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EVOLUTION OF THE MADRO-TERTIARY GEOFLORA[1]

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> *With increasing knowledge we may in a good measure discriminate between the descendants of the ancient northern flora and those which come from the highlands of the southwest (Asa Gray, 1884).*

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INTRODUCTION

General Statement

By Early Tertiary time[2] the vegetation of North America comprised three geofloras, each of which represents a major vegetation type of wide geographic extent and relative uniformity that maintained its essential identity through time and space. Occupying the southern half of the continent was the broadleafed evergreen Neotropical-Tertiary Geoflora; at the north was the temperate, mixed deciduous Arcto-Tertiary Geoflora; and between them, centered in the southern Rocky Mountains and adjacent Mexico, the sclerophyllous and microphyllous Madro-Tertiary Geoflora was

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[2] A geological time scale is reproduced in the Appendix to this review.

making its initial appearance. Evidence for the existence of these geofloras comes from a reconstruction of individual fossil floras of Tertiary age scattered throughout the region. These floras now number well over 200, and the genera identified in them with reasonable certainty total approximately 800, among which are distributed several thousand species. The conditions under which each fossil flora existed can reasonably be inferred by comparing the fossils with living species (Chaney, 1938; Cain, 1944). Such inferences rest on the basic assumption that the derived entities of the present do not differ substantially in their ecological relations from those of the past. This assumption is reinforced by the fact that assemblages of species still exist which closely resemble the fossil floras. For example, the Goshen flora of Oregon closely parallels the existing Panamanian savanna forest (Chaney and Sanborn, 1933), the Chalk Bluffs of California resembles the subtropical forests of southern Mexico (MacGinitie, 1941), the Mascall of Oregon shows relationship to the modern swamp cypress forest of the central Mississippi basin (Chaney, 1958), and the Tehachapi of southern California is closely related to the oak woodland, chaparral and thorn scrub vegetation of southwestern North America (Axelrod, 1939). Thus the modern environments where fossil floras find close analogues are generally similar to those of the past.

Studies of the numerous fossil floras that comprise each geoflora have provided evidence to substantiate three important facts: *a*) the geofloras are mostly disparate in respect of generic composition and, hence, in adaptive mode; *b*) they show gradual modifications in floristic composition in response to changing Tertiary environment; and *c*) their boundaries have shifted systematically during the period. Being in contact for the long procession of generations that have occurred, it would be surprising if species of some genera in each geoflora had not become adapted to environments within the normal range of each. This is frequently true, yet the boundaries of the geofloras were well defined during time. The persistence of each over wide areas, and the constant distinction between them through time, suggest a long period of evolution prior to the Cenozoic. The floras of Cretaceous age support this view, for they contain many species closely related to phylads in the Tertiary Geofloras.

Although the history of the Arcto-Tertiary and Neotropical- Tertiary Geofloras has received considerable attention (see summary by Chaney, 1947), the record of the Madro-Tertiary Geoflora, which developed in a dry zone between them, has not been assembled in detail. Thus in the following pages are gathered data relative to its evolution, both in time and in space. The Madro-Tertiary Geoflora had already appeared on the drier borders of the North American tropics by the Middle Eocene, and probably occupied much of the southwestern United States and adjacent Mexico by the close of the Oligocene. It extended its range northward and southward, as well as eastward and westward, in response to expanding dry climate in the succeeding Miocene epoch, and it attained an even wider distribution during the Pliocene as semiarid climate continued to spread. The particular time it invaded a given region depended chiefly on climate, as determined by position with respect to latitude, mountains and the ocean. It was largely in the later Pliocene, as environmental diversity became more pronounced over western America, that the geoflora was segregated into a number of derivative communities of more restricted occurrences. Some Madro-Tertiary species survived down to the present in areas of their Tertiary distribution and became adapted to climates which differ from those of the Tertiary. But others that formerly ranged northward into California, Nevada, Utah, Colorado and Oklahoma now find their nearest relatives only in the mild-winter areas to southward, notably in the mountains from southern Arizona to western Texas, and in the structurally continuous ranges farther south which comprise the Sierra Madre of Mexico. It was from these mountains of southwestern North America, where many relicts of the Madro-Tertiary Geoflora now survive, that the term "Madro-" was derived. The name also seems appropriate because this region apparently was the general area of both its early evolution and subsequent radiation.

Historical Review

In his essay on "Forest Geography and Archaeology," Asa Gray (1878) pointed out that the temperate North American flora probably had an holarctic origin, a viewpoint which has been fully substantiated by paleobotanical research. It generally has been forgotten, however, that Gray was also the first to suggest that the semiarid flora of the western United States may have had an origin in northern Mexico (1884). Subsequently, Hemsley (1888), Harshberger (1912), Clements (1920) and others have stated that certain modern plants and plant communities in the western United States originated in northern Mexico. This conclusion was based solely on inferences drawn from the discontinuous occurrence of many identical and closely related species in present woodland, chaparral, desert and thorn scrub vegetation of southwestern North America.

Although such similarities suggest that the flora and vegetation of this broad region comprise an historical unit, the geological history of all groups nonetheless shows that modern distributions can not, in themselves, form a basis for inferring the centers of origins of species or floras (and faunas), or of their routes and times of migration. The present day occurrence of similar and vicarious species of manzanita, juniper, piñon, walnut, live oak, sycamore, cottonwood and madrone, as well as numerous herbs and grasses (see Clements, 1936 for lists) that range from California to western Texas and southward into Mexico tells us only that there is a relation. Whether it is to be traced to *a*) a common center of dispersal from the north with migration southward along the Cascade-Sierra Nevada and Rocky Mountain axes to their present areas; or *b*) to a center or radiation from Mexico, with migration northward into the southwestern United States; or *c*) to an origin in the area of the present desert at a time when desert environment was not in existence, with subsequent restriction to their modern areas owing to gradual desiccation; or *d*) to an origin in southern California, and migration southeastward to Texas and Mexico; or *e*) vice-versa; or *f*) whether it has been in all (or some) of these, as well as other directions, can not be determined from present distributional evidence, as has been suggested (Mason, 1947: 210). Nor can the time or times of migration over the region be inferred from the present ranges of phylads linking distant areas. Decisions in these matters must rest on historical facts. These are the past occurrences of fossil plants closely related to living species, supplemented by geologic data which provide evidence bearing on past land-sea relations, topography and climate during the period of existence of the particular unit (flora or species) under consideration.

During the past two decades many Tertiary floras have been studied that contain species closely similar to those now comprising the oak woodland, conifer woodland, chaparral, plains grassland, thorn scrub and subdesert vegetation of southwestern North America. The fossil floras provide critical data concerning the origin, migration and evolutionary history of these semiarid communities. The first paleontological evidence of these relations was based on the discovery that certain fossil plants in the Pliocene rocks of southern California are closely similar to species living in southern Arizona and regions to the east and south (Axelrod, 1934, 1937). In searching for other fossils of similar affinity in the few Late Tertiary floras then known from western North America, it was found that Pliocene floras in Oklahoma, Texas, Colorado, central Nevada and central California all contained plants related to species characterizing vegetation types now in more southerly areas (Axelrod, 1938). Furthermore, it was shown that species represented in Miocene floras of southern California occurred to northward only in the younger Pliocene floras (Axelrod, 1939). This established the general direction and time of migration of a part of semiarid vegetation in the far West.

This group of fossil plants having close relatives in northern Mexico and bordering areas was first referred to as a North Mexican element (Axelrod, 1938), and then renamed the Sierra Madrean Element (Axelrod, 1939). Several years later, in reviewing all the Late Tertiary floras then known in the far West, the semiarid to subhumid vegetation was designated the Madro-Tertiary Flora (Chaney, 1944a), of which the Sierra Madrean Element is a part. More recently the term Flora has been changed to Geoflora, since the latter is more nearly descriptive of this and other Tertiary vegetation units which have continuity in time and space (Chaney, 1958). A fossil flora from a given locality thus represents but a small sample of a geoflora, and records only a minor stage in its history. From a study of successively younger floras, first in local areas and then in bordering regions, consecutive stages in the evolution of a geoflora may be reconstructed.

Today we can discern only the broader aspects of the historical development of the subhumid to semiarid vegetation types that comprise the Madro-Tertiary Geoflora. Although considerable data relative to its history are assembled in the following pages, many problems remain. Only in years to come, when relatively complete Tertiary cliseres are known from many more areas—and particularly from the southwestern United States and northern Mexico—shall we comprehend its history more clearly.

COMPOSITION

Morphologic Aspects

Madro-Tertiary species have been identified in the following genera, grouped here according to families:

- Pinaceae
  - *Pinus* (nut pines and closed-cone pines)
- Cupressaceae
  - *Cupressus*
  - *Juniperus*
- Gnetaceae
  - *Ephedra*
- Palmaceae
  - *Erythea*
  - *Sabal*
  - *Washingtonia*
- Yuccaceae
  - *Yucca*
- Salicaceae
  - *Populus*
  - *Salix*
- Juglandaceae
  - *Juglans*
- Fagaceae
  - *Quercus* (live oaks, scrub oaks)
- Ulmaceae
  - *Celtis*
- Moraceae
  - *Ficus*
  - *Morus*
- Berberidaceae
  - *Mahonia*
- Papaveraceae
  - *Dendromecon*
- Lauraceae
  - *Persea*
  - *Umbellularia*
- Platanaceae
  - *Platanus*
- Crossosomataceae
  - *Crossosoma*
- Saxifragaceae
  - *Philadelphus*
  - *Ribes*
- Rosaceae
  - *Amelanchier*
  - *Cercocarpus*
  - *Holodiscus*
  - *Lyonothamnus*
  - *Peraphyllum*
  - *Photinia*
  - *Prunus*
    - *Emplectocladus*
    - *Laurocerasus*
  - *Purshia*
  - *Vauquelinia*

Leguminosae
Acacia
Amorpha
Cercis
Conzattia
Eysenhardtia
Leucanea
Lysiloma
Piscidia
Pithecolobium
Prosopis
Robinia

