. Clearly, if a fossil flora has numerous sclerophyllous shrubs, as well as oaks, pines, madrones, and laurels that obviously formed a sclerophyllous woodland, the shrubs may only have formed a rich understory in it, rather than contributing chiefly to chaparral. And thirdly, examination of sclerophyllous vegetation in the subhumid parts of the United States, Mexico, and the extended Mediterranean (Tethyan) region shows that in every area there are numerous transitions from sclerophyll woodland with a rich understory of shrubs and small trees, through scattered woodland trees in sclerophyllous shrublands, to essentially pure chaparral- or macchia-covered slopes.

Since all these stages commonly occur in proximity and are regularly gradational, it is apparent that sclerophyllous shrublands are basically successional, whether in regions of severe summer drought (California, Spain) , or ample summer rain (Arizona, Nuevo Leon, N. Turkey) . The data suggest chaparral and macchia formed only local brushlands that were basically seral to woodland during the Tertiary, although local edaphic sites were temporarily favorable for shrubs. The initial spread of extensive brushlands most probably coincided with rapid uplift of mountains with steep slopes during the late Pliocene and Quaternary (Axelrod, 1958: 498) .

Tectonism.—Commencing in the later Pliocene, intense orogeny affected the regions where chaparral and macchia are prominently developed today. This not only includes California (with uplift of the Sierra Nevada, Coast Ranges, Transverse and Peninsula ranges), but central Arizona-New Mexico (uplift of Mogollon Plateau) , and eastern Mexico (uplift of Sierra Madre Oriental) . Furthermore, the extended mountainous alpine systems reaching from the Mediterranean eastward through Turkey and Iran to the Himalayas, was also uplifted late in the Cenozoic.

The rapid appearance of steep mountain slopes in areas of subhumid climate favored the spread there of shrubs over trees. Owing to natural updrafts, fires resulting from lightning or volcanism would now be more effective than in the earlier terrains of gentle relief. However, most slopes would soon revert chiefly to woodland with a rich sclerophyllous understory of small trees and shrubs, as can be seen today in numerous relict areas (see lists above) . In some unique edaphic situations *[i.e.,* marble outcrops in a granitic terrain; serpentine; metamorphosed Archean basement intruded by younger plutonics; acidic volcanic rocks *(i.e.,* rhyolite) overlying carbonates], shrubs no doubt were favored, as they are today. Although such areas of chaparral and macchia may have formed local "edaphic climaxes," they were relatively subordinate and probably transient with respect to woodland—even on outcrops of ultrabasics, as may be seen today in many areas in California.

Climate.—The spread of local patches of chaparral at the expense of woodland was increasingly favored by the drier climates of the later Quaternary interglacial ages. Since summer rainfall characterized regions of present mediterranean climate into the early Pleistocene, the adaptive advantage of a shrub- over a tree-habit has appeared only recently. In areas of present mediterranean climate the lowlands were under pluvial conditions during the ice ages. At these times, chaparral and macchia were restricted to the advantage of forest and woodland. This is shown by the early Pleistocene record in southern California where forest descended fully 3,000 ft to the floors of the interior valleys that are now surrounded by chaparral-covered mountain slopes (Axelrod, 1966) . In Tunis-Algeria oak woodland and macchia shrubs descended into regions presently desert (Arambourg *et al.*, 1953) . Clearly, areas of chaparral and macchia in the present regions of mediterranean climate were not so large in the ice ages, or the Neogene, as today.

Progressively drier climates developed during the successive interglacial ages because mountains were being elevated creating rainshadows, and stronger temperature contrasts were developing as the oceans became colder. As a result, the high-velocity, hot and dry winds (santa anas; siroccos) that descend from the continental interior into areas of mediterranean climate during the late summer and autumn were progressively strengthened during the later interglacials. At such times humidity is very low, there is little moisture in the soil, and these times of drought and potentially high fire hazard favor sclerophyllous shrubs, especially on drier slopes. The most favorable time for natural chaparral expansion probably was during the Xerothermic (Hypsithermal) period (8,000-4,000 BP) when climate was drier and warmer than at present. In California, numerous xerophyllous taxa spread from the interior to the coastal strip, and some still survive there on warm, exposed slopes (Axelrod, 1966: 42-55). We may infer that "santa ana weather" was more pronounced during the Xerothermic period than at present, and that natural fires fanned by high winds in terrains of steep slopes would have favored the temporary spread of brush over woodland. As climate moderated in more recent times, woodland trees reestablished in areas formerly brushland.

Fire.—Chaparral is maintained by fire today, its frequency determining if oak woodland or chaparral or grassland dominates, especially on the drier south-facing slopes. Total incineration of trees and shrubs by raging fires on steep slopes greatly accelerates erosion during heavy rains in the following wet seasons. This makes conditions unfavorable for trees by removing soil and litter, and creating dry barren to semibarren outcrops wholly stripped of soil. The spread of chaparral is especially favored by the great fire storms that rage late in the year when humidity is very low, when soil moisture is low, and when brisk to stiff (20-30 mi/hr) winds (santa anas, siroccos) are prevalent and continue for several days. These conflagrations that leave slopes totally devoid of plants create temporarily more arid conditions by the burning of litter, the reduction of mineral matter, and the removal of soil following heavy rain. Clearly, shrubs are favored over trees, though some (oak, pine, etc.) may persist in protected canyons or on favorable (north) slopes, as may be seen today in numerous areas (see lists above).

Following fire, shrubs often sprout prior to the first rain, and may cover the slopes rather quickly. However, it is doubted that this adaptation originated in response to fire cf. Jepson, 1925: 7). As discussed earlier, the sprouting habit is frequent in many woody plants in mesic sclerophyllous forests where fire is not frequent, forests which (ancestrally) produced the taxa that contribute to sclerophyllous oak woodland and chaparral today. Although fire became more frequent as steep slopes arose in the Quaternary, and especially during the drier parts of the interglacial ages, the conditions that perpetuate chaparral today are largely the result of man's diverse activities, of which fire is only one.

Man.—Study of the rich herbaceous vegetation that "suddenly" appears after fire has swept areas of chaparral in the Coast Ranges of California shows that the seedlings largely are from viable seed present in the soil before fire, and not from dispersal from adjacent open areas (Sweeney, 1956). Of the 217 annuals identified in chaparral burns, Sweeney (1956: 193-205) reports 196 are common in adjacent open sites where they contribute to grassland or to oak-savanna vegetation. This implies chaparral has invaded areas that formerly were open, which is consistent with evidence in other areas that shrubs spread into grassland following overgrazing—which is prevalent in the Coast Ranges. Isolated patches of grassland and oak savanna that regularly alternate with chaparral in the Coast Ranges and Sierra Nevada foothill belt lend further support to this interpretation. Furthermore, a good herbaceous cover appears after fire in the more extensive brushlands of southern California (Horton & Kraebel, 1955: 258) . In addition, relict patches of oak-grassland (or oak-walnut grassland) are in the chaparral zone. They are in the Piru Mountains near Oak Flat Guard Station; near Whiteacre Peak to the west; on Hwy. Interstate 5 at the head of Weldon Canyon 2.5 mi south of Newhall; in the Santa Monica Mountains, in shale-valleys and on cooler canyon slopes; in the San Gabriel Mountains near the mouth of Dalton Canyon; south of Palomar Mountain to Roderick Mountain; and also rather widely in San Diego County. In this regard, Dodge's (1975) study of vegetation associated with fire history in San Diego County shows that the region was largely open in the early days. As judged from reliable historical records, the spread of chaparral corresponds to the introduction of heavy grazing by cattle and sheep on the coastal slope in the late 1700's, and in the back country after the 1850's. At that time, patches of chaparral were confined chiefly to local rocky sites and to those of shallow soil, as is inferred here for the Neogene and earlier times as well.

Additional evidence that sclerophyllous shrublands (chaparral, macchia, matorral) as well as sage and semidesert scrub have largely spread under man's aegis, has been discussed by Aschmann (1973b) for Latin America, by Darby for Europe (1956), and also by Naveh & Dan (1973) for Israel. In this regard, it is significant that in the Izmir region (Menemen to Kusadasi) where rainfall is only 25-28 inches (640-710 mm), reforestation of the semibarren landscape covered with a degraded macchia is progressing readily. The native *Pinus brutia* is planted in the fall just as the rains commence. The trees grow rapidly and readily in what obviously was once their native landscape (as judged from relict stands) prior to clearing for lumber and agriculture, and subsequent degradation by grazing (goats, sheep) and resultant erosion.

My brief observations across the subhumid parts of much of the Madrean-Tethyan region indicate sclerophyllous shrublands are largely man-made, and are not a climatic climax, either in areas with summer drought or summer rain. This agrees with the view expressed by Turrill (1929) that extensive brushlands (of the Balkan peninsula) are "rarely if ever natural climatic climaxes. They either represent the undergrowth of forests from which the high trees have been removed by lumbering or other modes of destruction, or they are stages of subseres (p. 144) . . . . (Macchie) is often historically the undergrowth of destroyed forests, frequently of *Pinus halepensis* (or *brutia)* (p. 144). . . . The macchie are very frequently themselves a stage in a subsere started by the biotic factor of human activity. It is certain that for extensive stretches of lowland and hill zone in the Mediterranean domain the natural climax formation is *Pinus halepensis* high-forest with macchia undergrowth. All stages between this and treeless macchie may be studied in Greece and other parts of the Mediterranean domain (p. 146). . . . " A similar view is expressed by Hooker (in Hooker & Ball, 1878: 20) .

"The scarcity of trees in this country (Morocco) is mainly due to the mischievous interference of man. The same ignorant greed of the herdsman, who to procure a little meagre herbage for goats sets fire to wide tracts of brushwood, that has reduced whole provinces of Spain to a desert condition, has been equally busy and equally effectual in Morocco." The recent study of Crete by Zohary & Orshan (1965: 13) reaches a similar conclusion. "The present vegetal landscape of Crete is largely the outcome of man's intereference during millenia. As at present, . . . forests are unable to regain their area.... Nowadays the evergreen xerophyllous . . . maquis and garigue dominate. They suggest that the tremendous change of vegetation both in distribution and composition that took place . . . is due to man's destructive activity." Similar conditions also are well documented for Greece in recent works by Harris & Vita-Finzi (1968) and by Higgs & Vita-Finzi (1966). As the latter have pointed out (Higgs & Vita-Finzi, 1966: 29) : "... the erosion of the soils from the hills, which ... had begun at least as early as Middle Palaeolithic times, had probably by Neolithic times already decreased the pasturage potential. . . . That such a change had taken place was noted by Plato (who wrote) `During these 9,000 years many severe storms have occurred and the soil swilled away from the higher regions . . . leaving only the skeleton of the land...: " A very similar story can be pieced together across the southwestern United States and adjacent Mexico, whether in the summer-dry western, or in the summer-wet eastern part of the region.

BIOGEOGRAPHY

Broadleaved sclerophyllous vegetation appears to have had a similar history in North America and Eurasia. Its taxa, which originated from ancestors in mesic evergreen forests, adapted to expanding dry climate across low—middle latitudes. By the later Paleogene, sclerophyllous vegetation formed a broad, nearly continuous belt across each continent. It was then restricted by spreading drier and colder climates to relict areas of subhumid, mild-winter climate. Decreasing summer rain in the west eliminated taxa from the emerging mediterranean-climate areas, confining them to the eastern, summer-wet regions. This history of the broadleaved sclerophyllous belt bears directly on three problems that are now considered. The first pertains to an explanation of the floristic links between sclerophyllous vegetation zones in North America and Eurasia (Axelrod, 1972, 1973) ; the second concerns the relation of the spreading sclerophyllous zone to the problem of the disjunct "Appalachian" deciduous hardwoods in the Mexican cloud forests; and the third raises the problem of the relation between the sclerophyllous zone and source of the Canary Island laurel forest.

MADREAN-TETHYAN LINKS

As noted earlier, taxa now common to the sclerophyllous floras of California and the Mediterranean region include species of *Arbutus, Cercis, Cupressus, Juniperus, Helianthemum, Myrica, Pinus, Platanus, Prunus* (*Laurocerasus*), *Quercus* (evergreen) and *Styrax.* In addition, the summer-wet region of Arizona-New Mexico has species of *Bumelia, Cercis, Platanus, Sageretia* and *Sapindus* that are either represented by related taxa in the Mediterranean region, or occurred there and in California-Nevada during the Neogene. Furthermore, in the Sierra Madre of Mexico, the latter genera are now associated with *Arbutus, Clethra, Ilex, Myrica, Persea, Pistacia* and *Sabal* that either occur in the Mediterranean region today, or were there and also in California during the Neogene—and presumably earlier as well.