Rutaceae
Castelea
Xanthoxylum

Burseraceae
Bursera

Euphorbiaceae
Acalypha
Euphorbia

Anacardiaceae
Malosma
Pistacia
Pachycormus
Rhus
Schmaltzia
Tapiria

Aquifoliaceae
Ilex

Sapindaceae
Cardiospermum
Dodonaea
Sapindus
Thouinia

Celastraceae
Schaefflera

Hippocastanaceae
Ungnadia

Rhamnaceae
Ceanothus
Condalia
Colubrina
Rhamnus
Zizyphus

Passifloriaceae
Passifloria

Fouquieraceae
Fouquiera

Meliaceae
Trichilia

Sterculiaceae
Fremontia

Garryaceae
Garrya

Oleaceae
Fraxinus
Forestiera

Ericaceae
Arbutus
Arctostaphylos

Clethraceae
Clethra

Rubiaceae
Chiococca
Randia

Verbenaceae
Petrea

Bignoniaceae
Chilopsis

Compositae
Baccharis
Bahia
Brickellia

They chiefly comprise dry subtropic to warm temperate alliances closely related to species living in southwestern North America. These species must have been adapted to an environment quite different from that occupied by the Arcto-Tertiary or Neotropical Tertiary Geofloras because any suite of Madro-Tertiary leaf fossils differs markedly in gross morphology from those representing the other geofloras. Bailey and Sinnott (1915, 1916) have shown that there is a close correlation between leaf morphology and the environment of modern floras: large leaves with entire margins and thick textures are common in humid tropical regions; medium-sized leaves with incised or lobed margins and thinner textures are more frequent in temperate areas; and plants with small leaves are found chiefly in semiarid regions. A number of paleobotanists, including Berry (1916), Chaney and Sanborn (1933), Potbury (1935), MacGinitie (1941) and Dorf (1942), have compared foliar characters of fossil and modern floras on this basis and have demonstrated that leaf morphology gives a good clue to the environment under which the fossil flora was living.

Leaves of most Madro-Tertiary species commonly are one-half to a third as large as those representing species of the Arcto-Tertiary Geoflora, and fully one-third to one-fourth the size of those produced by the commoner plants comprising the Neotropical-Tertiary Geoflora. Whereas the Arcto-Tertiary Geoflora lived under a temperate climate of from 35 to 60 inches annual rainfall with moderate ranges of seasonal temperature, the Neotropical-Tertiary Geoflora survived under a climate having in excess of 80 inches yearly rain and uniformly high yearly temperature. It is apparent that Madro-Tertiary plants reflect an adaptation to low yearly rainfall, high summer temperature and long periods of sunshine, conditions ideal for optimum development of microphylls.

Madro-Tertiary plants indicate that they were adapted to dry climate in still other ways. To judge from their nearest living relatives, the fossil species of *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Dendromecon*, *Fremontia*, *Garrya*, *Quercus* (live and scrub oaks), *Rhamus*, *Rhus* (*Schmaltzia*, *Malosma*) and *Vauquelinia* were drought-resistant sclerophylls, thriving under a climate of limited seasonal rain, hot summers and prolonged sunny periods. In addition, there are small-leafed Madro-Tertiary plants that have medium- to thin-textured leaves, for instance, in *Acacia*, *Bursera*, *Cardiospermum*, *Colubrina*, *Condalia*, *Fouquieria*, *Pithecolobium* and *Randia*. They probably were deciduous, dropping their leaves and leaflets in the season of minimum rain, which coincided chiefly with the cool period during most of their recorded history.

Taxonomic and Adaptive Relations

The bulk of the geoflora is made up of derivative tropical and warm temperate types that seem to have evolved in response tc subhumid environments within or marginal to the tropics. Most of its genera belong to families that are adapted chiefly to tropical or border-tropical to warm temperate environments, such as Palmaceae, Yuccaceae, Fagaceae, Moraceae, Burseraceae, Leguminosae, Rutaceae, Lauraceae, Euphorbiaceae, Anacardiaceae, Sapindaceae, Passifloraceae, Sterculiaceae, Clethraceae, Rubiaceae and Bignoniaceae. These families now find most of their genera in tropical regions, and the geological record shows that they have been primarily tropical groups from the time angiosperms first appeared in the record in abundance, on down to the present day, a span of fully 100 million years. The more primitive living types (species, genera) of these families occur more frequently than not in the moister tropical regions, and those that range into cooler or drier areas marginal to the tropics commonly represent derived types in terms of their general taxonomic and adaptive relations (Bews, 1927). Significantly, not only are many Madro-Tertiary plants related to species of tropical families that are found now chiefly in drier areas bordering the tropics, but these living relatives represent highly specialized types in their respective genera, both in an ecologic and a morphologic sense. Among these are:

Fossil Species	Related Living Species
Palmaceae	
Sabal mohavensis	*S. uresana-mexicana*
Moraceae	
Ficus edenensis	*F. cotinifolia*
Ficus sp.	*F. palmeri*
Morus symmetrica	*M. microphylla*

Fossil Species	Related Living Species
Lauraceae	
Persea coalingensis	*P. podadenia*
Leguminosae	
Acacia n. sp.	*A. californica*
Cercidium edenensis	*C. floridum*
Eysenhardtia pliocenica	*E. polystachya*
Leucanea californica	*L. microcarpa*
Lysiloma n. sp.	*L. candida*
Pithecolobium mohavense	*P. mexicanum*
Prosopis mohavensis	*P. juliflora*
Euphorbiaceae	
Euphorbia mohavensis	*E. hindsiana*
Burseraceae	
Bursera n. sp.	*B. laxiflora*
Bursera n. sp.	*B. microphylla*
Sapindaceae	
Dodonaea californica	*D. angustifolia*
Sapindus oklahomensis	*S. drummondii*
Thouinia striacata	*T. pringlei*
Clethraceae	
Clethra petiolaris	*C. arborea*
Rhamnaceae	
Colubrina lanceolata	*C. arborea*
Condalia coriacea	*C. parryi*
Zizyphus florissanti	*Z. obtusifolia*
Rubiaceae	
Randia mohavensis	*R. thurberi*
Compositae	
Baccharis beaumontii	*B. sergiloides*

In addition, many Madro-Tertiary genera are derivative types of preponderantly tropical alliances that show adaptations to drier areas within or marginal to the tropics:

Palmaceae	*Erythea, Washingtonia*
Fagaceae	*Quercus* (live and scrub oaks)
Lauraceae	*Umbellularia*
Papaveraceae	*Dendromecon*
Leguminosae	*Cercidium, Lysiloma, Eysenhardtia*
Rutaceae	*Castelea*
Anacardiaceae	*Malosma, Pachycormus,* *Schmaltzia, Tapiria*
Rhamnaceae	*Ceanothus, Condalia, Karwinskia*
Sterculiaceae	*Fremontia*
Bignoniaceae	*Chilopsis*

Others belong to small, highly specialized, monotypic families that are confined largely to the drier environments of southwestern North America. They include *Crossosoma* in the Crossosomataceae, *Garrya* in the Garryaceae, and *Fouquieria-Idria* in the Fouquieriaceae. These families also appear to have been derived from basically tropical groups.

In contrast to these numerous Madro-Tertiary taxa (species, genera, families) of tropical alliances, some of the families represented in the Madro-Tertiary Geoflora have had a long history in association with the Arcto-Tertiary Geoflora. Among these are the Aceraceae, Fagaceae, Juglandaceae, Platanaceae, Rosaceae, Salicaceae, Saxifragaceae and Ulmaceae. They have been referred to an holarctic center of origin, chiefly because many of their genera are known from Cretaceous rocks in high latitudes, and they then migrated gradually southward to middle latitudes during the Tertiary as an integral part of the Arcto-Tertiary Geoflora (Chaney, 1947). Thus the possibility arises that some of the species of genera representing temperate families in the Madro-Tertiary Geoflora are derivative Arcto-Tertiary plants that evolved in response to dry climate. The Madro-Tertiary species of *Acer*, *Amelanchier* and *Rosa*, in particular, seem to represent such a group as judged from their relations to Arcto-Tertiary plants.

There is evidence to suggest, however, that during the Cretaceous and Early Tertiary the present day temperate families typical of the Arcto-Tertiary Geoflora were represented by numerous types that were also adapted to subtropical and warm temperate environments. For example, species of *Alnus, Acer, Celastrus, Cercidiphyllum, Cornus, Fraxinus, Hydrangea, Liquidambar, Nyssa, Quercus, Rhus, Salix* and *Ulmus* were associated with *Acalypha, Artocapus, Calyptranthes, Cedrela, Cinnamomum, Cryptocarya, Cupania, Dalbergia, Ficus, Inga, Mallotus, Meliosma, Persea, Phytocrene, Rhamnidium, Sabalites* and *Terminalia* in the Early Eocene Chalk Bluffs flora of California (MacGinitie, 1941). Such relations are not peculiar but are displayed regularly by the Cretaceous to Early Tertiary floras of southern Alaska, Washington, Montana, Colorado and Dakota. It is pertinent that most of these so-called temperate families find more primitive living members of their respective genera in warmer regions, and some of them, including evergreen to nearly-evergreen species of *Acer, Alnus, Betula, Platanus, Prunus, Quercus* and *Ulmus*, range well into tropical areas. In addition, many of these temperate families appear on morphological evidence to have been derived from alliances that are largely tropical today, and which appear to have always been adapted to tropical environments. Among these are the following:

Chiefly Temperate Families	Probable Ancestral Alliance
Aceraceae	Sapindales
Betulaceae	Hamamelidales
Juglandaceae	Sapindales
Rosaceae	Dilleniaceae-Magnoliales
Saxifragaceae	Rosaceae
Ulmaceae	Hamamelidales

Furthermore, many of the species or genera typical of the Arcto-Tertiary Geoflora are temperate to warm temperate isolates of preponderantly tropical groups, for example:

Ailanthus	Simarubaceae
Cedrela	Meliaceae
Cercis, Cladrastris, Gymnocladus, Robinia, Sophora	Leguminosae
Cocculus	Menispermaceae

Dilodendron	Sapindaceae
Diospyros	Ebenaceae
Exbucklandia, Hamamelis, Liquidambar	Hamamelidaceae
Gordonia	Theaceae
Halesia	Styracaceae
Lindera, Persea, Sassafras	Lauraceae
Liriodendron, Magnolia	Magnoliaceae
Paliurus	Rhamnaceae
Ptelea	Rutaceae
Tilia	Tiliaceae
Vitis	Vitaceae