An example of this relationship is provided by the early Miocene (Burdigalian) flora of Majorca (Arenes & Depape, 1956) , dominated by broadleaved sclerophyllous taxa. These include *Phoenix* and *Sabal* among the palms, and evergreen dicots such as *Laurus, Myrica, Persea, Pistacia, Quercus, Sapindus* and *Zanthoxylum* that are similar to living species and are represented by related (ancestral?) taxa in the Oligocene and Eocene floras of southern Europe (lists in Arenes & Depape, 1956). Most of the fossils are allied to species in the American Miocene and Oligocene. The Majorca flora compares well in general physiognomy with the evergreen oak-laurel-palm woodland of coastal southern to central California, as represented by the Carmel, Puente and Modelo floras. The following genera in the Miocene of southern California have rather similar species in the Majorca flora-*Sabal, Myrica, Persea, Pistacia, Quercus* and *Zanthoxylum,* and *Sapindus* is represented in the Pliocene there.

Additional links with the Mediterranean region appear to be represented in the American Paleogene floras; few were identified by earlier workers probably because they were not searched for. In this regard, Moore (1973) gives credence to the record of *Phoenix* in the Eocene of Texas (Berry, 1914) . *Zanthoxylum (= Fagara)* in the late Eocene-Oligocene of the Gulf States (Berry, 1916b, 1924) has comparable species in the Miocene-Oligocene of the Mediterranean, and in the Mint Canyon flora of southern California as well. In the drier interior, several species in the Eo-Oligocene Florissant flora (MacGinitie, 1953) of Colorado display relationship with those now only in the Mediterranean region, or in Mexico- the Mediterranean-southwest Asia. Among these, *Quercus orbata* appears similar to the fossil *Q. cruciata* of southern Europe; *Cotinus fraterna* resembles C. *coggygria* of the Mediterranean pine-oak woodland and macchia that ranges east into China; *Rhamnites pseudo-stenophyllus* shows relationship to *Rhamnus* in California *(R. rubra),* eastern Mexico *(R. pinetorum),* and the Mediterranean *(R. oleoides, R. lycioides);* and *Daphne septentrionalis* resembles *D. oleoides* of the Mediterranean scrub and *D. giradldi* or *D. tangutica* of western China. The Oligocene *Platanus stenoloba* from Montana (Becker, 1969) shows considerable relationship to *P. orientalis* of the eastern Mediterranean, as well as to its nearest relative, *P. racemosa* of California and Baja California.

In California, the Chalk Bluffs flora of early Eocene age is reported to have *Nerium* (MacGinitie, 1941). The leaf of *Myrtus oregonensis* from the Miocene of central California has been compared with leaves of the living Mediterranean M. *communis* Lesquereux (1883), but the resemblances now appear largely superficial (H. Schorn, oral communication, June, 1974) . The widespread *Arbutus idahoensis* in the Miocene of the West shows affinity with *A. canariensis,* though it has shorter petioles. It was a regular member of broadleaved sclerophyll vegetation in the Miocene, and was associated with sclerophyllous trees and evergreen shrubs *(Ceanothus, Cercocarpus* and *Heteromeles)* in the Pliocene. In the Blue Mountains flora it is recorded with *Pinus tiptoniana,* represented by several cone impressions and numerous 2-needled fascicles that closely resemble those of the living *P. halepensis* and *P. brutia* of the Mediterranean sclerophyllous zone (Chaney & Axelrod, 1959) . The madrone and pine evidently contributed to a broadleaved sclerophyll vegetation with *Quercus* and *Lithocarpus* on warmer slopes adjacent to a mixed conifer-hardwood forest that inhabited moister, cooler sites in the region.

Apart from these, fossil live oaks in southern Europe are considered by Andreánszky (1962b) similar to taxa (sect. Virentes: *cf. Q. virginiana, virens)* now in the coastal Atlantic and Gulf States. In their analysis of the early Miocene (Burdigalian) flora of Majorca, Arenes & Depape (1956) note that *Q. drymeia* resembles some Mexican oaks *(Q. xalapensis, lancifolia, sartorii),* and that *Myrica balearica* shows some relationship to M. *California* and to other species as well. Several authors *(i.e.,* Grangeon, 1958; Arenes & Depape, 1956) have compared *Quercus elaena* with *Q. phellos.* All these specimens should be reexamined so as to verify the suggested relations.

The data suggest that an ancient sclerophyllous flora adapted to subhumid climate inhabited lower–middle latitudes in the Paleogene, stretching along the shores of the Tethyan region and across southern North America (Fig. 1) . The links are relicts of effective migration across the middle Atlantic, for it was narrower in the Paleogene (Phillips & Forsyth, 1972; Dietz & Holden, 1970) . Dispersal was aided by micro-continents (Azores), and by volcanic islands along the mid-Atlantic Ridge and its flanks that were rafted subsea as the ocean basin widened and deepened. In addition, migration during the Paleogene was favored by the lower latitude of the east coast (Fig. 1) , and especially by the ENE orientation of the Appalachian axis, having since been rotated to its NE trend (Phillips & Forsythe, 1972; Walper & Rowett, 1972) . This orientation (Fig. 2) produced more numerous warm, dry sites for migration, especially on granite-gneiss domes, "shale barrens," and other suitably hard rocks scattered through the Piedmont.

That land areas at low–middle latitudes had warm, subhumid climate is indicated by latitudinal position marginal to the subtropical high pressure belt, marked now by the Azores High. This belt of dry descending air extended farther west during the Paleogene than at present. North America was low, high cordilleras had not yet been elevated, the Americas were widely separated by ocean, the Tethys was broad, and the global latitudinal thermal gradient was much less than that of today—all implying a broader zonal distribution than now exists. A belt of dry climate is confirmed by the thick evaporite sections in the late Cretaceous and Paleogene of the Gulf States (Green, 1961; Lotze, 1964; Kozary *et al.,* 1968), in northern Mexico (Imlay, 1944), and in the western interior as shown by the Green River Formation (Bradley, 1948, 1964) , as well as in the Paleogene from Spain to India and southwest China (Strakhov, 1960; Green, 1961; Lotze, 1964; Kozary *et al.*, 1968). Furthermore, the fossil floras of all these areas have comparatively small- to moderate-sized sclerophyllous leaves (see Berry, 1916b, 1924; MacGinitie, 1969; Dilcher, 1973; Andreánszky, 1962a, 1962b; Arenes & Depape, 1956; Grangeon, 1958; Vasilevskaya, 1957), implying adaptation

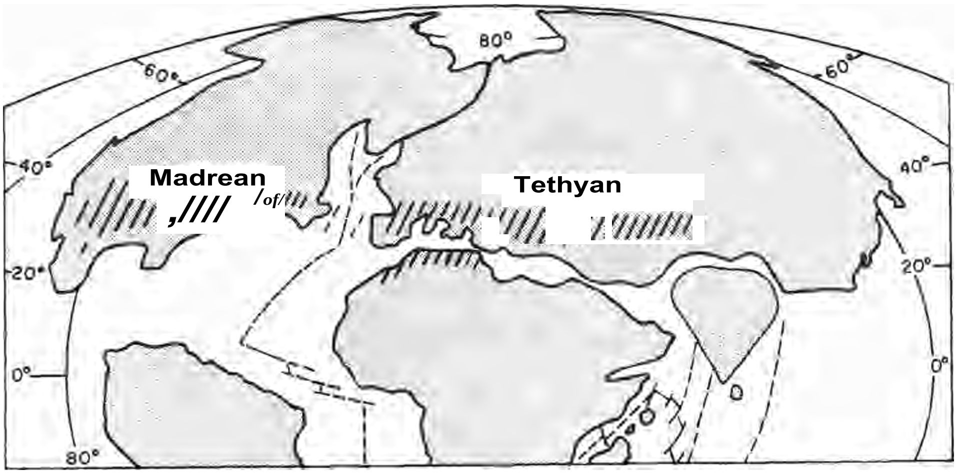


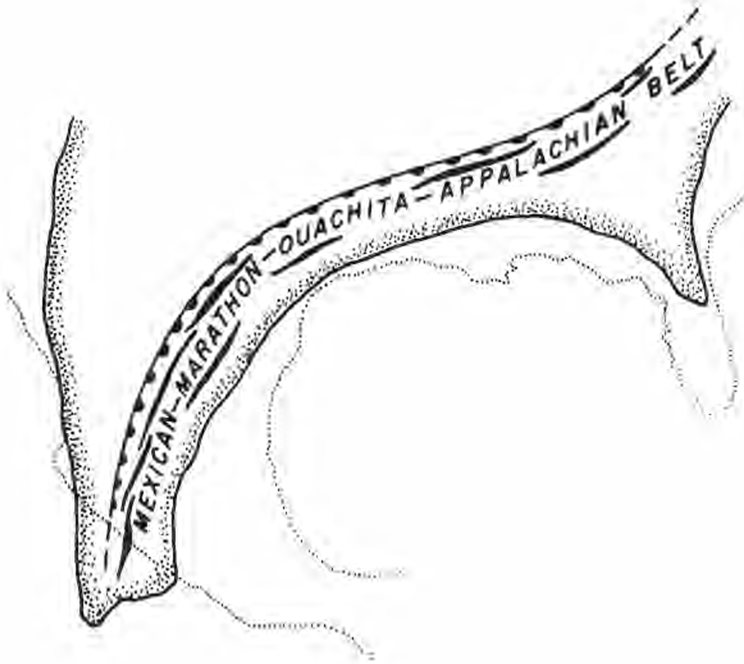
FIGURE 1. Early Tertiary positions of the continents and areas (hachured) potentially occupied by Madrean-Tethyan sclerophyllous vegetation (marine embayments, not shown). Somewhat modified *(i.e.,* India) from Dietz & Holden (1970). For other reconstructions, see Phillips & Forsyth (1972) and Briden *et al. (1974).*

to a climate of much sunshine, moderate (subhumid) summer precipitation, and high evaporation.

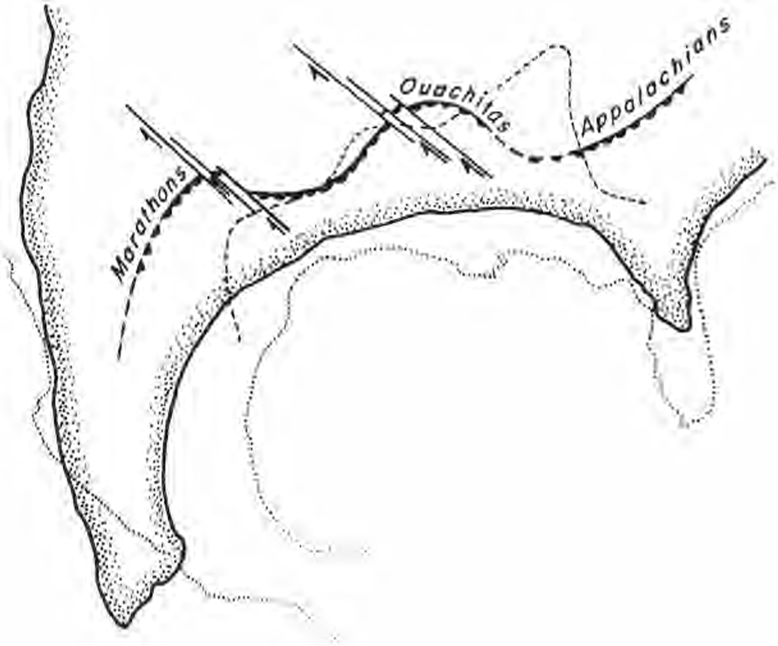
The potential for migration across this region may be inferred from the occurrence today on the granite-gneiss domes of the Piedmont and in the "Fall Line Sand Hills" at the edge of the Piedmont of some 200 taxa, few of which are found elsewhere in the eastern United States. McVaugh (1943) reviewed these distributions and emphasized that many of them find their affinities in the Mississippi Valley, the Ozarks, or in the western United States and Mexico. He draws an analogy (p. 140) between their distribution and that of the black oaks which also have few species in the moister, colder Blue Ridge, but many in the Piedmont-inner Coastal Plain, the Ozarks and southwestern North America. The plants in these edaphically dry areas, both perennials and annuals, include *Agave, Forestiera, Eriogonum, Hedyotis, Lotus, Oenothera, Portulaca, Schoenolirion, Sedum, Talinum, Trifolium* and *Yucca.* Other species in the southeastern United States that are rare and not restricted to the granite-gneiss domes are isolated representatives of genera typical of the west, distributed in *Aristida, Brickellia, Astragalus, Cnidoscolus, Eriogonum, Eryngium, Gilia, Krameria, Muhlenbergia, Nolina, Opuntia, Penstemon, Stillingia, Stipa* and *Xerophyllum.* Many of them are in the "Fall Line Sandhills" which form a narrow belt at the edge of the Piedmont. The "shale barrens flora" farther north (West Virginia-Pennsylvania) and higher up in the Appalachians shows a similar floristic content (Keener, 1970) , though it is not so rich inasmuch as it is in a colder region. Species of *Eriogonum, Oenothera* and *Phlox* are attributed to a southwestern source.