These and other relations have led to the suggestion that the Arcto-Tertiary Geoflora probably evolved chiefly from tropical alliances that gradually became adapted to temperate environments (Axelrod, 1952a). The data also suggest that the Madro-Tertiary Geoflora probably derived some of its plants from these "temperate" families which, during Cretaceous and Paleocene times, were represented by types that were common in warm temperate to subtropical forests. The Madro-Tertiary plants belonging to these "temperate" families include the following:

Fossil Species	Similar Living Species
Salicaceae	
Populus fremontii *Populus lamottei*	*P. fremontii* (group)
Populus sonorensis	*P. monticola*
Salix edenensis *Salix taxifoloides*	*S. hindsiana-taxifolia*
Juglandaceae	
Juglans beaumontii	*J. rupestris*
Juglans nevadensis	*J. californica*
Ulmaceae	
Celtis kansana	*C. reticulata*
Celtis n. sp.	*C. pallida*
Platanaceae	
Platanus paucidentata *Platanus florissanti*	*P. racemosa-wrightii*

Fossil Species	Similar Living Species
Saxifragaceae	
Philadelphus minutus	*P. microphylla*
Rosaceae	
Cercocarpus antiquus	*C. betuloides*
Cercocarpus holmesii	*C. paucidentatus*
Cercocarpus linearifolius	*C. ledifolius*
Holodiscus idahoensis	*H. dumosus*
Prunus (Emplectocladus) prefremontii	*P. fremontii*
Prunus (Emplectocladus) prefasciculata	*P. fasciculata*
Prunus (Laurocerasus) mohavensis	*P. lyonii*
Prunus (Laurocerasus) n. sp.	*P. ilicifolia*
Lyonothamnus mohavensis	*L. floribundus*
Vauquelinia coloradensis	*V. californica*
Vauquelinia liniara	*V. angustifolia*
Oleaceae	
Fraxinus edenensis	*F. dipetala*
Fraxinus millsiana	*F. anomala*

All of them are specialized in terms of their taxonomic and adaptive relations. This suggests a long period of evolution on the drier margins of the tropics, a region where they occur today and an area where all their fossil relatives lived in the past.

Thus in terms of its composition, Madro-Tertiary plants seem principally to represent derivative tropical and warm temperate alliances of the Neotropical-Tertiary Geoflora that evolved in response to subhumid environments within or marginal to the tropics. A few of its species apparently were derived from temperate Arcto-Tertiary plants that gradually became adapted to drier climates in the Middle and Late Tertiary. Since numerous genera of these temperate families were more broadly adapted to subtropical and warm temperate environments in the Cretaceous and Early Tertiary, however, most Madro-Tertiary plants representing these alliances may also have evolved from them at an early date on the drier margins of the tropics.

EARLY EVOLUTION

The history of the Madro-Tertiary Geoflora is only partly known. Relatively continuous sequences of fossil floras in southern California, central California, western Nevada and southern Oregon provide much evidence of its Middle and Late Tertiary history in those areas. But in regions to the south and east, Middle and Late Tertiary floras are largely unknown, and the more abundant Cretaceous and Early Tertiary floras of that region do not provide us with records of Madro-Tertiary vegetation (but see below). From the facts in hand, and from the inferences which may be drawn from them, it is possible to outline in a provisional way the broader aspects of its evolution. The following analysis is presented in two parts: *1*) the time of its earliest appearance as a distinct geoflora, and its relations to other geofloras at that time; *2*) inferences as to its probable earlier history in terms of *a*) ancestral types in older floras, *b*) area and environment, and *c*) mode of evolution. The occurrence of floras to which reference is made is shown in the accompanying figures, and Table I outlines the relative ages of Tertiary floras now known to contain Madro-Tertiary plants.

Earliest Records

Evidence supplied by the Green River and Florissant floras of the central Rocky Mountain region indicates that the Madro-Tertiary Geoflora was already in existence during the latter part of the Early Tertiary. Among the Middle Eocene Green River plants (Brown, 1934) that seem to represent the earliest records of Madro-Tertiary species in moderate numbers are:

Woodland

Celtis, *Pinus* (nut pine), *Platanus* (*Aralia*), *Rhus*, *Vauquelinia.*

Arid Subtropic Scrub

Cardiospermum, *Cassia*, *Dodonaea*, *Eopuntia*, *Maytenus*, *Mimosites*, *Passiflora*, *Randia*, *Thouinia.*

Abundant data, both geological and paleobotanical, suggest that a seasonally-dry, warm temperate to subtropical climate characterized the Green River lowlands (Bradley, 1929; Brown, 1934;

EPOCHS	"AGE STAGE"		CALIFORNIA		GREAT BASIN	ROCKY MOUNTAINS	HIGH PLAINS
	Mammalian	Molluscan	Central	Southern			
PLEISTOCENE	Blancan	San Joaquin	Sonoma-Napa San Joaquin				Channing, Texas
PLIOCENE	Hemphillian	Etchegoin Jacalitos	Etchegoin Oakdale Petaluma Mulholland Jacalitos	Pico Mount Eden Piru Gorge Anaverde	Verdi Cache Valley Truckee-Hazen	Creede, Colo.	Vincent Ranch, Kan.
	Clarendonian	Neroly-Cierbo	Black Hawk Carmel; Table Mt; Remington Hill; Valley Spr.	Mill Creek Puente; Ricardo Mint Canyon	Esmeralda Alvord Creek Fallon; Middlegate; Chloropagus Aldrich Station	Silver Cliff, Colo.	Laverne, Okl. Clarendon, Texas
MIOCENE	Barstovian	Briones		Puddingstone Dam Topanga	Buffalo Canyon		
	Hemingfordian	Temblor		Tehachapi			
	Arikareean	Vaqueros					
OLIGOCENE	Whitneyan	Blakeley			Lower Elko	Antero, Colo.	
	Orellan	Lincoln				Florissant, Colo.	
	Chadronian	Keasey					
EOCENE	Duchesnean	Tejon					
	Uintan						
	Bridgerian	"Transition" Domengine				Green River, Colo. & Utah	
	Wasatchian	Capay					
PALEOCENE	Clarkforkian	Meganos					

---- Present variable usage of EPOCHS by Mammalian and Molluscan paleontologists in the Western United States.

TABLE I

Relative ages of floras containing Madro-Tertiary plants.

Chaney, 1944c). The Green River sediments have also yielded members of the Arcto-Tertiary Geoflora, as represented by pollen of *Abies, Acer, Alnus, Carpinus, Carya, Fagus, Sequoia* and *Ulmus* (Wodehouse, 1932; 1933). This temperate forest probably lived in cooler upland areas bordering the Green River basin, sites from which relatively few leaves or seeds would be transported into the lowlands. The Green River also includes species of *Cassia, Chrysobalanus, Dioon, Ficus, Geonoma, Musophyllum, Oreodaphne* and *Sabal*, comprising relicts of the Neotropical-Tertiary Geoflora. The leaves representing some of these species are smaller than those of related types in the Early Eocene and Paleocene floras of the nearby region. This suggests they had become adapted to a climate drier than that which prevailed there earlier.

The Early Oligocene Florissant flora of Colorado (MacGinitie, 1953) contains numerous Madro-Tertiary plants. Among those recorded are species in the following genera, grouped here according to the vegetation type they probably represented:

Woodland and Savanna
Arbutus, Celtis, Dodonaea, Morus, Quercus (*live oak*), *Platanus, Rhus, Sapindus, Stipa, Vauquelinia*

Chaparral
Ceanothus, Cercocarpus, Colubrina, Mahonia, Quercus (scrub oak), *Schmaltzia*

Thorn Scrub
Bursera, Caesalpinia, Colubrina, Euphorbia, Prosopis, Tephrosia, Thouinia, Zizyphus

MacGinitie's analysis indicates that these communities occupied the drier, well-drained slopes and interfluves bordering Florissant lake. Woodland and chaparral were scattered on the warmer, south-facing slopes, extending up the flanks of nearby volcanos. Thorn scrub (possibly a mesquite grassland) inhabited well-drained flats and seasonally-dry watercourses at lower altitudes. More mesic sites along the lake shore and in bordering valleys were dominated by members of the temperate Arcto-Tertiary Geoflora, as represented by species of *Abies, Acer, Carpinus, Carya, Celastrus, Cephalotaxus, Chamaecyparis, Crataegus, Pinus, Populus, Rosa, Sequoia, Tilia, Ulmus* and *Vitis*. A few plants, including species of *Astronium*, *Bursera*, *Cedrela* and *Oreopanax*, appear to be relicts of the Neotropical-Tertiary Geoflora that dominated this region earlier in the period.

Thus the Green River and Florissant floras indicate that *a*) during the Early Tertiary the Madro-Tertiary Geoflora was in ecotone with the Arcto-Tertiary and Neotropical-Tertiary Geofloras, a relation which has persisted down through the Cenozoic; *b*) it comprised plants that were adapted to a dry environment between these geofloras, a relation which is still in existence; *c*) the occurrence in Eo-Oligocene rocks of Madro-Tertiary species that are closely similar to modern types suggests that the history of the geoflora probably extends back into Paleocene if not into Cretaceous time. These conclusions raise for discussion the earlier, and speculative, history of the Madro-Tertiary Geoflora.

Ancestral Types

We have noted that this geoflora is made up chiefly of derivative subtropical to warm temperate types that seem to have evolved in drier environments marginal to the tropics. The problem thus arises as to whether there are taxa possibly ancestral to Madro-Tertiary types in the Cretaceous and Paleocene floras of North America, plants that presumably were becoming adapted to relatively drier areas during those times. The sorts of plants we are interested in finding in these older floras are those that seem to be ancestral to Madro-Tertiary species in the sense that they apparently represent members of lineages that evolved gradually into typical Madro-Tertiary plants. The Late Cretaceous Vermejo flora of New Mexico and Colorado (Knowlton, 1917) has several species that appear to be close forerunners of Madro-Tertiary phylads, as does the Paleocene Raton (Knowlton, 1917) of the same region:

Vermejo Species[3]	Related Madro-Tertiary Species	Related Living Species
Diospyros ? *leei* Knowlton (pl. 48, fig. 2)	*Quercus convexa; Q dayana*	*Q. virginiana* phylad

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[3] In this and the following list the original names are retained for the Cretaceous and Paleocene species, although many of them were determined incorrectly by the earlier workers; since this is not a taxonomic paper, it seems best not to bury any formal name changes here.