McVaugh (1943) concluded that since a large proportion of these xeric species either have the greater parts of their ranges south and west of the Piedmont, or belong to genera that are best developed in the southwestern United States and the highlands of Mexico, they probably were derived from those semi-arid regions.

A


MEXICAN-MARATHON-OUACHITA-APPALACHIAN BELT

B


Marathons
Ouachitas
Appalachians

As he notes, these are not recent distributions for some of the genera are monotypic and confined to the granitic-gneiss domes (*Diamorpha* and *Amphianthus)* and other taxa are represented there by unique, isolated species in their respective genera, notably in *Isoetes, Juncus, Agrostis, Talinum* and *Sedum.* The distinctness of many of the eastern Piedmont species suggests invasion probably occurred in the Tertiary, as does the relict occurrence of some, notably *Sageretia* in xeric coastal sites of Carolina (see Tables 2, 3), or the discontinuous occurrence of clusters of *Helianthemum* species (Table 3) in each area which have diverged since migration.

The evidence reviewed above indicates subhumid climate probably formed a more or less continuous belt across the entire region into the later Paleogene prior to the counter-clockwise rotation of the Appalachian axis (and North America) to its more northerly bearing (Fig. 2) . At that time, dry sites may have supported ancestral species of the sclerophylls now discontinuous between southern Eurasia and North America *(Arbutus, Juniperus, Cupressus, Bumelia, Pistacia, Quercus, etc.)* . In this regard, Gray (1960b) notes pollen of *Ephedra* is sufficiently abundant in the late middle Eocene Claiborne Formation of Alabama to suggest that it probably was derived from shrubs on local drier sites nearby. She suggests beach dunes near the coast, though *Ephedra* may also have inhabited xeric edaphic sites in the foothill belt to the north. Of the pollen genera listed by Gray, species of the following now contribute to sclerophyllous vegetation: *Celtis, Ilex, Juglans, Ficus, Myrica,* Myrtaceae, *Ocotea,* Palmae, *Quercus* and *Sapindus.* Several of these, as well as possible grains of Ericaceae, are recorded from the Claiborne of Hot Springs County, Arkansas (Saunders *et al.,* 1974). Clearly, a search of the pollen record may disclose other sclerophylls of subhumid requirements inhabited the region. According to the thesis adopted here, these would be Tethyan or Madrean in distribution at present.

In regard to dry sites in the region, the Middle Miocene Calvert flora of Virginia and the District of Columbia (Hollick, 1904; Berry, 1909, 1916a) provides additional critical evidence. Most of the leaves are very small (nanophyll to leptophyll) and a number of them are entire and coriaceous as well—features indicative of dry conditions. These fossils are so poorly illustrated that the specimens must be examined before the determinations of Hollick and Berry can be accepted. Nonetheless, both of them recognized affinities with plants in the Southwest. In this regard, the legumes have very small leaflets and appear to represent several genera, possibly *Diphysa, Caesalpinia* and *Leucaena.* Other taxa include evergreen oaks, a possible sumac, a probable *Ceanothus* (Berry's

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4-

FIGURE 2. Walper & Rowett (1972) propose: A. The Appalachian-Mexican folded belt trended north-south during Late Paleozoic time. B. The Gulf of Mexico owes to separation of the American plates in the Permo-Triassic transition; in conjunction with the formation of the Caribbean, the opening of a sphenochasm produced the Mississippi embayment; accompanying large left-lateral displacement shifted segments of the eastern mobile belt to their present positions. Prior to counter-clockwise rotation of North America following the Eocene, larger areas of exposed dry slopes faced south for occupation by xerophyllous plants in these displaced segments.

Phyllites), and a presumed *Ilex.* Equally notable, there is no evidence here for a rich mixed mesophytic forest. Although some of the taxa are referred to *Ulmus, Berchemia* and *Pieris,* their very small leaves remove them from any relation with typical members of those genera; others are very fragmentary. In discussing the assemblages, Berry noted the flora from Richmond, Virginia suggests a low coastal area boredered by cypress swamps. But that at Good Hope Hill, District of Columbia, has small-leaved oaks, *Ilex, Vaccinium,* numerous legumes and *Ceanothus? (Phyllites)—all* suggesting a region of dry edaphic conditions, possibly coastal dunes. This clearly implies that drier rocky sites at the Fall Line, situated only a few miles west, probably supported a xeric flora.

Evidence of a drier climate in the early and middle Miocene is also provided by the rich vertebrate faunas of northern Florida (Goin, 1958; Olsen, 1962; Estes, 1963; Puri & Vernon, 1964) . Some of the fossil mammals (kangaroo rat, badger) indicate relatively dry open country. However, the sedentary herpetofauna probably provides a better indication of environment than the more rapidly evolving mammals. In discussing the origin of the herpetofauna, Goin (1958) assigns a number of taxa to Southwestern and Mexican sources, including a large percentage of big snakes and numerous lizards. He also emphasizes that *Scaphiopus,* a toad of desert affinities, has been in Florida since the middle Miocene (17 m.y.) . Although it has lived there continuously in a region where there are abundant ponds, lakes and streams, it has retained its habit of breeding only in temporary water. The tadpoles transform at rates that indicate drying puddles, implying that its breeding habits have remained basically unchanged since the Miocene, though it has been isolated from arid regions where this habit is obligatory for at least 12-13 m.y. Since some of the taxa *(i.e.,* kangaroo rat, badger, desert toad, tortoise) indicate dry sites, it appears that northern Florida as well as lowland areas north to Maryland were essentially a dry savanna-prairie region, which is consistent with the presence of large browzers and grazers in the mammalian faunas, including antelopes, horses, rhinocerotids, camelids and others.

The biologic evidence of dry climate is consistent with that provided by geologic and marine paleontologic evidence. Alt (1974) has noted that high level gravels of the southeastern United States, aligned along the Orangeburg scarp reaching from Virginia south to the Trail-Lake Wales Ridge in central Florida, appear to be remnants of coalescing alluvial fans laid down chiefly by braided streams on a pediplain surface during middle Miocene under dry climate. Deposition of montmorillonite-sepiolite-attapulgite clay minerals in the contemporaneous Hawthorn Formation is consistent with an arid source area. In addition, phosphate deposits in the Hawthorn are considered the result of upwelling of deep, cold waters along the shelf edge of the east coast during the Miocene.

Gibson's (1967) study of the paleoenvironment of the phosphatic marine strata of North Carolina in the Pungo River Formation (a lateral equivalent of the Calvert), and in the Yorktown Formation which overlies the Pungo River unconformably, was interpreted primarily from planktonic foraminifera. Two very different temperature regimes are indicated for the region during deposition. The Pungo River (age = *Globogerinatella insueta* zone, or 22-23 m.y.; see Bandy &

Ingle, 1970: fig. 4) and the lower part of the Yorktown (age = *Globorotalia menardia* zone, or 13 m.y.; see Bandy & Ingle, 1970: fig. 4) contain a cool water benthonic fauna and a dominantly cool water planktonic fauna, both quite different in composition from synchronous subtropical faunas in Florida. During late Yorktown deposition, the benthonic faunas become warm temperate to almost subtropical and have many species that are also in Florida at that time. The faunal relations thus indicate the pre-late Yorktown hydrographic regime was different from the present one, with warm currents situated farther south and with a circulation pattern similar to the present appearing only late during Yorktown deposition (~ 13 m.y.) .

To explain these features, as well as those along the entire coastal strip that call for dry climate, Alt (1974) proposed that if the prevailing westerlies dominated over the southeastern states during the Miocene, the entire paleogeographic assemblage (phosphate deposition, diatomites, clay minerals, relict pediplains, paleoclimatic indications) could have a common cause. This would be possible if the continent had relatively low relief, as is now known to have been the case; the western cordillera was elevated appreciably only in the later Tertiary and Quaternary. Coupled with warmer oceans in the west, the principal atmospheric pressure systems would not be so strong as those of today, and the westerlies might well flow east across the continent, bringing a drier climate to the east coast (see Willett & Saunders, 1959: 199-204) .

The sclerophyllous taxa of subhumid requirements that are now discontinuous between the subhumid climates of southern Eurasia and North America presumably were eliminated from the Appalachian axis and its western extensions (Ouachita, Marathon Mts.) by spreading colder climates commencing in the late Miocene (post-late Yorktown) . In this regard, mild winters typified the western interior well into the Neogene, as shown by the occurrence of *Cedrela, Cordia, Meliosma* and evergreen oaks in the late Miocene of northwestern Nebraska (MacGinitie, 1962), by *Sabal* in the Pliocene of northern Texas (Chaney & Elias, 1936: 12) , and by alligators and other cold-sensitive vertebrates (Hibbard, 1960) and molluscs (Taylor, 1960) in the High Plains well into the later Pliocene.

Fossil and modern floristic evidence not only imply there was east-west migration of sclerophyllous taxa, geologic evidence indicates that it was favored by climate, island stepping-stones, and by continental orientation. The efficacy of migration is demonstrated by the affinities of the modern flora of the Azores. Situated on the mid-Atlantic Ridge 1,000 miles west of Lisbon, it has numerous native Mediterranean taxa that reached there by long-distance transport (Wallace, 1880: 248–253) . There also are some endemics in the Azores allied to species in the Mediterranean region. They indicate earlier migrations followed by evolution in isolation, or survival under the insular maritime climate and extermination on the continent. Although trans-Atlantic links between areas of subhumid climate are not numerous today, the occurrence of larger numbers into the Neogene is consistent with migration between the sclerophyllous belts which were at least discontinuous across the area.

Present evidence suggests that interchange across the Madrean-Tethyan region was relatively restricted, inasmuch as comparatively few taxa (so far as now known) *were* common to these areas in the Paleogene. This is implied also by the occurrence of distinctive taxa in each region which appear to have originated in their respective areas (Raven, 1973) . Thus the Californian sector has *Adenostema, Arctostaphylos, Carpinteria, Ceanothus, Cercocarpus, Cneoridium, Dendromecon, Fremontodendron, Garrya, Lyonothamnus* and *Simmondsia,* most of which range into summer-rain areas to the south and east. In like manner, the Tethyan area is distinguished by its *Ceratonia, Olea, Chamerops, Laurus, Myrtus* and *Phillyrea* that are typical of woodland and macchia vegetation and also extend into summer rain areas to the east. A further indication of the distinctness of the floras during much of the past is provided by the live oaks that are so numerous in each area. They are not closely related, but belong to different sections and tribes. Presumed similarities, such as the older grouping of *Quercus chrysolepis, Q. virginiana* and *Q. ilex* into Sect. *Ilex,* are the result of homoplasy—not close genetic relationship. Similarly, each area has "closed-cone pines," yet they are now known to represent very different sections (Critchfield & Little, **1966;** Little & Critchfield, 1969). The distribution of Tertiary pines and oaks that required subhumid climate may have been restricted chiefly by the problem of transport across water barriers.

Although the preceding data appear to clarify the much-discussed relations of sclerophyllous woody taxa that are discontinuous now between the Californian and Mediterranean regions, it must be reemphasized that they make up only a small fraction of the total floras of these regions. There is a tremendous discontinuity and dissimilarity between the Madrean and Tethyan floras, as might be expected in view of their progressively wider separation by water and distance during Tertiary time. Not only are the woody floras quite distinct, the majority of the herbaceous taxa also differ, as cogently reviewed by Raven (1971, 1973) . These differences in both the woody and herbaceous floras of the Madrean-Tethyan regions indicate they are relatively ancient, and that the links between them did not involve much long distance dispersal. The closer correspondence of woody taxa between the Madrean-Tethyan regions in Tertiary time stems chiefly from a more favorable climate and terrain for a wider distribution. Later they were eliminated in the mediterranean regions and elsewhere as climate with summer rain contracted, and as drier steppe and desert climates expanded.