Vermejo Species	Related Madro-Tertiary Species	Related Living Species
Ficus leei Knowlton (pl. 39, fig. 6)	*F. edenensis, F.* sp.	*F. palmeria; F. brandegei*
Laurus coloradensis Knowlton (pl. 45, fig. 3)	*Persea coalingensis*	*P. podadenia*
Sabal montana (pl. 32, fig. 3)	*Sabal mohavensis*	*S. uresana-mexicana*
Salix plicata Knowlton (pl. 37, figs. 6, 7)	*S. payettensis-edenensis*	*S. exigua phylad*
Sterculia coriacea Knowlton (pl. 48, fig. 1)	*Platanus paucidentata-florissanti*	*P. wrightii-racemosa*
Raton Species[a]		
Aralia coloradensis (pl. 107, fig. 2)	*Platanus paucidentata*	*P. racemosa*
Ficus neoplanicostata Kn. (pl. 73, fig. 4; pl. 74, fig. 2)	*Colubrina lanceolata*	*C. arborea*
Juglans sapindoides (pl. 65, fig. 5) *Laurus ratonensis* (pl. 91, figs. 2-4)	*Persea coalingensis; P. florissanti*	*P. podadenia; P. hartwegii*
Sabalites spp. pls. 56-60)	*Sabal miocenica*	*S. uresana-mexicana*
Sterculia berryana Knowlton (pl. 102, figs. 3-4)	*Platanus florissanti*	*P. wrightii* aff.

In addition, the Late Cretaceous Laramie flora of the Denver basin (Knowlton, 1922) contains specimens of a narrow-leafed form of *Karwinskia* (= *Rhamnus brittoni* Knowlton) similar to those produced by the living *K. humboldtiana-parvifolia,* and the Eocene Barilla Mountains flora of west Texas (Berry, 1919) includes leaves of the *Quercus virginiana* plexus (= *Ilex barillensis* Berry). The Early Eocene Wilcox flora[4], which lived on the shores of an embayment that occupied the lower Mississippi Valley, provides further critical data (Berry, 1916, 1930). In addition to tropical savanna forest, the flora includes species of mangrove swamp, lagoon border and beach jungle associations. Several members of the latter community, which largely occupied the drier sandy ridges in the region, appear to be precursors of Madro-Tertiary types:

Wilcox species	Related Madro-Tertiary Species	Related Living Species
Berchemia eocenica (PP 156, pl. 33, f. 12-14)	*Karwinskia californica*	*K. humboldtiana-parvifolia*
Bumelia pseudotenax (PP 91, pl. 100, f. 2)	*B. beaverana*	*B. lanuginosa*
Dillenites serratus (PP 91, pl. 45, f. 2)	*Thouinia striacata*	*T. pringlei*
Dodonaea knowltoni (PP 91, pl. 64, f. 3)	*D. californica*	*D. viscosa angustifolia*
Fagara eocenica (PP 91, pl. 55, f. 6)	*Xanthoxylum* n. sp.	*X. clava-herculis*

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[4] In terms of the continental-time-scale for North America, the Wilcox may be Paleocene, rather than Early Eocene in age.

Wilcox species	Related Madro-Tertiary Species	Related Living Species
Oreodaphne puryearensis (PP 91, pl. 83, f. 1)	*Persea coalingensis-florissanti*	*P. podadenia; P. hartwegii*
Rhamnus eolignitícus (PP 91, pl. 69, f. 4)		
Pithecolobium eocenica (PP 91, pl. 45, f. 2)	*P. miocenica*	*P. dulce*
Reynosia praenuntia longiopetiolata (PP 156, pl. 46, f. 1)	*Clethra petiolaris*	*C. lanata*
Sabalites grayana (PP 91, pl. 12, f. 1, 2; pl. 14, f. 1)	*Sabal miocenica*	*S. uresana; S. mexi*cana

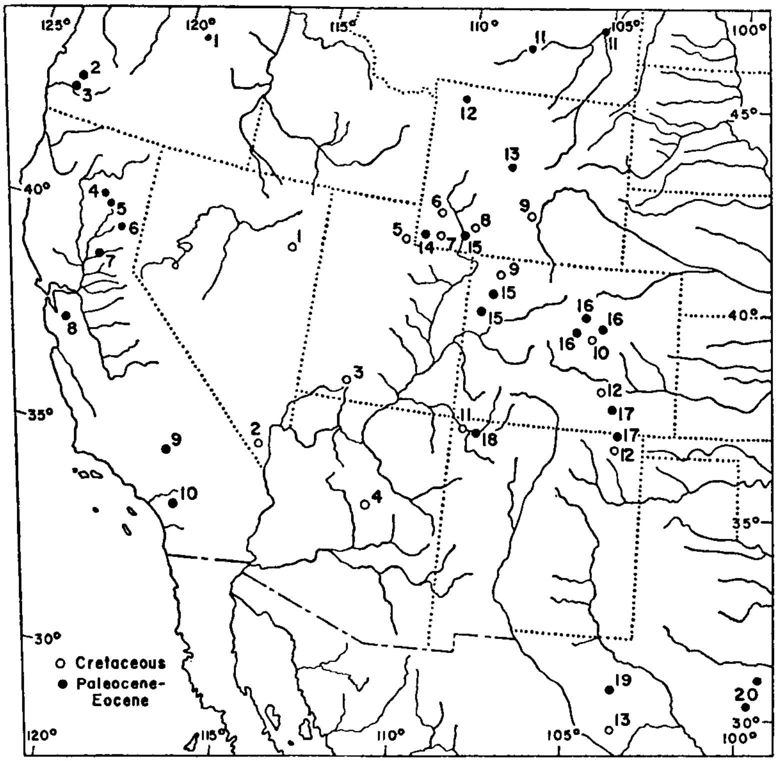
There also are a number of other plants in the Wilcox flora, including species of *Ficus* and *Quercus*, and numerous Leguminosae, that are not now known to have closely related species in the Madro-Tertiary Geoflora but which are presumed to have formed an important part of it on the basis of the occurrence of related phylads in its derivative communities.

These Cretaceous and Paleocene plants showing relationship to Madro-Tertiary lineages belong to genera that have a wide occurrence today, and their past distribution was greater. They differ from Middle and Late Cenozoic Madro-Tertiary species chiefly in having somewhat larger (though still relatively small) leaves and leaflets, and in some cases there also are subtle differences in details of nervation or margin. Although they resemble more mesic living species of their genera than do typical Middle and Late Cenozoic Madro-Tertiary plants, their modern relatives nonetheless occur regularly in seasonally dry subtropical and warm temperate regions, and they belong to phylads that apparently link them with Madro-Tertiary species. Since these Paleocene and Cretaceous plants seem to be ancestral to Madro-Tertiary types, we may appropriately ask: Where did they undergo their evolution?

Area and Environment

The occurrence of ancestral Madro-Tertiary types in the Cretaceous and Early Tertiary floras of southwestern North America indicates that the geoflora had its early evolution in this general region. This conclusion is supported by the fact that ancestral Madro-Tertiary plants are not known in the temperate Cretaceous floras of high latitudes or in the humid tropical floras on the east and west coasts of the continent during this interval. We have noted also that the general taxonomic and adaptive relations of the Madro-Tertiary alliances suggest that their early evolution was chiefly in response to dry climate. Thus it is critical that on climatic grounds southwestern North America is a region where relatively drier conditions have regularly existed, for at low-middle latitudes on the western sides of the continents a high-pressure system typically develops and results in less frequent rain.

The Paleocene and Late Cretaceous floras that have been reported from this area are shown in Fig. 1. Although they are not numerous, they nonetheless afford evidence with respect to regional lowland environments. The Paleocene Animas (Knowlton, 1924) and Raton floras (Knowlton, 1917) of northern New Mexico and adjacent Colorado are lowland and subtropical in character, as is the Denver flora of central Colorado (Knowlton, 1930). To the southeast, the younger Eocene flora from the Barilla Mountains in western Texas is generally of similar aspect (Berry, 1919). To the west, the Paleocene Goler flora from the Mojave Desert is lowland and tropical (U. C. Mus. Pal.), and resembles the Raton, as does the Wilcox flora from the Gulf region (Berry, 1916, 1930; Ball, 1931). The fact that all these floras show relationships to one another indicates that environmental conditions were generally similar over this broad region during the early Tertiary. They also clearly point to the absence of a high cordillera in the western interior and demonstrate that migration was readily possible across the region.



FOSSIL FLORAS

Paleocene-Eocene (●)

1 Clarno
2 Comstock
3 Goshen
4 Montgomery Cr.
5 Moonlight
6 La Porte
7 Chalk Bluffs
8 Tesla
9 Goler
10 Alberhill
11 Ft. Union
12 Yellowstone
13 Wasatch
14 Evanston
15 Green River
16 Denver
17 Raton
18 Animas
19 Barilla Mts.
20 Indio

Late Cretaceous (○)

1 Conners Pass
2 Willow Tank
3 Kanab Cr.
4 Coal Cr.
5 Coalville
6 Aspen
7 Frontier
8 Black Buttes
9 Medicine Bow
10 Laramie
11 Fruitland
12 Vermejo
13 Aguja

Fig. 1

Some important Cretaceous and Early Tertiary floras in southwestern North America.

Since the low-middle latitudes in the western parts of the continents have always been relatively the driest parts of the earth, we may infer that the Paleocene floras across these latitudes, instead of comprising a broad expanse of tropical or subtropical rain forest, chiefly represented tropic savanna. This suggestion finds support in the climatic implications of the better-known Eocene floras of California and Oregon (MacGinitie, 1941; Chaney and Sanborn, 1933), which indicate that the Pacific border was a tropic savanna in the Early Tertiary, with rain concentrated chiefly in the warm season (MacGinitie, 1937). Since the floras of southwestern North America are situated at lower latitudes, rainfall probably was more seasonally distributed there than in the Pacific border area from central California northward. This raises the possibility that local subhumid areas existed in the region, especially on the lee slopes of low ranges. One need only examine the tropics today in areas away from the wet lowland floodplains to see that diverse drier environments may occur throughout the region. Dry (deciduous) tropic forest and scrub occur frequently to leeward of only low ranges in such areas. Clearly, we would expect to find little evidence of them in the known Paleocene floras because the high water tables on the lowland floodplains, where they were living, would tend to give them a more mesic aspect than that which may actually have existed in nearby parts of these basins.