The trans-Atlantic links between the Madrean-Tethyan regions were more or less indirect and discontinuous because direct migration of sclerophyllous taxa adapted to subhumid climate was not possible around the North Atlantic. That area was humid and temperate during the Tertiary, supporting mesic conifers and deciduous hardwoods of Arcto-Tertiary alliance. In this regard, many Arcto-Tertiary genera of woody plants common to the Mediterranean and California regions have important roles in sclerophyll-border communities, notably species of *Acer, Aesculus, Alnus, Clematis, Cornus, Crataegus, Fraxinus, Juglans, Populus, Prunus, Rosa, Rubus, Salix, Viburnum* and *Vitis.* All of them inhabited moister sites in the ecotone with the sclerophyllous vegetation of the Madrean and Tethyan provinces, but are unrelated historically to the origin of sclerophyllous taxa and vegetation. Many temperate taxa are derivatives of species in Arcto-Tertiary forests that have persisted in the regions of present summer drought by functional adaptation: by shifting into the moistest sites—along streambanks, seepages, and cool northerly-facing slopes. The species are distinct endemics in most cases, and usually represent different sections of their respective genera, as noted above for the evergreen oaks and the closed-cone pines. This distinctness extends notably to the herbaceous alliances (see Raven, 1971, 1973) . Even though there are numerous genera of herbs and forbs common to each region, as in *Achillea, Allium, Aster, Carduus, Crepis, Delphinium, Festuca, Filago, Galium, Geranium, Iris, Lotus, Plantago, Poa, Rumex, Stipa* and many others, the species are only distantly related and frequently belong to distinct tribes or sections of their respective groups, which are characteristically Mediterranean or Californian though some may be Madrean or Tethyan, having a wider distribution. When we turn to family relations we find that some have their chief centers of evolution in the California region, notably Boraginaceae, Cruciferae, Hydrophyllaceae, Onagraceae. and Liliaceae. In the Mediterranean region, the Caryophyllaceae, Leguminosae and Umbelliferae are proportionally more important, and several of the Californian families (Hydrophyllaceae, Polygonaceae, Onagraceae, Polemoniaceae) are not as well represented there. These differences parallel those displayed by taxa in trans-Atlantic forests today. Differentiation across the inner tropics commenced in the Late Cretaceous (Turonian) when Africa and South America finally parted company, and a forest with many common taxa was severed. Since then, related taxa at the level of genera, tribes and families have gradually emerged in each region, and account in large measure for the distinctness of the New and Old World tropical floras. In addition, the elimination of presently Old World taxa from the New World, and of some American taxa from the Old World tropics following the Eocene, accounts also for the increasing floristic differences between the African-Asian and American tropical floras during the Tertiary. In the same way, though in much lesser degree because of its more recent occurrence, the temperate deciduous and conifer-hardwood forests of eastern North America and Europe were rather similar into the late Miocene. As colder climates isolated them in later times, their taxa have continued to differentiate, but the wide floristic differences today result chiefly from the wholesale elimination of American taxa in western Europe during the glacial ages.

Thus, the floristic evidence as now known supports the view that past Madrean-Tethyan connections have been minor but important; the fossil record may be expected to disclose more of them. The long period of separation of these regions of subhumid, warm temperate climate by major climatic and ocean barriers has led to the development of unique sclerophylls in each area, to the formation of unique tribes or sections of "large" genera that still link these regions, and to significant differences in the proportional representation of some families in these areas.

MEXICAN CLOUD-FOREST

The spread of a belt of xerophyllous woodland vegetation over low—middle latitudes following the middle Eocene bears directly on the problem of the age of the disjunct occurrence of numerous "Appalachian" taxa in the mountains of Mexico and central America. These include mesophytic species of *Acer, Carpinus, Carya, Cercis, Cornus, Fagus, Hamamelis, Ilex, Liquidambar, Myrica, Nyssa,* *Ostrya, Prunus* and *Tilia* in Mexico that are identical or closely related to taxa in the eastern United States. The age of the disjunction has been disputed, chiefly because of the absence of a record. Some have favored the early Tertiary (Berry, 1926; Axelrod, 1939, 1950, 1960; Clements, 1936) , others the Miocene (Graham, 1972; Martin & Harrell, 1957; Chaney, 1936) and some the Pleistocene (Deevey, 1949; Dressler, 1954; Sharp, 1953) .

Recently, Graham (1973) discovered the pollen of temperate genera (*Abies, Picea, Alnus, Celtic, Fagus, Juglans, Myrica, Liquidambar, Populus* and *Quercus)* in the middle Miocene Paraje Solo Formation near Coatzacoalcos on the coast of Veracruz, Mexico. Hence, he concluded temperate deciduous hardwoods had migrated there from the Appalachian area by the Miocene, or possibly earlier. However, this interpretation does not take into account the fact that whereas these taxa make up deciduous hardwood forests in the Appalachian region today, in Mexico and Central America most of them are subordinate members of forests in which evergreen dicots dominate (Hernandez *et al.,* 1951; Miranda & Sharp, 1950) . Clearly, the occurrence of these "Appalachian" deciduous hardwoods in the Mexican and Central American cloud forests is not due to their southward migration and entry into an evergreen forest previously without them, as implied by Graham (1972, 1973) and others as well *(i.e.,* Chaney, 1936; Martin & Harrell, 1957; Braun, 1950) .

These temperate rainforests have persisted there in modified form since the early to middle Eocene, at which time they extended northward to central California, Oregon, Wyoming, Colorado, as well as into the Appalachian region. Although deciduous hardwoods are recorded from the Appalachian area (Brown, 1944; Gray, 1960b), they dominated forests in the uplands, where climate was cooler (Axelrod, 1965: 164) . At low to middle altitudes they were members of a temperate rainforest (or cloud forest) like that now on the eastern escarpment of Mexico, a forest in which evergreens are prominent. This Eocene forest was replaced at altitudes near sea level by the northern fringe of a subtropical forest that lived under a dry winter season during the middle Eocene (Dilcher, 1973) .

The Tertiary cloud-forest of the eastern United States lost numerous evergreen dicots and some deciduous hardwoods as colder climate developed during the Tertiary, and especially during the Quaternary when ice sheets reached south to Lat. 37°. The surviving relict forests that are related to those of the Mexican highlands are not solely the "cove forests" of the Appalachians, but the lowland Southern Mixed Hardwood Forest (Quarterman & Keever, 1962; Monk, 1965) that has a few relict evergreens *(Ilex, Myrica, Persea, Quercus* and *Symplocos)* mixed with the deciduous hardwoods. Not only is it more similar in physiognomy to the temperate Mexican rainforests, it lived under a climate of similar warmth (*ET* 58-62), whereas the Appalachian cove forests are in a colder climate (*ET* 54-56), one which in Mexico supports oak-pine or pine forests of different composition. Apart from the few evergreens in the Southern Mixed Hardwood Forest that indicate relations to the south, the bryophytes and ferns of the escarpment-gorge region of the Blue Ridge in North and South Carolina display a strong Mexican affinity (Cooper & Hardin, 1970; Billings & Anderson, 1966) . They appear to have survived because the escarpment-gorge area faces south. As a result, warm moist air moving up the gorge gives increased (and high) orographic precipitation and the mild Gulf air damps temperature extremes. Hence the region has the most equable climate in the southeastern states, as noted earlier (Axelrod, 1967b: 27) . Thus, some of the groundlayer "tropical" bryophytes and ferns managed to survive the Quaternary cold waves, but few of the evergreens did.

The evidence now available suggests that in the Eocene temperate rainforests dominated by a mixture of evergreen dicots and deciduous hardwoods covered the central United States, extending southward into Central America on highlands along the present axis of the Sierra Madre Occidental. As noted earlier (Axelrod, 1960: 268), high altitudes are not required: all altitudinal thermal zones are narrower under conditions of highly equable climate (Axelrod, 1965, 1968) . The taxa that were in the Mexican region have persisted there in scarcely modified form. They spread into the Sierra Madre of eastern Mexico as it was elevated in the late Cenozoic (Schuchert, 1935; Guzman & de Cserna, 1963; de Cserna, 1960) , at which time their area in the western Sierra Madre was reduced by spreading dry climate. On this basis, the pollen of deciduous hardwoods recorded from the Miocene of Veracruz (Graham, 1973) did not make up a deciduous forest in Mexico like that of the present Appalachians, nor did species from such a forest migrate south to become associated with broadleaved evergreens. They contributed to a temperate rainforest situated in the mountains farther west, and well above the tropical lowland rainforest that lived at sea level at Coatzacoalcos, an area to which they were transported. Thus, there appears to be no direct evidence for migration of forest species from the Appalachian region into the Sierra Madre Oriental. Rather, the relations seem explicable by the local differentiation and survival as specialized outliers of a forest that extended across North America into later Paleogene time, at least in local areas. The presumed problem of migration between the southeastern United States and northern Mexico thus appears to be non-existent. The Appalachian taxa are disjunct by default: their earlier associates were eliminated from the region by decreasing temperateness of climate.

This analysis may account for the major anomaly in the composition of the modern temperate forests in eastern Asia and eastern North America. The lowlands from central Japan to northern Taiwan, and coastal and southern China south of the Yangtze are covered with a temperate rainforest composed of evergreen dicots and a sprinkling of deciduous hardwoods, captioned Evergreen Broad-leaved Forest by Wang (1961) . It has no close counterpart in the eastern United States in areas of similar climate except along the outer coastal strip from central Florida into North Carolina. Inland, areas with slightly colder winters are occupied by the Southern Mixed Hardwood Forest which has fewer evergreens and in which deciduous hardwoods are more frequent (Quarterman & Keever, 1962; Monk, 1965) . This forest is clearly ecotonal to the dominantly deciduous forests farther north and to the evergreen forests to the south or coastward, and in this sense may be compared with the Mixed Mesophytic Forest of China (Wang, 1961) .

It was decreasing temperateness (see Bailey, 1960, 1964) following the Oligocene that eliminated numerous broadleaved evergreens from the eastern

United States, and left an impoverished, dominantly deciduous hardwood forest over the lowlands there. The climatic differences are especially emphasized when areas of similar effective temperature (ET) are compared, as Tokyo and Washington, D.C., or Augusta, Georgia and Kagoshima, Kyushu Island. As shown by Bailey (1966: 193; see also Vahl & Humlum, 1949), Tokyo has 460 hours of the year with temperatures below 32°F (0°C) as compared with 745 hours at Washington, and 568 hours with temperatures above 80°F (26°C) as compared with 1033 at Washington, yet the warmth of climate is very similar in each area (ET = 57.5°F or 14.2°C at Tokyo, 57.2°F or 14.0°C at Washington). Other examples of temperateness in areas of similar warmth have been noted elsewhere (Axelrod, 1964: 53–59, 1967b: 5–12, 1968: 717–718; Axelrod & Bailey, 1968: 595–599).

CANARIAN LAUREL FOREST

Many of the unique woody plants that make up the laurel forest of the Canary Islands are represented by very similar (or the same) species in Neogene floras scattered from Spain to western Georgia in the southern USSR (Depape, 1922; Bramwell, 1972; Sunding, 1970; Takhtajan, 1969; Kolakovskii, 1964). The notion that the Pliocene species migrated to the Canaries from the Mediterranean, pervades most discussions of their origin. However, this does not account for the fact that during the late Miocene and Pliocene Canarian taxa in the Mediterranean region lived adjacent to forests composed dominantly of conifers and deciduous hardwoods that are not now in the Canaries, but throughout the temperate parts of Holarctica.

The Pliocene floras of southern Europe (see Depape, 1922, 1928) show that members of the Canarian laurel forest lived with, or were close to, members of 3 floristic groups that are no longer in the Mediterranean basin. These include (1) subtropicals (Buettneria, Cinnamomum, *Celtis*, Myrsine, Raphiolepis, *Sapindus* and Sterculia) that are now in the moister parts of Africa and Asia; (2) temperate conifers and deciduous hardwoods that are now found in eastern North America (Carya, Liquidambar, Liriodendron, Morus, Magnolia, Nyssa, Robinia, Sassafras, Taxodium and *Ulmus*); and (3) temperate alliances that are now chiefly in eastern Asia, with some extending discontinuously to the Colchic region (*Albizzia*, Carpinus, Cercidiphyllum, Diospyros, Gleditsia, Glyptostrobus, Juglans, Parrotia, *Ulmus* and Zelkova). Members of all these groups live in regions of ample summer rainfall, and imply similar conditions for the Canarian taxa that lived with them in the Mediterranean region into the close of the Tertiary. In addition, each Pliocene flora has species that have persisted in the more temperate parts of southern Europe (Acer, Aesculus, Alnus, Clematis, Cornus, Crataegus, Fraxinus, Populus, Ulmus and Vitis), interfingering with Mediterranean sclerophyllous vegetation in moister sites at lower warmer levels, but most of them are not recorded from the Canarian region. Furthermore, a good number of the typical broadleaved sclerophylls of the Mediterranean (Ceratonia, Chamerops, Myrtus, Nerium and Quercus) are not now members of the Canarian flora. Throughout the Pliocene, taxa of the Canary Island laurel forest were associated with species of these floristic elements in the Mediterranean province. Farther north, Canarian taxa rapidly decreased and disappeared for climate there was too cold for them as judged from the increasing numbers of deciduous hardwoods and conifers, and from the general absence there of taxa that suggest warm temperate climates (Depape, 1922, 1928; Szafer, 1964).

It has generally been assumed that the taxa of the Canarian laurel forest migrated to the insular region, and that they have survived there under mild marine climate where they are removed from cold. They are confined to the cool fog-belt that shrouds the windward, north side of the islands during summer. This reduces evaporation and fog-drip keeps the soil moist, which also aids in the persistence of these subtropical relicts. The absence of numerous taxa that were their associates into the later Pliocene of the Mediterranean, and now survive chiefly in eastern Asia or eastern North America is understandable in terms of the lack of sufficient summer rain to support them. Nonetheless, the question arises as to how the seeds of laurels *(Apollonias, Laurus, Ocotea* and *Persea)* were carried there yet none of the numerous species of *Quercus* that were associated with them in the Mediterranean Pliocene—and are still common in the Mediterranean basin—managed to make the trip. Furthermore, many species that were associated with the Canarian taxa in the Mediterranean inhabit moist sites in that region today *(Acer, Alnus, Crataegus, Fraxinus, Smilax,* etc.) in areas that are marginally mediterranean in terms of climate, yet they are not in the Canaries either.

The reason why deciduous hardwoods and conifers of Arcto-Tertiary alliance are absent from the Canary Islands is apparent from the composition of the Miocene and Oligocene floras of the Mediterranean region. The Cervera of Spain (Bataller & Depape, 1950), the Majorca from the Balaeric Islands (Arenes & Depape, 1956), and the Sinigallia flora from central Italy (Massalongo & Scarabelli, 1859) are entirely dominated by broadleaved sclerophylls, including forerunners of endemics that now typify the Canarian laurel forest. Equally important, conifers or deciduous hardwoods of temperate requirements are almost totally absent from these floras. They were then situated farther north in central Europe (or at higher altitudes), and appeared in the lowlands of the Mediterranean region only in the late Miocene (Depape, **1928;** Arenes & Depape, 1956). This regional distribution of vegetation suggests that the Canarian laurel forest is only a remnant of the rich laurophyllous vegetation that dominated the area from the southern shores of Europe southward into Africa into the late Miocene, following which it was replaced largely by temperate Arcto-Tertiary forests as colder climates developed, and then by sclerophyllous Mediterranean vegetation.

This inference finds support in two lines of evidence. In the first place, the fossil floras that inhabited the broad Saharan region, as based on numerous studies of fossil woods (reviewed by Aubréville, 1970), were composed of dominantly tropical families from Paleocene into Miocene time. Of the 20-odd families so far identified, not one is diagnostic of temperate environments; only one (Fagaceae) has many species *(Quercus)* represented in temperate climates, yet they also range deeply into the subtropics and tropics. The alliances in the Saharan region from Paleocene into the Miocene are mostly related to the present African tropical flora, including taxa in the Annonaceae, Arecaceae (Palmae),

FIGURE 3. Disjunct ranges of some Canarian taxa in eastern Africa and border areas. These may date from the Oligo-Miocene when dry climate commenced to spread across the continent. *Galopina (Rubiaceae)* and *Cliffortia (Rosaceae)* of southeast Africa are related to the Canarian *Phyllis* and *Bencomia,* respectively.

Celastraceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Euphorbiaceae, Hamamelidaceae, Icacinaceae, Lauraceae, Moraceae, Myrtaceae, Proteaceae, Rutaceae, Sapindaceae, Sterculiaceae and Ternstroemiaceae.

The numerous papers of Louvet (1963, 1964, 1965, 1966, 1967, 1968, 1972) and Koeniguer (1966, 1967a, 1967b, 1967c, 1967d, 1967e) on the fossil woods of Tinehert in the Algerian Sahara near Fort Flatters, at the latitude (28°) of the Canaries, show that from the late Eocene into the Miocene that area supported a tropical flora composed of Combretaceae, Leguminosae and Meliaceae. The Meliaceae woods are similar to *Lovoa* and *Entrandrophragma,* large trees in the dense and humid Guinea-Congonese forest. And *Anogeissuxylon* compares with *Anogeissus* which is found today chiefly in wooded savannas. The woody flora implies alternating savanna and rainforest on the Tinehert plateau in the Oligocene and early Miocene, with palms and numerous woody Leguminosae also present. For the Oligocene, Koeniguer & Louvet (1968) describe *Endandrophragmoxylon* from eastern Fez and near Constantine, implying rainforest along the southern Tethyan shore from Tunis to Egypt. The evidence also indicates a pan-Saharan distribution for *Sterculioxylon* which has been recorded in Rio de Oro, Egypt, Somalia and Libya. Wood of *Dombeyoxylon* also had a wide distribution, including Algeria, southern Morocco, lower Egypt and Syria, implying an environment like that of the living *Dombeya* in the Guinea-Sundanese savannas.

The occurrence of these tropical and subtropical alliances in the present Saharan region into the early Miocene implies laurophyllous forests of the Canary Islands were derived chiefly from the mesic Tertiary rainforests and savannas of Africa proper. This is consistent with the distribution of a number of the Canarian taxa that are found elsewhere only in the eastern tropics (Fig. 3) , as noted by Hooker & Ball (1878), by Ceballos & Ortuno (1951: 45), and illustrated by

Bramwell (1972) and Sunding (1970) . Among these, *Dracaena* is represented elsewhere by over 150 species in the Paleotropics, yet the Canarian *D. draco* finds is nearest allies in 3 closely related species in Abyssinia, Somalia and Socotra. The pantropical *Sideroxylon* has 100 species, yet the Canarian S. *marmulano is* most nearly allied to taxa in South Africa (Natal), Reunion and Socotra. *Apollonias* has a related species only in southern India (Kerala, Madras) . Several other taxa have their nearest relatives only in eastern and southern Africa (Hooker & Ball, 1878: 411; Lems, 1960) though they are not all confined to the laurel forest. These disjunctions are range restrictions in response to the spread of dry climate across northern Africa and southwest Asia following late Oligocene time, a view expressed earlier by Hooker (in Hooker & Ball, 1878: 417): "Finally, the *Dracaena,* together with the tropical trees of *Myrsineae, Sapotaceae* (in Madeira) , and *Laurineae,* and the Egypto-Arabian types, suggest the hypothesis that at a very remote period these and many other plants of warmer and damper regions flourished in the area included in North-West Africa and its adjacent islands, and that they have been expelled from the continent by altered conditions of climate, but have been preserved in the more equable climate and more protected area of the Atlantic Islands."

The second line of evidence that suggests the Canarian laurel forest was derived from tropical forests of adjacent Africa comes from plate tectonics. Both Africa and Europe moved northward during the Tertiary (Dietz & Holden, 1970; Phillips & Forsyth, 1972), as determined from polar position measured by remnant magnetism in rocks, from the age of the ocean floor, and from lines of volcanos that show direction of movement. In the South Atlantic, the Walvis Ridge and Rio Grande Ridge are lines of volcanoes that erupted from the Walvis thermal center along the mid-Atlantic ridge, and were then transported northward by the moving ocean-floor. Present evidence indicates that in the early Eocene (50 m.y.) the site of the Canaries was near Lat. 18° and moved to its present position at Lat. 28° by the middle Miocene when the African plate collided with southern Europe, Sicily being a piece of Africa (Barberi *et al.,* 1974) .

North Africa with the Canarian area has therefore been carried northward out of the tropical zone to a position at its margin. Thus, the Oligocene to middle Miocene floras of north Africa-southern Europe are tropical to subtropical because they were situated farther south, and have moved to their present positions. Hence, the Paleogene trend toward cooling was due at least in part to continental movement, as noted earlier by Hamilton (1968). As for the Canaries, they are composed of two discordant island groups. The low eastern Canaries are continental, but the western volcanic islands are oceanic (Dash & Bosshard, 1969; Rona & Nalwalk, 1970; Dietz & Sproll, 1970). Volcanism that created the western Canaries (Gran Canary, Tenerife, La Palma, etc.) commenced in the middle Miocene (Abdel-Monem *et al.,* 1972) and probably is symptomatic of the continuing deformation of the Atlas Mountains (Kames *et al.,* 1973). These islands no doubt were quickly stocked by laurophyllous trees and shrubs from the bordering continent. This was via the present low eastern Canaries which are continental and were attached then to the mainland as shown by the remains of ratites there (Sauer & Rothe, 1972) . Dates of volcanic rocks on Lanzarote and

Fuerteventura (Abdel-Monem *et al.,* 1971) show their ages reach down to the early Miocene (20 m.y.). Thus, it is likely that laurel forests occupied the eastern Canaries by at least this time, invading the western volcanic islands as soon as they appeared in the middle Miocene (16 m.y.) . These forests presumably lost numerous taxa as summer rains decreased, as spreading aridity eliminated forests from the low eastern Canaries and from the lowlands of the western volcanic islands, and as colder climates developed during the Pleistocene. Even today cold spells occasionally affect banana plantations over the lowlands. That forests actually inhabited the region is clear from the notice by Schmincke (1968) that stems of bamboo and palm are in the Pliocene rocks of Gran Canary.

It is now evident why the temperate Arcto-Tertiary deciduous hardwoods and conifers that are associated with Canarian laurel forest taxa in the late Miocene and Pliocene in the Mediterranean region are not in the Canaries. The temperate forest did not penetrate southward in the Miocene into lowland Africa, or to the Canarian region, simply because the area was subtropical to tropical. As the African plate moved northward in the Neogene, subtropical laurophyllous forests were carried to the ecotone with Arcto-Tertiary forests, with the latter also having been displaced southward by cooling climate. The Canarian laurel forest is clearly relict to judge from our present understanding of forest history in northern Africa. On this basis, the high percentage of diploids in the flora which reflects antiquity (Bramwell, 1972) becomes understandable, as does the woody habit of much of the flora, the numerous ferns and lianas in it, and the widely disjunct relations of some of its unique taxa. The sclerophyllous evergreen shrubs in it that also contribute to the adjacent macchia further support the opinion that taxa of chaparral and macchia vegetation were derived early in the Tertiary from alliances that contributed to similar laurophyllous forests that were then spread widely across low middle latitudes in both Eurasia and North America.

SUMMARY AND CONCLUSIONS

Broadleaved sclerophyllous taxa that contributed to evergreen woodland and chaparral (or macchia) vegetation occur today in areas with winter rain and summer drought (California, Spain) , summer and winter precipitation (Arizona-New Mexico, eastern Mediterranean) , summer rain and winter drought (eastern Mexico, northwestern India), and with rainfall rather well distributed through the year (northern coast, Turkey) . On each continent, the areas of sclerophyllous vegetation share identical and paired species (or varieties), but are separated now by steppe, grassland and desert climates.

Sclerophyllous taxa entered the fossil record in the middle Eocene, replacing more mesic ones of the earlier dominant laurophyllous forests. The sclerophyllous shrubs and small trees were derived from alliances in laurophyllous forests and many of them contribute to these forests today. Since the adaptive structural features (sclerophylly, small leaves, sprouting habit, deep root system) of chaparral-macchia taxa are also common to related species in mesic laurophyllous forests, they certainly did not originate in response to summer drought, and probably not to pyrogenic conditions. Further perfection of adaptations (sunken stomata, reduced leaf size, thicker leaves, etc.) to drier conditions presumably took place on lee slopes, in intermontane valleys, and in mineral-deficient sites. Hence, as summer precipitation decreased during the later Tertiary these sclerophylls were preadapted to live in a climate of progressively increasing summer drought.

The basic adaptive structural features of sclerophyllous taxa are therefore not specialized and derived but are ancient and possibly primitive. From an evolutionary standpoint, broadleaved evergreen sclerophylls may best be regarded as "generalists" for they live in diverse environments in which their structural adaptations are rather similar, but in which their functional adaptations adjust as environment changes.

During late Paleocene to early Neogene time, sclerophyllous vegetation extended largely across each continent at low-middle latitudes, inhabiting a broad belt of subhumid climate with summer rain. Many sclerophyllous taxa that are now only in summer-wet areas of the Tethyan and Madrean provinces were formerly in the west, where summer-dry mediterranean climates developed more recently.

The existence of chaparral and macchia over wide areas as "climax" vegetation in the Tertiary seems unlikely. Brushlands were present locally in poor sites ("edaphic climaxes") , and temporarily after natural fires (lightning, volcanism), but they were chiefly seral to oak-pine-laurel woodlands with a rich understory of sclerophyllous shrubs and small trees. Similar communities thrive today in areas where there is summer rainfall like that during the Neogene which then typified the present areas of mediterranean climate.

Chaparral and macchia spread primarily in response to late Pliocene and Quaternary orogenic events which created steep mountain slopes that favored raging fires during the dry season, followed by erosion, soil impoverishment, and the temporary displacement of woodland by shrubland.

The post-glacial Xerothermic period (8,000-4,000 B.P.) greatly favored shrubs in areas previously covered with sclerophyllous woodland, and accounts for some chaparral expansion. However it has been man's destructive activities that resulted in the replacement of sclerophyllous woodland by chaparral today, though most of these are seral potentially.