The Middle to Late Cretaceous floras of the western United States reflect a cooler climate than that indicated by the succeeding Paleocene floras which occupied generally the same areas (Fig. 1). The subtropical to tropical types which are so common in the Paleocene floras are less abundant in those of Cretaceous age, and the latter contain more numerous warm temperate angiosperms as well as conifers which are rare to absent in the Paleocene floras. On climatological grounds, it would follow that slightly drier conditions may be postulated for the southwestern part of the continent during the Cretaceous. But even at that time subhumid environments could not have been very widespread, for the presence of tree ferns (*Temskya*) in the Upper Cretaceous rocks in southern Nevada shows that area was well-watered and that extremes of drought were not yet in existence. The Cretaceous floras from southern Utah (Lesquereux, 1887), south-central Arizona (Lesquereux, 1887), northeastern Arizona (Gregory, 1917, p.

75) and northern New Mexico (Knowlton, 1917) provide no evidence of low rainfall. As mentioned above for the Paleocene forests, this is probably due to their occurrence in lowland basins of high water tables, which would give them a more mesic facies than communities on nearby better-drained slopes.

The nature of the marine Cretaceous rocks in northern Mexico provides compelling evidence for the existence of seasonally-dry continental environments in southwestern North America. At many localities the marine sections are characterized by frequent occurrence of salt and gypsum beds of moderate thickness (Imlay, 1944). This indicates accumulation in basins that were barred intermittently and situated in a region of seasonally dry climate of high evaporation, as is found on the margins of the tropics today. Since the salines occur at some localities inter-fingered with continental rocks, it is apparent that the bordering lands also were subject to seasonal drought under tropic savanna climate. The absence of evaporites in rocks of similar, as well as slightly younger (Late Cretaceous-Paleocene), age in the southwestern United States probably means that the marine basins of that area were open and hence unsuited to saline accumulation, not that conditions of high evaporation were absent.

Geologic data thus reinforce our earlier inferences, based on climatic and paleobotanic evidence, that dry tropical to warm temperate climates existed over the region. Rainfall may have been as low as 35 or 40 inches in local areas on the lee slopes of low, discontinuous mountains scattered through the area. Rocky sites and well drained sandy-to-gravelly tracts provided by the retreating inland sea (Fig. 2) could be expected to produce local edaphic situations that were effectively drier. Hence available evidence indicates that many marginal tropical to warm temperate alliances may have been adapting to scattered drier areas in southwestern North America from Middle Cretaceous (or earlier) into Paleocene time.

Mode of Early Evolution

From an evolutionary standpoint, this inferred setting for phylads ancestral to Madro-Tertiary plants would have been particularly well suited for mega- (or quantum) evolution (Simpson, 1953; Stebbins, 1950). There are two major facts that bear directly on this problem: *a*) dry environments were restricted in area and not extreme in type during the Cretaceous and Paleocene, they commenced to expand in the Early Eocene, were becoming more widespread in the Middle Eocene, and continuously increased in area and in degree of severity during the rest of the Cenozoic (Axelrod, 1952a, fig. 14); *b*) the Madro-Tertiary Geoflora is clearly adapted to dry climate. It is apparent, therefore, that the trend toward the development of hotter and drier climates over southwestern North America would favor rapid evolution of any preadapted types, for the expansion of a new climate corresponds to the appearance of a new adaptive zone. It is pertinent also that evidence recently has been presented to show that aridity may be a powerful stimulus to evolution (Stebbins, 1952).

Rapid evolutionary divergence of ancestral Madro-Tertiary phylads from more mesic tropical types would be promoted by isolation, owing to their restriction to scattered drier sites. At this early date isolation would have been not unlike that which occurs today in insular regions, areas where rapid evolution is known to have occurred: habitat discontinuity produces moderate-sized or even small populations in which isolated demes interchange genes only occasionally, a situation favorable to genetic drift and hence rapid evolution. In addition, ecological differentiation of habitats is quite marked in dry regions and increases with the degree of aridity. Thus even a moderate trend toward aridity in the Cretaceous or Paleocene, a span of some 60 million years, would have tended to further promote isolation and hence speciation. And with normal climatic fluctuation imposed on a secular trend, we might well expect the occasional merging of marginal habitats and their populations, and hence further genetic change. In addition, the number of specialized adaptive types that exist in marginal dry tropical areas is quite large (see Shreve, 1951, p. 34). Since selective pressure would rise in response to any trend toward a more extreme (hotter and drier) climate, whether due to wide secular or local topographic changes (or both), many new mutations might be expected to have a high selective value, owing to the diversity of adaptive types possible.

Thus rapid evolution of these early Madro-Tertiary phylads is understandable on the basis of an organism-environmental inter-

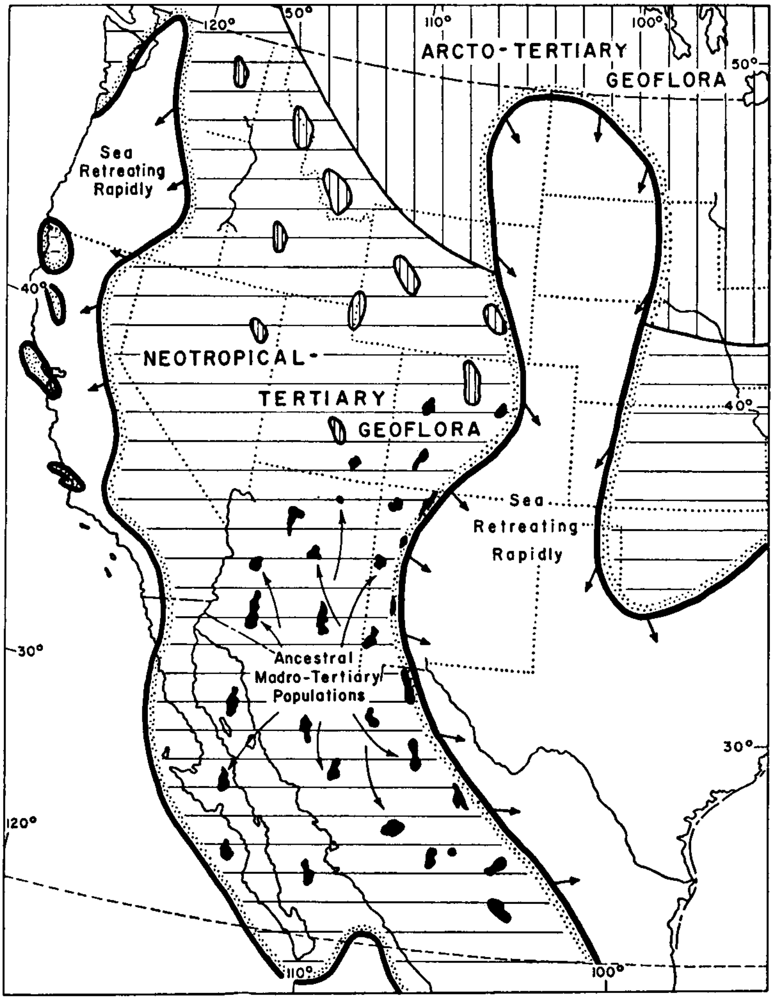


Fig. 2

Inferred distribution of ancestral Madro-Tertiary plants in pre-Eocene time.

relationship as outlined by Simpson (1953) and Stebbins (1950), for here we are dealing with a direct relationship between morphological specialization and a continued differentiation of new habitats imposed by a gradual trend toward increased drought and heat. The development of successively more extreme dry environments following the Early Eocene would result in continued strong selection and in further evolution. Marginal subtropical to warm temperate types preadapted to semiarid and arid environments would thus evolve progressively (macro- or phyletic evolution) into types better adapted to survive under increasingly drier habitats. An evolutionary setting of the type visualized would be expected to promote the differentiation of numerous, yet very distinct, novel species, genera and small families—taxons of a type well represented in the Madro-Tertiary Geoflora (see Composition). Hence it is not surprising to find that by the close of the Early Tertiary, as shown by the Green River and Florissant floras, many Madro-Tertiary plants were commencing to spread widely over the lowlands as dry climates expanded, and the types they represent appear to be basically stabilized and typical of the geoflora. The inferred pre-Eocene occurrence of the Madro-Tertiary Geoflora is depicted in Fig. 2, which shows scattered, ancestral Madro-Tertiary populations centered in southwestern North America during the later Cretaceous and early Paleocene. The land-sea relations shown here are necessarily generalized because the seas were retreating rapidly during this interval.

As mentioned above, this early evolution involved not only the development of many novel taxonomic entities but also numerous adaptive types, each with a wide array of specialized structures. Judging from the composition of the geoflora, these probably included plants with swollen bases for water storage (*Idria*, *Bursera*); winter-deciduous (*Acacia*, *Populus*, *Platanus*, *Juglans*, *Salix*) and drought deciduous (*Aesculus*, *Bursera*, *Cercidium*, *Prosopis*) types; fleshy, water-storage types of candelabra, free-branching and cylindrical form (Cactaceae); and many others. In the herbaceous groups, which are largely unrecorded, we may infer that the taxa included forerunners of the numerous adaptive forms represented in the dry regions today, ranging from perennials to bulbous storage types, short-lived annuals and many others.

Summary

The preceding theoretical discussion, sketching the probable early history of the Madro-Tertiary Geoflora, may be summarized as follows:

1. Taxonomic and adaptive relations of Madro-Tertiary plants suggest that they were derived chiefly from tropical and warm-temperate alliances that became adapted to drier environments on the margins of the tropics.

2. Species that appear to represent ancestral members of Madro-Tertiary phylads occur in small numbers in the lowland Cretaceous and Paleocene floras of southwestern North America and border areas.

3. Geologic, paleoclimatic and paleobotanic evidence indicate that this region was chiefly a lowland area, characterized by subtropical to warm temperate climate, with seasonal rainfall prominent in the western sector. Discontinuous low ranges existed along the axis of the present western cordillera.

4. Scattered dry sites, such as sandy tracts and rocky slopes, as well as local dry areas to the lee of low ranges, may be inferred for the region.

5. Madro-Tertiary plants probably were evolving in these areas (4 above) from Middle Cretaceous (or earlier) through Paleocene time, a span of fully 60 million years.

6. Spatial isolation probably was imposed by their restriction to discontinuous drier areas over southwestern North America, an isolation analogous to that seen in insular regions today.

7. With a strong linear component to selection imposed by a trend toward expanding dry climate, many novel taxonomic and adaptive types would be expected to have come into existence, adapting rapidly to the expanding new zone.

8. Thus when the Madro-Tertiary Geoflora is first recorded in moderate numbers (Green River, Florissant), its species and genera were already clearly delineated, highly-evolved types, well adapted to seasonally dry climate.

POST-EOCENE HISTORY IN THE FAR WEST

Migration

We have now shown that the Madro-Tertiary Geoflora had come into existence over southwestern North America by the Early Cenozoic, at which time it occupied a position between the Arcto-Tertiary and Neotropical-Tertiary Geofloras. Although the relative spatial relations of these geofloras remained rather stable, their positions changed rapidly following the Eocene. In response to factors that are still obscure but which were clearly global in scope, dry climates commenced to expand after the Eocene. The Madro-Tertiary Geoflora migrated widely over the region as dry climates developed on an increasingly larger scale during the succeeding epochs of the Tertiary. However, it became dominant in different areas at various times in its history, depending chiefly on geographic position and time. The time it assumed dominance in a province can be determined for regions where relatively complete sequences of floras, or cliseres, are available for comparison; they record the gradual displacement of the more mesic Arcto-Tertiary and Neotropical-Tertiary Geofloras by the Madro-Tertiary Geoflora as dry climates expanded. We shall summarize here only the Miocene and Pliocene aspects of the problem in the far West. Using all the data in hand, the floral succession shows that the geoflora attained optimum development in different provinces as follows:

MOHAVIA. The Madro-Tertiary Geoflora was already the dominant vegetation in southeastern California by Early Miocene time (Axelrod, 1939). The time it first invaded the area is not now known, though it is clearly post-Paleocene, for the Goler flora of this area represents tropical forest. The absence of humid subtropical to warm temperate relicts in the Early Miocene of southeastern California suggests that the geoflora may have already been well established there by the Middle Oligocene, and possibly by Middle Eocene time.

CENTRAL GREAT BASIN. Madro-Tertiary vegetation became conspicuous over the lowlands of the region in Late Miocene time (Axelrod, 1940a, 1940b, 1956). The more mesic Arcto-Tertiary forest was largely eliminated from slopes near the basins of deposition by the close of the epoch, leaving a dominant oak and conifer woodland and chaparral over the lowlands.

NORTHERN GREAT BASIN. Madro-Tertiary plants are rare in the Late Miocene; they increased in numbers during the Early Pliocene (Axelrod, 1944f) but probably never wholly supplanted the Arcto-Tertiary Geoflora in this cooler, more northerly region (Axelrod, 1944g).

CENTRAL SIERRAN PIEDMONT. Madro-Tertiary plants were beginning to invade the central Sierran foothill area in the Late Miocene (Condit, 1944a, b), they increased in numbers in the Early Pliocene, and soon dominated the area as temperate forest was restricted to cooler and moister sites at higher levels (Axelrod, 1944c).

WEST-CENTRAL CALIFORNIA. Madro-Tertiary plants appeared in the region in appreciable numbers only in the later part of the Early Pliocene (Axelrod, 1944a). They assumed dominance over the lowlands in the Middle Pliocene, at which time Arcto-Tertiary plants lived on bordering cooler and moister slopes (Axelrod, 1944b). With cooling climate later in the epoch, they became subordinate to surviving species of the Arcto-Tertiary Geoflora (Axelrod, 1944d, 1950b).

These data make it possible to calculate roughly its rate of migration. Measurement of the rate is determinable from the time required for migration from a known center of radiation to a distant region where it eventually attained dominance in response to the development of favorable climatic conditions over the lowlands. It is apparent that:

1. The Madro-Tertiary Geoflora migrated from Mohavia to southern Oregon, a distance of 600 miles, during the interval from the Early Miocene to the Early Pliocene (items 1, 3 above).
2. It migrated from Mohavia to west-central California, a distance of 300 miles, during the interval from the Early Miocene to the Middle Pliocene (items 1, 4, 5 above).

Its more rapid movement over the interior was made possible by the relatively drier, sunnier climate to the lee of the Sierra Nevada-

Cascade axis which formed only a low barrier at this time (Axelrod, 1957; Chaney, 1944b). The coastward slopes were mesic for a longer interval, and hence the Arcto-Tertiary Geoflora dominated there into a later stage.

The Miocene and Pliocene epochs represent a span of approximately 27 million years, with the latter having a duration of essentially 11 million years (see Appendix 1). On this basis, and the estimates are only approximate, it may be concluded that the Madro-Tertiary Geoflora required 16 million years to migrate the 600 miles from Mohavia to southern Oregon. This is an average rate of .0037 mile per century, or about 2.37 inches a year. It took 18 million years to migrate the 300 miles to west-central California, at an effective rate of .0016 mile per century, or 1.05 inches per year. These are maximum rates, however, for, as noted above, we may infer that the geoflora probably was in the Mohave area by the Middle Oligocene, possibly in the Middle Eocene, some 10 to 20 million years prior to its first known records in that region.

Late Tertiary Evolution

SPECIES

FOLIAR STRUCTURES

Leaves of most Madro-Tertiary plants in Miocene and Pliocene floras so closely resemble those produced by modern species that they are essentially indistinguishable. In some instances, however, there is evidence of a gradual reduction in leaf size during the Middle and Late Tertiary. This relation is found, besides other genera, in *Amelanchier, Acer, Cercocarpus, Philadelphus, Platanus, Populus, Prunus, Rosa* and *Ribes*, species of which occur in semiarid woodland, chaparral and semidesert vegetation. Under the influence of increasing drought and longer periods of sunshine with high evaporation following the Eocene, the evolutionary trend in these genera involved *a*) gradual reduction in leaf area, *b*) development (in *Acer, Platanus, Ribes*) of deeper sinuses and narrower lobes, *c*) suppression of marginal teeth (*Amelanchier, Cercocarpus, Populas, Rosa*), *d*) development of a thicker texture, and *e*) by inference, the appearance of a drought-deciduous habit (*Amelanchier, Ribes*) (Axelrod, 1944f: 241-243). It is not now known whether all these species were common in areas well removed from the Arcto-Tertiary—Madro-Tertiary ecotone, though some of them were. In any event, they reflect a climate quite different from that indicated by related species of the same genera in the humid, temperate areas occupied by the Arcto-Tertiary Geoflora. Figs. 3, 4 and 5 illustrate these shifting morphologic types that developed in response to the trend toward increased aridity.

On the other hand, certain Miocene species of *Cercocarpus, Prunus* (*Laurocerasus*), *Lyonothamnus* and *Quercus* from interior localities have leaves that average somewhat smaller than the norm of the living insular species which most nearly resemble them. Pliocene records of these species from more coastal situations are nearly intermedite in size between the Miocene and the modern (Fig. 6). This may mean that as ancestors of such living insular endemics as *Cercocarpus traskii, Lyonothamnus floribundus, Prunus* (*Laurocerasus*) *lyonii* and *Quercus tomentella* migrated coastward, larger leaves gradually evolved in response to milder oceanic climate (Axelrod, 1944b: 119). Nonetheless, the validity of such a conclusion rests now on negative evidence. Discovery of more numerous floras in both interior and coastal stations may show that the small-leafed species were limited to the interior and that the larger leafed species occurred only in coastal or near coastal sites. If so, it would indicate that the present endemics were represented by several closely related species in different environments.

As noted earlier, many Madro-Tertiary species appear to be derivatives of typically tropical families that became adapted to increasing aridity on the margins of the tropics. It is pertinent that the Miocene and Pliocene species of these subtropic types are most like plants living in the drier, and generally more extreme, environments occupied by the genera they represent, including *Acacia, Bursera, Celtis, Cardiospermum, Condalia, Eysenhardtia, Ficus, Lysiloma, Morus, Passiflora, Pithecolobium* and *Randia.* Related living species of these genera which occur in more humid and equable areas commonly have larger leaves or leaflets, as do those of the fossil species in the Eocene and older floras. Morphological evidence supplied by the floral and fruiting structures of living species of these genera suggests that the species in the drier regions more frequently than not comprise the derived and specialized types in their respective alliances. Since this trend parallels