The present mediterranean climates are therefore not causally related to the origin of chaparral taxa as adaptive types for the taxa are much older than the climate—a condition to which they were preadapted. Functionally, woody taxa adapted simply by shifting germination and seedling establishment into earlier months as the dry season gradually lengthened during the later post-glacial ages.

The history of sclerophyllous vegetation throws light on three biogeographic problems. First, the links between sclerophyllous taxa in North America and southern Eurasia are more numerous when considered in terms of taxa in areas outside of summer-dry mediterranean climates, and when it is recalled that they were more numerous and widespread in the Tertiary. The trans-Atlantic links resulted from east-west migration which was favored by a narrower ocean that had numerous islands, by a more easterly-trending Appalachian axis with scattered dry sites (granite-gneiss domes, shale barrens) , and by a more continuous broadly-zoned subhumid climatic belt. There are hints of sclerophyllous links in the foothill belt of the Appalachians during Paleogene and Neogene times. Dry edaphic sites in that area still support Madrean taxa that have been there a long time, as judged from their uniqueness. Others presumably were eliminated by the trend to lower temperature, and by the counterclockwise rotation of the continent which eliminated many favorable warm exposures.

Linking sclerophyllous taxa were not abundant because barriers were operative —climate to the north (colder, wetter, longer photoperiod) and water to the east—west—yet they were far more numerous than at present. The Madrean-Tethyan floras are largely distinct today, each region having its unique, autochthonous taxa. As with the sclerophylls, dissimilarity of the herbaceous and perennial floras also implies long separation: if the same genera occur in each region the taxa usually belong to different tribes or sections. This applies also to the temperate Arcto-Tertiary taxa that bordered the Madrean-Tethyan province to the north. Some of them survived in modified form in the Madrean-Tethyan ecotone by shifting functionally to the local, moister and cooler sites within the broadleaved sclerophyll zone.

Second, as Madro-Tertiary woodland spread with expanding dry climate over southwestern North America, temperate rainforests of Mexico-Central America were isolated from those in the western and eastern United States by the middle Oligocene, or possibly earlier. Decreasing summer rain and increasing cold eliminated rainforest taxa in the west, whereas in the East colder winters decimated frost-sensitive evergreen dicots, creating a dominantly deciduous-hardwood forest there. The deciduous hardwoods in the Mexican cloud-forests are therefore relict: they did not migrate there from the Appalachians to enter a forest previously without them, as others have maintained. Elimination of evergreen dicots left a dominantly deciduous hardwood forest in the eastern United States. It finds no counterpart in areas of similar warmth in China-Japan because cold did not so greatly affect that region where forests of similar warmth (ET) have more numerous evergreen dicots.

Third, a rich laurophyllous forest ancestral to the present Canarian laurel forest covered much of North Africa and the south shore of Europe into the Middle Miocene. It probably invaded the eastern Canaries in the early Miocene (20 m.y.) and then the western high volcanic islands as they were built up in the middle Miocene (15-16 m.y.) . This laurophyllous forest was progressively impoverished as summer rain decreased and as winter temperatures were lowered later in the Cenozoic. It still has several alliances with relatives in the eastern tropics that have survived in this mild fog-belt climate. Thus, taxa of the Canarian laurel forest element in the Late Miocene and Pliocene floras of southern Europe, which were in ecotone with the rich Arcto-Tertiary deciduous hardwood-conifer forest, did not migrate 800 + miles (~ 1300 km) south to give rise to the present Canarian laurel forest, as generally maintained.

LITERATURE CITED

ABDEL-MONEM, A., N. D. WATKINS & P. W. GAST. 1971. Potassium-argon ages, volcanic stratigraphy and geomagnetic polarity history of the Canary Islands: Lazarote, Fuerteventura, Gran Canaria, and La Gomera. Amer. Jour. Sci. 271: 490-521.

——— 972. Potassium-argon ages, volcanic stratigraphy and geomagnetic polarity history of the Canary Islands: Tenerife, La Palma, and Hierro. Amer. Jour. Sci. 272: 805-825.

ALT, D. 1974. Arid climatic control of Miocene sedimentation and origin of modern drainage, southeastern United States. Pp. 21-29, in R. Q. Oaks, Jr. & J. R. duBar (editors), Post-Miocene Stratigraphy Central and Southern Atlantic Coastal Plain. Utah State Univ. Press, Logan, Utah.

ANDREANSZKY, G. 1962a. Das Trockenelement in der Alttertiären Flora Mitteleuropas auf grund Paläobotanischer Forschungen in Ungarn. Vegetatio 11: 95-111.

______. 1962b. Das Trockenelement in der Jungertertii ren Flora Mitteleuropas. Vegetatio 11: 155-172.

ANDREWS, E. C. 1913. The development of the natural order Myrtaceae. Proc. Linn. Soc. New South Wales 38: 529-568.

______. 1914. The development and distribution of the natural order Leguminosae. Jour. Roy. Soc. New South Wales 48: 333-407.

______. 1916. The geological history of the Australian flowering plants. Amer. Jour. Sci. 249: 171-232.

ARAMBOURG, C., J. ARENES & G. DEPAPE. 1953. Contribution a l'étude des floras fossiles Quarternaries de l'Afrique du Nord. Arch. Mus. Nat. Hist., ser. 7, T 2: 1-85.

ARENES, J. & G. DEPAPE. 1956. La flore burdigalienne des isles Baleares (Majorque). Rev. Gen. Bot. 63: 347-390.

ASCHMANN, H. 1973a. Distribution and peculiarity of Mediterranean ecosystems. Pp. 11-19, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

1973b. Man's impact on the several regions with Mediterranean climates. Pp. 363-371, in F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

AUBRÉVILLE, A. 1970. La flore tropicale Tertiaire du Sahara. Adansonia, n.s. 10: 9-14. [See bibliography.]

AXELROD, D. I. 1937. A Pliocene flora from the Mount Eden beds, southern California. Publ. Carnegie Inst. Wash. 476: 125-183.

______. 1939. A Miocene flora from the western border of the Mojave Desert. Publ. Carnegie Inst. Wash. 516: 1-128.

1950. The evolution of desert vegetation in western North America. Publ. Carnegie Inst. Wash. 590: 215-306.

1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24: 433-509.

______ 1960. The evolution of flowering plants. Pp. 227-305, *in* S. Tax, (editor), Evolution after Darwin. Vol. 1, The Evolution of Life. Univ. Chicago Press, Chicago, Illinois.

1964. The Miocene Trapper Creek flora of southern Idaho. Univ. Calif. Publ. Geol. Sci. 51: 1-180.

______. 1965. A method for determining the altitudes of Tertiary floras. Paleobotanist 14: 144-171.

1966. The Pleistocene Soboba flora of southern California. Univ. Calif. Publ. Geol. Sci. 60: 1-108.

______. 1967a. Geologic history of the Californian insular flora. Pp. 267-315, in R. N. Philbrick (editor), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Bot. Garden, Santa Barbara, Calif.

______. 1967b. Quaternary extinctions of large mammals. Univ. Calif. Publ. Geol. Sci. 74: 1-42.

______. 1967c. Drought, diastrophism and quantum evolution. Evolution 21: 201-209.

______ 1968. Tertiary floras and topographic history of the Snake River basin, Idaho. Bull. Geol. Soc. Amer. 79: 713-734.

______. 1972. Edaphic aridity as a factor in angiosperm evolution. Amer. Naturalist 106: 311-320.

______ 1973. History of the Mediterranean ecosystem in California. Pp. 225-277, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

1974. Plate tectonics in relation to the history of the angiosperm vegetation in India. Birbal Sahni Inst. Paleobot. Spec. Publ. 1: 5-18.

______ & H. P. BAILEY. 1968. Cretaceous dinosaur extinction. Evolution 22: 595-611.

______ & P. H. RAVEN. 1972. Evolutionary biogeography viewed from plate tectonic theory. Pp. 218-236, *in* J. H. Behnke (editor), Challenging Biological Problems. Directions toward their Solution. Oxford Univ. Press, New York.

BAILEY, H. P. 1960. A method of determining the warmth and temperateness of climate. Geogr. Ann. 42: 1-16.

———. 1964. Toward a unified concept of the temperate climate. Geogr. Rev. (New York) 54: 516-545.

1966. The mean annual range and standard deviation as measures of dispersion of temperature around the annual mean. Geogr. Ann. 48A: 183-194.

———. 1972. On the recognition of climatic similarities in global perspective. Origin and Structure of Ecosystems. IRP IPB, Techn. Rep. 73-4: 1-12.

BANDY, O. L. & J. C. INGLE, JR. 1970. Neogene planktonic events and radiometric scale, California. Special Pap. Geol. Soc. Amer. 124: 131-172.

BANERJEE, D. 1968. Siwalik microflora from Punjab (India). Rev. Paleobot. Palynol. 6: 171-176.

BARBERI, F., L. CIVETTA, P. GASPARINI, F. INNOCENTI, R. SCANDONE & L. VILLARI. 1974. Evolution of a section of the Africa-Europe plate boundary: Paleomagnetic and volcanological evidence from Sicily. Earth & Planetary Sci. Lett. 22: 123-132.

BATALLER, J. R. & G. DEPAPE. 1950. Flore Oligocene de Cervera, Catalogne. Anales de la Escuela de Peritos Agric. y de Especialidades Agropecuaries y de los Serv. Tecn. de Agric. 9: 1-60.

BEADLE, N. C. W. 1966. Soil phosphate and its role in moulding segments of the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47: 992-1007.

BECKER, H. F. 1961. Oligocene plants from the upper Ruby River Basin, southwestern Montana. Mem. Geol. Soc. Amer. 82: 1-127.

——— 1969. Fossil plants of the Tertiary Beaverhead basins in southwestern Montana. Palaeontographica, Abt. B, Paläophytol. 127: 1-142.

BERRY, E. W. 1909. A Miocene flora from the Virginia coastal plain. Jour. Geol. 17: 19-30.

———. 1914. Fruits of a date palm in the Tertiary deposits of eastern Texas. Amer. Jour. Sci. 187: 403-406.

. 1916a. The physical conditions indicated by the flora of the Calvert Formation. U. S. Geol. Surv. Prof. Pap. 98-F: 61-73.

———. 1916b. The flora of the Catahoula sandstone. U. S. Geol. Surv. Prof. Pap. 98-M: 227-251.

———. 1924. The middle and upper Eocene floras of southeastern North America. U. S. Geol. Surv. Prof. Pap. 92: 1-206.

——— 1926. Pleistocene plants from North Carolina. U. S. Geol. Surv. Prof. Pap. 140-C: 97-119.

BILLINGS, W. D. & L. E. ANDERSON. 1966. Some microclimatic characteristics of habitats of endemic and disjunct bryophytes in the southern Blue Ridge. Bryologist 69: 96-95.

BOULAY, N. 1890. Flore pliocene des environs de Theziers. Mém. Acad. Vaucluse 8: 1-70.

BRADLEY, W. H. 1948. Limnology and the Eocene lakes of the Rocky Mountain region. Bull. Geol. Soc. Amer. 59: 635-648.

———. 1964. Geology of the Green River formation and associated Eocene rocks in southwestern Wyoming and adjacent parts of Colorado and Utah. U. S. Geol. Surv. Prof. Pap. 496-A: 1-86.

BRAMWELL, D. 1972. Endemism in the flora of the Canary Islands. Pp. 141-159, *in* D. H. Valentine (editor), Taxonomy, Phytogeography and Evolution. Academic Press, New York.

BRAUN, E. L. 1950. Deciduous Forests of Eastern North America. The Blakeston Co., Toronto and Philadelphia. 596 pp.

BRIDEN, J. C., G. E. DREWRY & A. G. SMITH. 1974. Phanerozoic equal-area world maps. Jour. Geol. 82: 555-574.

BROWN, R. W. 1944. Temperate species in the Eocene flora of the southeastern United States. Jour. Wash. Acad. Sci. 34: 349-351.

BUDANTSEV, L. Y. 1957. The Eocene flora of the Pavlodar Priirtyshie. Pp. 177-198, in Collection of Works in Memory of A. N. Krystofovich. Moscow and Leningrad. [In Russian.]

BURBIDGE, N. T. 1960. The phytogeography of the Australian region. Austral. Jour. Bot. 8: 75-212.

CAIN, S. A. 1944. Foundations of Plant Geography. Harper & Bros., New York. 556 pp.

CEBALLOS, L. & F. ORTUNO. 1951. Vegetation y Flora Forestal de Las Canarias Occidentales. Inst. Forest Invest. Exp., Madrid. 465 pp.

CHANEY, R. W. 1936. Plant distribution as a guide to age determination. Jour. Wash. Acad. Sci. 26: 313-324.

———. 1938. Paleoecological interpretations of Cenozoic plants in western North America. Bot. Rev. 4: 371-396.

———. 1947. Tertiary centers and migration routes. Ecol. Monogr. 17: 139-148.