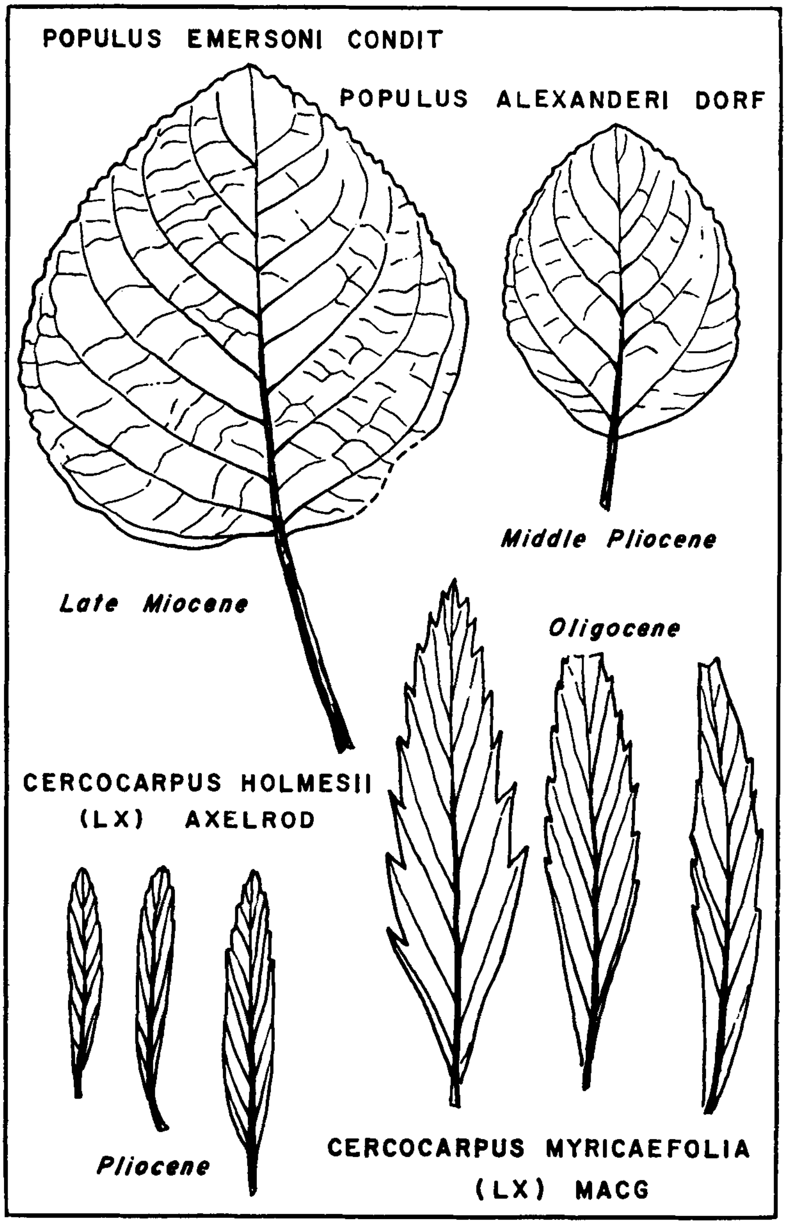


Fig. 3

Reduction in leaf size during the Late Tertiary.

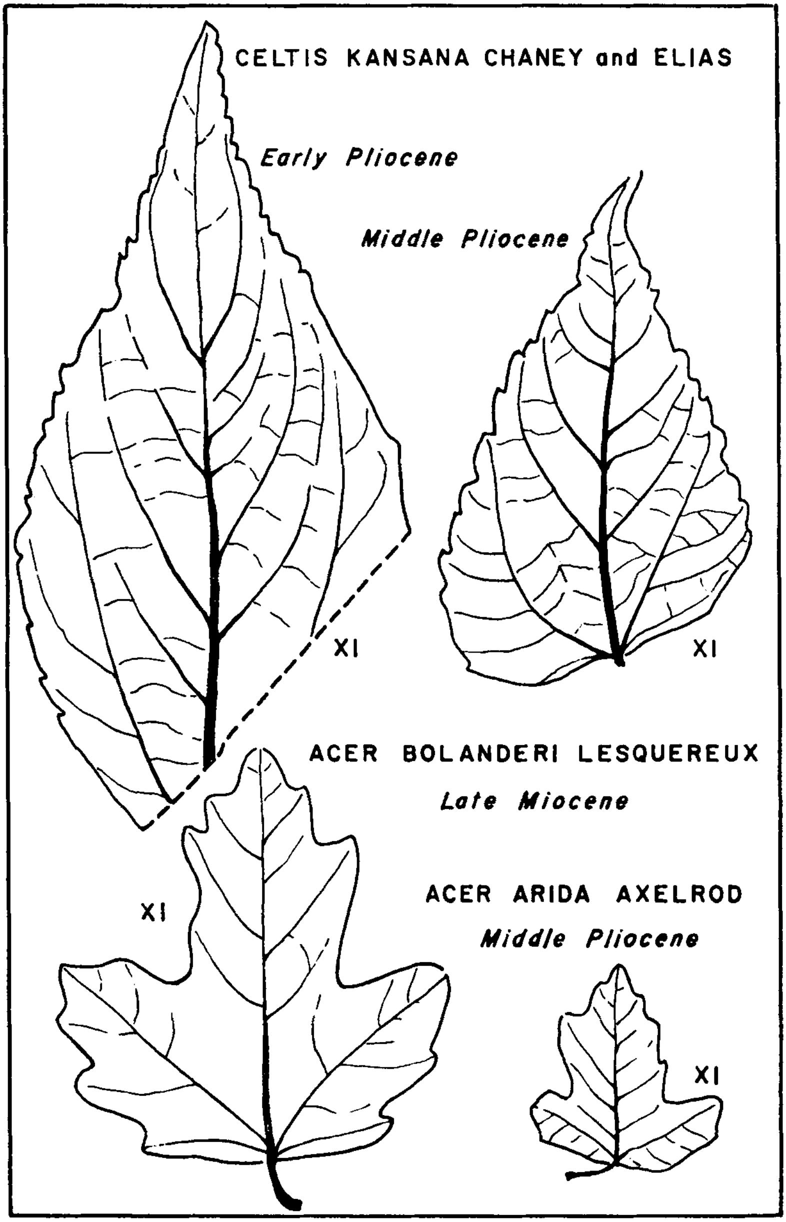


Fig. 4

Reduction in leaf size during the Late Tertiary.

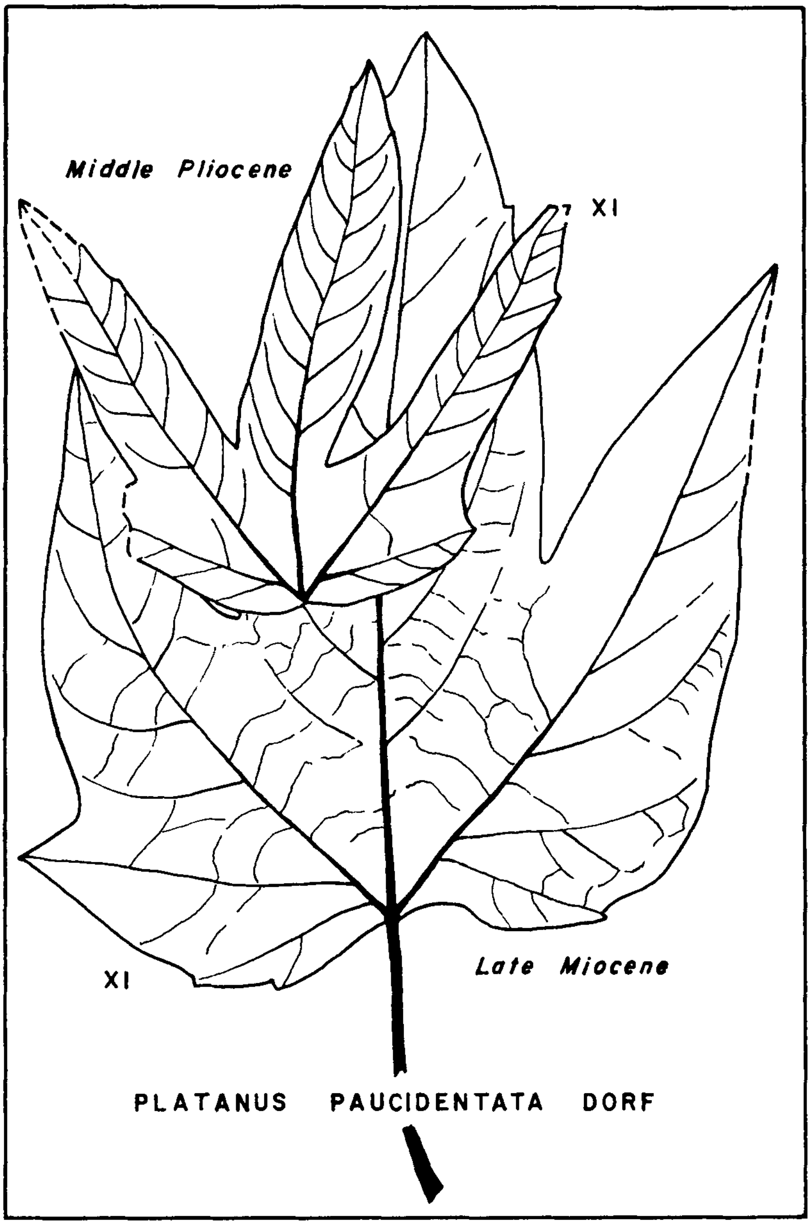


Fig. 5

Reduction in leaf size during the Late Tertiary.

that toward smaller foliar organs, which is also displayed by these tropic phylads as they are traced into drier areas, both trends probably developed in concert.

FRUITING STRUCTURES

A nearly continuous record of evolutionary change is provided by seeds of grasses and boraginaceous herbs in rocks of the Arikaree, Hemingford and Ogallala groups of the High Plains, distributed from South Dakota to northern Texas (Elias, 1942). Elias referred most of the fossil grasses to the Stipeae, and a few to the Paniceae. Species of Stipeae chiefly represent the extinct genera *Stipidum* and *Berriochloa*, which Elias considered ancestral to modern species of *Stipa* (and some of its subgenera) that arose from them in the Late Pliocene. The extinct genus *Parastipidium* gave rise to *Nassella* and *Oryzopsis* in the Middle and Late Pliocene, respectively. Seeds of the boraginaceous herb *Biorba* are regarded as ancestral to the living *Lithospermum* and *Anchusa*, which came into existence in the Quaternary. *Krynitzskia* has been in existence since the Early Pliocene and has also given rise to the related genus *Lappula*. Full details of the phyletic sequences are illustrated in his fine monograph (Elias, 1942, pl. 17). Owing to their abundance, excellent preservation, wide distribution and rapid evoluton, the seeds provide a good index to age and have been used to zone the rocks of the High Plains.

Elias noted that there was a comparatively normal rate of evolution from Early Miocene into Early Pliocene time, followed by an outburst of speciation in the Middle Pliocene. This evolutionary activity probably was in response to the rapid expansion of semiarid climate over the western United States at that time, which was the driest part of the Tertiary (Axelrod, 1948). These Middle Pliocene steppe types had only a brief history, disappearing in the Late Pliocene as climate became moister.