——— & M. K. ELIAS. 1936. Late Tertiary floras from the High Plains. Publ. Carnegie Inst. Wash. 476: 1-46.

——— & D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau. Publ. Carnegie Inst. Wash. 617: 1-237.

CHATTERJEE, D. 1947. Influence of east Mediterranean region flora on that of India. Sci. & Cult. 13(1) : 9-11.

CHELIDZE, L. T. 1970. Flora tufogennykh otlozheniy Vale. [The fossil flora of the tufogenic rocks of Vale (Caucasus, southern Georgia)1. Akad. Nauk Gruz. SSR, Inst. Paleobiol. 107 pp.

CLEMENTS, F. E. 1916. Plant Succession: an analysis of the development of vegetation. Publ. Carnegie Inst. Wash. 242: 1-512.

——— 1936. The origin of the desert climax and climate. Pp. 87-140, in T. H. Goodspeed (editor), Essays in Geobotany in Honor of William Albert Setchell. Univ. Calif. Press.

COOPER, A. W. & J. W. HARDIN. 1970. Floristics and vegetation of the gorges of the southern Blue Ridge escarpment. *In* P. C. Holt (editor), The Distributional History of the Biota of the Southern Appalachians. Part II: Flora. Virginia Polytechn. Inst. State Univ., Res. Div. Monogr. 2: 291-330.

CROWELL, J. C. 1962. Displacement along the San Andreas fault, California. Special Pap. Geol. Soc. Amer. 71: 1-61.

CRITCHFIELD, W. B. & E. L. LITTLE, JR. 1966. Geographic distribution of the pines of the world. U. S. D. A. Forest Serv. Misc. Publ. 991. 97 pp.

DARBY, H. C. 1956. The clearing of the woodland in Europe. Pp. 183-216, in W. L. Thomas, Jr. (editor), Man's Role in Changing the Face of the Earth. Univ. Chicago Press, Chicago, Illinois.

DASH, B. P. & E. BOSSHARD. 1969. Seismic and gravity investigations around the western Canary Islands. Earth & Planetary Sci. Lett. 7: 169-177.

DE CSERNA, Z. 1960. Orogenesis in time and space in Mexico. Geol. Rundschau 50: 595-605.

DEEVEY, E. S., JR. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Amer. 60: 1315-1416.

DEPAPE, G. 1922. Recherches sur la flore Pliocene de la Vallee du Rhone. Ann. Sci. Nat. Bot. Ser. 10.4: 73-265.

——— 1928. Le monde des plantes a l'apparition de l'homme en Europe occidentale flores récentes en France, des Pays-bas, d'Angleterre. Ann. Soc. Sci. Bnixelles, Ser. B. 48: 39-101.

& D. BRICE. 1965. La flore Oligocene de Cervera, Spain. Extr. Ann. Soc. Geol. Nord Lille 85: 111-117.

DIETZ, R. S. & J. C. HOLDEN. 1970. Reconstruction of Pangaea: Breakup and dispersion of continents, Permian to Present. Jour. Geophys. Res. 75: 4939-4956.

——— & W. P. SPROLL. 1970. East Canary Islands as a microcontinent within the Africa-North America continental drift fit. Nature 226: 1043-1045.

DILCHER, D. L. 1973. A paleoclimatic interpretation of the Eocene floras of southeastern North America. Pp. 39-59, in A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Publ. Co., Amsterdam and New York.

DODGE, J. M. 1975. Vegetation changes associated with fire history in San Diego County, California. Ph.D. thesis, Univ. California, Riverside.

DORF, E. 1930. Pliocene floras of California. Publ. Carnegie Inst. Wash. 412: 1-122.

DRESSLER, R. L. 1954. Some floristic relationships between Mexico and the United States. Rhodora 56: 81-96.

EHLIG, P. L. & EHLERT, K. W. 1972. Offset of Miocene Mint Canyon Formation from volcanic sources along San Andreas Fault, southern California. Geol. Soc. Amer., Abstr. with Programs 4: 154.

EMBERGER, L. 1930. La vegetation de la region Mediterraneenne. Rev. Gen. Bot. 42: 641-662,705-721.

——— 1933. Nouvelle contribution a l'etude de la classification des groupements vegetataux. Rev. Gen. Bot. 45: 473-486.

ENGLER, A. 1904. Ober floristische Verwandtschaft zwischen dem tropischen Afrika and

Amerika, sowie über die Annahme eines versunkenen brasilianisch-äthiopischen Kontinents. Sitzungsber. Konigl. Preuss. Akad. Wiss. Berlin 9: 180-231.

———. 1914. Ober Herkunft, Alter and Verbreitung extremer xerothermer Pflanzen. Sitzungsber. Königl. Preuss. Akad. Wiss. Berlin 20: 564-621.

EsTEs, R. 1963. Early Miocene salamanders and lizards from Florida. Quart. Jour. Florida Acad. Sci. 26: 234-256.

GANSSER, A. 1964. Geology of the Himalayas. Interscience Publ., New York and London. 289 pp.

GIBSON, T. G. 1967. Stratigraphy and paleoenvironment of the phosphatic Miocene strata of North Carolina. Bull. Geol. Soc. Amer. 78: 631-650.

GOIN, C. J. 1958. Comments upon the origin of the herpetofauna of Florida. Quart. Jour. Florida Acad. Sci. 21: 61-70.

GRAHAM, A. 1972. Some aspects of Tertiary vegetational history about the Caribean basin. Mem. Symp. I Congr. Latinoamer. Bot., pp. 97-117.

1973. History of the arborescent temperate element in the northern Latin American biota. Pp. 301-314, in A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Publ. Co., Amsterdam and New York.

GRANGEON, P. 1958. Contribution a l'etude de la flore Stampienne de Lornagne. Rev. Sci. Nat. Auvergne 24: 41-100.

GRAY, J. 1960a. Late Tertiary microflora from the Basin and Range province, Arizona. Science 132: 147-148.

———. 1960b. Temperate pollen genera in the Eocene (Clairborne) flora, Alabama. Science 132: 808-810.

GREEN, R. 1961. Paleoclimatic significance of evaporites. Chap. 4, in A. E. M. Narin (editor), Descriptive Palaeoclimatology. Interscience Publ., New York.

GUZMAN, E. J. & Z. DE CSERNA. 1963. Tectonic history of Mexico. Mem. Amer. Assoc. Petrol. Geol. 2: 113-129.

HAMILTON, W. 1968. Cenozoic climatic change and its cause. Meteorol. Monogr. 8: 128-133.

HANES, T. L. 1965. Ecological studies on two closely related chaparral shrubs in southern California. Ecol. Monogr. 35: 213-235.

——— 1971. Succession after fire in the chaparral of southern California. Ecol. Monogr. 41: 27-52.

HARRIS, D. R. & C. VITA-FINZI. 1968. Kokkinopilos-a Greek badland. Geogr. Jour. (London) 134: 537-546.

HERNANDEZ, E., H. CRUM, W. B. Fox & A. J. SHARP. 1951. A unique vegetational area in Tamaulipas. Torrey Bot. Club Bull. 78: 458-463.

HIBBARD, C. W. 1960. An interpretation of Pliocene and Pleistocene climates in North America. Annual Rep. Michigan Acad. Sci. 62: 5-30.

limos, E. S. & C. VITA-FINZI. 1966. The climate, environment and industries of Stone Age Greece: Pt. II. Proc. Prehist. Soc., n. s. 32: 1-29.

HOLLICK, A. 1904. Systematic palaeontology: Plantae Angiospermae. Maryland Geol. Surv., Miocene: 483-486.

HOOKER, J. D. & J. BALL. 1878. Journal of a Tour to Morocco and the Great Atlas. Macmillan and Co., London. 490 pp.

HORTON, J. S. & C. J. KRAEBEL. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology 36: 244-262.

IMLAY, R. W. 1944. Cretaceous formations of central America and Mexico. Bull. Amer. Assoc. Petrol. Geol. 28: 1077-1195.

JEPSON, W. L. 1925. A Manual of the Flowering Plants of California. Univ. Calif. Press, Berkeley and Los Angeles. Sixth printing. 1238 pp.

JOHNSON, L. A. S. & B. G. BRIGGS. 1975. On the Proteaceae-the evolution and classification of a southern family. Bot. Jour. Linn. Soc.: in press.

KAMES, W. H., M. SAADI, E. EHRLICH & A. ALEM. 1973. Moroccan crustal response to continental drift. Science 180: 950-952.

KEENER, C. S. 1970. The natural history of the mid-Appalachian shale barren flora. *In* P. C. Holt (editor), The Distributional History of the Biota of the Southern Appalachians. Pt. II: Flora. Virginia Polytechn. Inst. State Univ., Res. Div. Monogr. 2: 215-248.

KITAMURA, S. (editor). 1964. Plants of West Pakistan and Afghanistan. Results Kyoto Univ. Sci. Exped. Karakoram & Hindukush, 1955. Vol. 3: 1-283.

KOENIGUER, J. C. 1966. Sur un bois fossile du continental terminal en Tinrhert (Sahara central) : *Leguminoxylon schenkii.* Congr. Nat. Soc. Savantes (90th). Sect. Sci., C. R. 2: 235-245.

______. 1967a. Sur un bois fossile de l'oligocène de Dor el Abd (Syrte) : *Bridelioxylon Arnouldii.* Congr. Nat. Soc. Savantes (91st), Sect. Sci., C. R. 3: 153-163.

. 1967b. Sur la presence de *Dombeyoxylon Owenii* dans le territorie de la Syrte. Congr. Nat. Soc. Savantes (91st), Sci. Sect., C. R. 3: 164-168.

______ 1967c. Sur la presence *Sapindoxylon* sp. dans le Tertiare du nord du Tibetsi. Congr. Nat. Soc. Savantes (91st), Sect. Sci., C. R. 3: 169-172.

______. 1967d. Sur tine Meliacee fossile nouvelle du tertiare de l'Algérie (Tinrhert) : *Lovoaxylon princeps.* Congr. Nat. Soc. Savantes (91st), Sect. Sci., C. R. 3: 178-180.

______ 1967e. Etude paleoxylologique du Rio de Oro: *Sapindoxylon Almelai, Caesalpinioxylon aff. Quirogae* Schenk, *Dombeyoxylon Oweni* (Carr.) Krause!. Notas Comun. Inst. Geol. Espana 96: 39-66.

& P. LOUVET. 1968. Sur la presence d'une Meliacee dans la Tertiare du Fezzan oriental: *Entandrophragmoxylon boureaui* Louvet. Paleobotanist 17: 33-35.

KOLAKOVSKII, A. A. 1964. Pliotsenovaya flora Kodora [A Pliocene flora of the Kodor River]. Akad. Nauk Gruz. SSR, Sukum. Bot. Sad. Monogr. 1: 1-209.

KOROVIN, E. 1932. Novyi tretichnyi tip semeistva Proteaceae iz Srednei Azii. Bot. Zurn. SSSR 17: 605-622. [Summary in Biol. Abstr. 11: 1018. 1937.]

KOZARY, M. T., J. C. DUNLAP & W. E. HUMPHREY. 1968. Incidence of salt deposits in geologic time. Special Pap. Geol. Soc. Amer. 88: 43-57.

KRYSTOFOVICH, A. N. 1929. Evolution of the Tertiary flora in Asia. New Phytol. 28: 303-312.

______. 1935. A final link between the Tertiary floras of Asia and Europe. New Phytol. 24: 339-344.

______. 1954. The origin of the xerophyllous plant formations in the light of paleobotany. In The Deserts of the USSR and Their Utilization 2: 583-569. Moscow and Leningrad. [In Russian.]

KUTUZKINA, E. F. 1974. Some representatives of the Mediterranean flora in the Upper Sarmat of the Krasnodar district. Bot. Zhurn. Akad. Nauk SSSR. 59: 251-260. [In Russian.]

LAKHANPAL, R. N. 1970. Tertiary floras of India and their bearing on the historical geology of the region. Taxon 19: 675-694.

LEMS, K. 1960. Floristic botany of the Canary Islands. Sarracenia 5: 1-94.

LEOPOLD, E. S. & H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pp. 147-200, *in* A. Graham (editor), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publ. Co., Amsterdam.

LESQUEREUX, L. 1883. The Cretaceous and Tertiary Floras. U. S. Geol. Surv. Territories vol. 8. 283 pp., 59 *pls.*

LEVYNS, M. R. 1964. Migration and origin of the Cape Flora. Trans. Roy. Soc. South Africa 37: 85-107.

LITTLE, E. L., JR. & W. B. CRITCHFIELD. 1969. Subsdivisions of the genus *Finns* (Pines) . U. S. D. A. Forest Serv. Misc. Publ. 1144. 51 pp.

LOTZE, F. 1964. The distribution of evaporites in space and time. Pp. 491-509, in A. E. M. Nairn (editor), Problems in Palaeoclimatology. John Wiley and Sons, New York and London.

LOUVET, P. 1963. Sur un Acajou fossile du Tertiare d'Algérie. *Entandrophragmoxylon Boureaui.* Congr. Nat. Soc. Savantes (88th), Sect. Sci., C. R. 2: 493-504.

______. 1964. Sur une Combretacee fossile nouvelle du Tinrhert (Algerie) : *Anogeissus Bussoni.* Congr. Nat. Soc. Savantes (89th), Sect. Sci., C. R. 1: 281-301,

______. 1965. Sur une Legumineuse fossile nouvelle du Tinrhert: *Afzelioxylon Kiliani.* Congr. Nat. Soc. Savantes (90th), Sect. Sci., C. R. 2: 317-332.

______. 1966. Sue une Meliancee fossile nouvelle du Tinrhert: *Lovoaxylon princeps.* Congr. Nat. Soc. Savantes (91st), Sect. Sci., C. R. 3: 189-197.

______ 1967. Sur une Combretacee fossile nouvelle du Tinrhet. *Combretoxylon euphorbioides.* Congr. Nat. Soc. Savantes (92nd), Sect. Sci., C. R. 3: 39-50.

______. 1968. Sur deux Meliacees fossiles nouvelles du Tinrhert: *Entandrophragmoxylon Normandii, Entandrophragmoxylon mkrattense.* Comité Tray. Hist. Sci. Mém. Sect. Sci. 2 Palaeobot.: 92-111.

______. 1972. Sur deux legumineuses fossiles du Tinrhert (Algerie). Congr. Nat. Soc. Savantes (93rd), Sect. Sci., C. R. 3: 23-37.

LOVELESS, A. R. 1961. A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. Ann. Bot. (London), n. s. 25: 168-184.

——— 1962. Further evidence to support a nutritional interpretation of sclerophylly. Ann. Bot. (London), n. s. 26: 551-561.

Lukose, N. G. 1969. Microfossils from the Middle Siwalik of Bihar, India. Jour. Palynol. 4: 107-112.

MacGinitie, H. D. 1941. A middle Eocene flora from the central Sierra Nevada. Publ. Carnegie Inst. Wash. 534: 1-178.

———. 1953. Fossil plants from the Florissant beds, Colorado. Publ. Carnegie Inst. Wash. 599: 1-198.

———. 1962. The Kilgore flora: A late Miocene flora from northern Nebraska. Univ. Calif. Publ. Geol. Sci. 35: 67-158.

———. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. Univ. Calif. Publ. Geol. Sci. 83: 1-202.

McVaugh, R. 1943. The vegetation of the granitic flat-rocks of the southeastern United States. Ecol. Monogr. 13: 119-166.

Makulbekov, N. 1972. The Eocene flora of northern Kazakhstan. (Œotsenovaya flora severnogo Kazakhstana). Alma Ata. 178 pp.

Mani, M. S. 1974. Ecology and Biogeography in India. W. Junk, The Hague. 773 pp.

Martin, P. S. & B. E. Harrell. 1957. The Pleistocene history of the temperate biotas in Mexico and eastern United States. Ecology 38: 468-480.

Massalongo, A. & G. Scarabelli. 1859. Studii sulla Flora Fossile e Geologia Stratigrafica del Senigalliese. Imola. 504 pp.

Meher-Homji, V. M. 1973. A phytoclimatic approach to the problem of mediterraneity in the Indo-Pakistan subcontinent. Feddes Repert. 83: 757-788.

Meusel, H. von. 1989. Beziehungen in der Florendifferenzierung von Eurasien and Nordamerika. Flora 158: 537-564.

———. 1971. Mediterranean elements in the flora and vegetation of the West Himalayas. Pp. 53-72, in P. H. Davis, P. C. Harper & I. C. Hedge (editors), Plant Life of South-west Asia. Bot. Soc., Edinburgh.

——— & R. Schubert. 1971. Beitrge zur Pflanzengeographie des Westhimalajs. I. Teil: Die Arealtypen. II. Teil: Die Waldgesellschaften. III. Teil: Die pflanzengeographische Stellung and Gliederung des Westhimalajas. Flora 160: 137-194,373-432,573-606.

Miranda, F. & A. J. Sharp. 1950. Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology 31: 313-333.

Monk, C. D. 1965. Southern mixed hardwood forests of northcentral Florida. Ecol. Monogr. 35: 335-353.

Mooney, H. A. & E. L. Dunn. 1970. Convergent evolution of mediterranean climate evergreen sclerophyll shrubs. Evolution 24: 292-303.

——— & A. T. Harrison. 1972. The vegetational gradient on the lower slopes of the Sierra San Pedro Martir in northwest Baja California. Madroño 21: 439-445.

——— & D. J. Parsons. 1973. Structure and function of the California chaparral-an example from San Dimas. Pp. 82-112, in F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

S. L. Gulmon, D. J. Parsons & A. T. Harrison. 1974. Morphological changes within the chaparral vegetation type as related to elevational gradients. Madroño 22: 281-285.

Moore, H. E., Jr. 1973. Palms in the tropical forest ecosystems of Africa and South America. Pp. 63-88, in B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D. C.

Mortenson, R. H. 1973. Ecologic variation in the leaf anatomy of selected species of *Cercocarpus*. Aliso 8: 19-48.

Muller, C. H. 1939. Relations of the vegetation and climatic types in Nuevo Leon, Mexico. Amer. Midl. Naturalist 21: 687-729.

Naveh, Z. & J. Dan. 1973. The human degradation of Mediterranean landscape in Israel. Pp. 373-390, in F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

Noss, M. A. 1963. Experimental studies on species relationships in *Ceanothus*. Publ. Carnegie Inst. Wash. 623: 1-94.

Olsen, S. J. 1962. The Thomas Farm Quarry. Quart. Jour. Florida Acad. Sci. 25: 142-146.

PHILLIPS, J. D. & D. FORSYTH. 1972. Plate tectonics, paleomagnetism, and the opening of the Atlantic. Bull. Geol. Soc. Amer. 83: 1579-1600.

PRAKASH, U. 1972. Palaeoenvironmental analysis of Indian Tertiary floras. Geophytology 2: 178-205.

PURI, G. S. 1947. Fossil plants and the Himalayan uplift. Jour. Indian Bot. Soc., M.O. P. Iyengar Commemoration Vol. 1946: 167-184.

——— 1960. Indian Forest Ecology. 2 Vols. Oxford Book and Stationary Co., New Delhi and Calcutta. 710 pp.

PURI, H. S. & R. O. VERNON. 1964. Summary of the geology of Florida and a guidebook to classic exposures. Florida Geol. Surv. Spec. Publ. 5: 1-312.

QUARTERMAN, E. & C. KEEVER. 1962. Southern mixed hardwood forest: climax in the southeastern Coastal Plain, U. S. A. Ecol. Monogr. 32: 167-185.

RAVEN, P. H. 1971. The relationship between "mediterranean" floras. Pp. 119-134, in P. H. Davis, P. C. Harper & I. C. Hedge (editors), Plant Life of South-west Asia. Bot. Soc., Edinburgh.

——— 1973. The evolution of Mediterranean floras. Pp. 213-224, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems-Origin and Structure. Springer Verlag, Berlin.

RONA, P. A. & A. J. NALWALK. 1970. Post-early Pliocene unconformity on Fuerteventura, Canary Islands. Bull. Geol. Soc. Amer. 81: 2117-2122.

RZEDOWSKI, J. 1966. Vegetación del estado de San Luis Potosi. Contr. Inst. Invest. Zonas Deserticas, Univ. Autonoma de San Luis Potosi 20: 1-291.

SAMPSON, A. W. 1944. Plant succession on burned chaparral lands in northern California. Univ. Calif. Agric. Exp. Sta. Bull. 685: 1-144.

SAUER, E. G. F. & P. ROTHE. 1972. Ratite eggshells from Lanzarote, Canary Islands. Science 176: 43-45.

SAUNDERS, W. B., R. H. MAPES, F. M. CARPENTER & W. C. ELSIK. 1974. Fossiliferous amber from the Eocene (Clairborne) of the Gulf Coastal Plain. Bull. Geol. Soc. Amer. 85: 979-984.

SCHMINCKE, H. U. 1968. Pliozäne, subtropische Vegetation auf Gran Canaria. Naturwissenschaften 55: 185-186.

SCHUCHERT, C. 1935. Historical Geology of the Antillean-Caribbean Region. John Wiley and Sons, New York. 811 pp.

SEDDON, G. 1974. Xerophytes, xeromorphs and sclerophylls: the history of some concepts in ecology. Biol. Jour. Linn. Soc. 6: 65-87.

SHARP, A. J. 1953. Notes on the flora of Mexico: world distribution of the woody dicotyledonous families and the origin of modern vegetation. Jour. Ecol. 41: 376-380.

SPECHT, R. L. 1969. A comparison of the sclerophyllous vegetation characteristics of mediterranean type climates in France, California and southern Australia. I. Structure, morphology and succession. Austral. Jour. Bot. 17: 277-292.

——— & P. RAYSON. 1957. Dark Island Heath (Ninety-Mile Plain, South Australia) . I. Definition of the ecosystem. Austral. Jour. Bot. 5: 52-85.

STEBBINS, G. L. 1952. Aridity as a stimulus to plant evolution. Amer. Naturalist 86: 33-44.

——— & A. DAY. 1967. Cytogenetic evidence for long continued stability in the genus *Plantago*. Evolution 21: 449-528.

STRAKHOV, N. M. 1960. Principles of Lithogenesis. 3 Vols. Transl. by J. P. Fitzsimmons. 1967. Oliver and Boyd, Edinburgh and London.

SUNDING, P. 1970. Elements in the flora of the Canary Islands and theories on the origin of their flora. Blyttia 28: 229-259.

SWEENEY, J. A. 1956. Responses of vegetation to fire: a study of herbaceous vegetation following chaparral fires. Univ. Calif. Publ. Bot. 28: 143-250.

SZAFER, W. 1946. The Pliocene flora of Kroscienko in Poland. Polska Akad. Umiejetn. Rozpr. Wydz. Mat: Przyr., Dział B, Nauki Biol. 72: 1-162.

TAKHTAJAN, A. 1958. The taxonomic study of the Tertiary fan palms of the USSR. Bot. Zuhrn. Akad. Nauk SSSR 43: 1661-1674.

———. 1969. Flowering Plants, Origin and Dispersal. Trans!. by C. Jeffrey. Smithsonian Inst. Press, Washington, D. C. 310 pp.

TAYLOR, D. W. 1960. Late Cenzoic molluscan faunas from the High Plains. U. S. Geol. Surv. Prof. Pap. 337: 1-94.

TURRILL, W. B. 1929. The Plant Life of the Balkan Peninsula: A Phytogeographical Study. Oxford Press, London. 490 pp.

UZNADZE-DGEBUADZE, M. D. 1948. The Eocene flora of the South Ural. Proc. Geol. Inst. Acad. Sci. Georgian SSR, Tbilisi 4: 161-182. [In Russian.]

VAHL, M. & J. HUMLUM. 1949. Vahl's climatic zones and biochores. Acta Jutlandica Aarskrift 21: 1-79.

VASILEVSKAYA, N. D. 1957. The Eocene flora of Badkhyz in Turkmenia. Pp. 103-175, in Collection of Works in Memory of A. N. Krystofovich. Moscow and Leningrad. [In Russian.]

WALLACE, A. R. 1880. Island Life or, The Phenomena and Causes of Insular Faunas and Floras, Including a Revision and Attempted Solution of the Problem of Geological Climates. Macmillan & Co., London. 526 pp.

WALPER, J. L. & C. L. **ROWETT.** 1972. Plate tectonics and the origin of the Caribbean Sea and the Gulf of Mexico. Trans. Gulf Coast Assoc. Geol. Soc. 22: 105-116.

WALTER, H. 1968. The Vegetation der Erde im Oko-physiologischer Betrachtung. II. Die gemässigten and arktischen Zonen. Gustav Fischer Verlag, Jena. 1001 pp.

——— 1973. Vegetation of the Earth in Relation to Climate and Eco-Physiological Conditions. Transl. by J. Weiser. The English Universities Press Ltd., London. 237 pp.

WANG, CHI-WU. 1961. The Forests of China, with a Survey of Grassland and Desert Vegetation. Maria Moors Cabot Foundation Publ. 5: 1-313.

WELLS, P. V. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23: 264-267.

WILLETT, H. C. & F. **SAUNDERS.** 1959. Descriptive Meteorology. Ed. 2. Academic Press, New York. 355 pp.

ZOHARY, M. & G. **ORSHAN.** 1966. An outline of the geobotany of Crete. Israel Jour. Bot. 14 (supplement) : 1-49.