Stebbins (1947) has suggested that most of the fossil Stipeae described by Elias represent *Piptochaetium*, a subgenus of *Stipa* confined now to the plains of Argentina and bordering areas. He notes that the seeds of *Stipidium* and *Nassela* described by Elias are well within the range of variation of living Argentine species. Although seeds of the Miocene grasses differ slightly from those of the modern species, those of the Pliocene species are closely

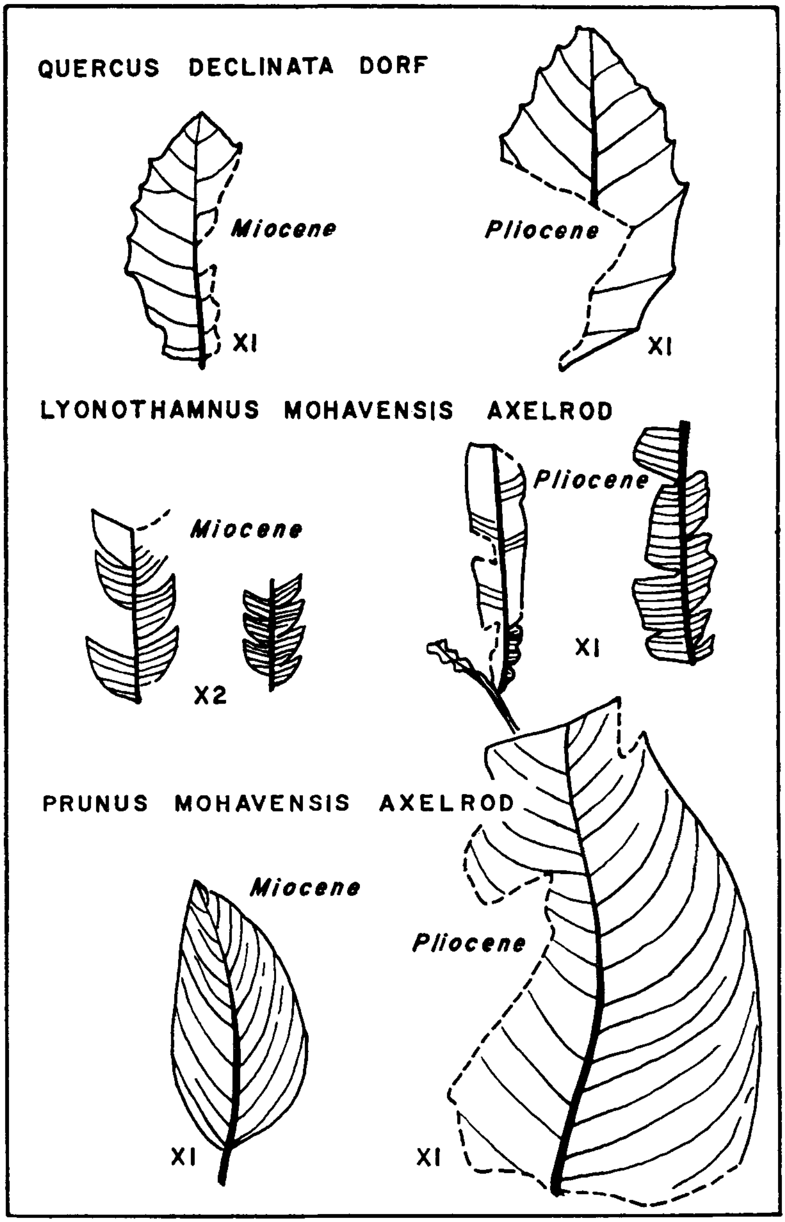


Fig. 6

Increase in leaf size during the Late Tertiary.

similar to present Argentine types. The relationship between Late Tertiary grasses of the High Plains and living Argentine species is not surprising. Many other genera are represented by paired species that have a discontinuous distribution between these areas today, and plants in the deserts bordering these regions show a similar distributional pattern (Johnston, 1940). As outlined elsewhere, they are not Cretaceous desert and steppe relicts, as suggested by Johnston (1940), but are probably the result of Late Tertiary long-distance migration (Axelrod, 1948:140-142; 1952b).

VEGETATION

Late in Cenozoic time diverse physical conditions developed rapidly over western North America in response to general regional uplift throughout the western half of the continent. The major mountain systems that now form high topographic barriers, including the Sierra Nevada, Coast Ranges, Transverse and Peninsular Ranges of California, the Cascades of Oregon and Washington, the Basin Ranges of Nevada, the central and southern Rocky Mountains, and the Sierra Madre of Mexico, largely assumed their present heights in the later Pliocene and Pleistocene. In addition, high interior plateaus (Anahuac, Colorado) and plains (High Plains) were also elevated. These geologic events were accompanied by major climatic alterations which were due in part to secular change as well as to local topographic effects (Axelrod, 1957:40-42). The principal secular climatic modifications involved a continued decrease in yearly rainfall over lowland areas, a shift in seasonal distribution in the far West to a period of winter rain, a general lowering of winter temperature, and greater ranges and extremes of temperature developed throughout the region. Adjustment to these topographic and climatic changes resulted in major alterations in the floristic composition and distribution of the Madro-Tertiary Geoflora. Thus it was chiefly in the Late Cenozoic that various woodland, chaparral, thorn scrub and desert communities were segregated from the geoflora to give rise to the modern associations that are now more or less in harmony with these new environments. In the following pages the evolution of some of the derived communities of the geoflora, chiefly woodland and chaparral vegetation, is reviewed.

WOODLAND

CALIFORNIA WOODLAND ELEMENT. Several distinctive communities comprise California woodland vegetation today. In central California the major ones include the live oak woodland of the coastal region and the digger pine-live oak woodland of the inner Coast Ranges and Sierran foothills. In southern California an endemic insular woodland characterizes the Channel Islands and extends southward to Guadalupe and Cedros Islands, a walnut-live oak woodland typifies the coastal area, and an Engelmann oak woodland the interior. The chaparral in each of these areas also differs.

During the Tertiary, fossil relatives of modern California woodland and chaparral species ranged more widely than do their living descendants. Some of the more important occurrences of these plants are listed in Table II and are shown in Fig. 7; those with distributions in California represent occurrences markedly different from those of their present counterparts. The Late Tertiary relatives of living California species were associated with plants that now characterize different woodland communites. For example, a number of typical California species, in genera such as *Arctostaphylos, Ceanothus, Cercocarpus, Garrya, Photinia, Quercus, Rhus* and *Styrax*, have close counterparts in the Great Basin (Table II lists fossil species and their modern relatives). Occurring with them were fossil representatives of the present day conifer-woodland, including piñon, juniper and a number of shrubs that characterize that community today (see below, Conifer Woodland Element). In addition, these floras contain Sierra Madrean Woodland species, in genera such as *Arbutus, Bumelia, Cercocarpus, Populus, Rhus* and *Robinia.*

In the same way the Late Tertiary floras of central California contain trees and shrubs whose modern descendants now survive there. But they were associated with species closely related to present day insular endemics of southern California, including *Lyonothamnus mohavensis* (*floribundus*)[5] and *Quercus declinata* (*tomentella*), as well as such plants as *Celtis kansana* (*reticulata*), *Prunus prefasciculata* (*fasciculata*), *Quercus convexa* (*engelmanii*), *Rhus* (*Malosma*) *prelaurina* (*laurina*) and *Rhus* (*Schmaltzia*)

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[5] Species in parenthesis on this and the following pages represent living plants most nearly related to the fossil species.

TABLE II

Components of the California Woodland and Chaparral Elements and Their Distribution

	Digger pine Woodland, Diablan-Mariposan Chap.	Walnut-Oak Woodland, Ynezian Chaparral	Engelmann oak Woodland, Cismontane Chaparral	Insular Woodland and Chaparral	Fossil localities
Arctostaphylos preglauca (glauca)	x	x	x	x	Esmeralda
Ceanothus precuneatus (cuneatus)	x	x	x	x	Verdi, Middlegate, Alvord Cr.
Ceanothus prespinosus (spinosus)				x	Mulholland, Mt. Eden, Piru Gorge
Celtis kansana (reticulata)			x		Mulholland, Oakdale
Cercis carsoniana (occidentalis)	x				Middlegate
Cercocarpus antiquus (betuloides)	x	x	x	x	Alvord Cr., Middlegate, Aldrich Station
Forestiera buchananensis (neomexicana)			x		Table Mtn.
Garrya gianellana (fremontii)	x				Chalk Hills
Juglans beaumontii (californica)		x			Truckee
Lyonothamnus mohavensis (floribundus)				x	Tehachapi, Mint Canyon, Mulholland, Valley Spr.
Photinia sonomensis (arbutifolia)	x	x	x	x	Alvord Creek
Pinus pieperi (sabiniana)	x				Pico, Mount Eden

TABLE II (Continued)

COMPONENTS OF THE CALIFORNIA WOODLAND AND CHAPARRAL ELEMENTS AND THEIR DISTRIBUTION

	Digger pine Woodland, Diablan-Mariposan Chap.	Walnut-Oak Woodland, Ynezian Chaparral	Engelmann oak Woodland, Cismontane Chaparral	Insular Woodland and Chaparral	Fossil localities
Prunus mohavensis (lyonii)				x	Tehachapi, Mint Canyon, Mount Eden, Piru Gorge
Prunus prefasciculata (fasciculata)			x		Mulholland
Quercus convexa (engelmanii)			x		Table Mt., Verdi, Sonoma, Mulholland
Quercus declinata (tomentella)				x	Sonoma, Mulholland, Weiser
Quercus dumosoides (dumosa)	x	x	x	x	Florissant
Quercus hannibali (chrysolepis)	x		x	x	Fallon, Aldrich Station, Middlegate, Weiser
Quercus pliopalmeri (palmeri)			x		Mulholland, Tehachapi
Quercus wislizenoides (wislizenii)	x		x	x	Fallon, Middlegate, Chloropagus
Rhus moragensis (ovata)		x	x	x	Mulholland, Esmeralda
Rhus preintegrifolia (integrifolia)		x		x	Mount Eden, Tehachapi
Rhus prelaurina (laurina)		x		x	Mulholland, Mount Eden, Mint Canyon, Anaverde
Styrax middlegatei (californica)	x				Middlegate

moragensis (*ovata*), whose descendants are typical now of southern California communities. These floras also had a Sierra Madrean Woodland Element, comprising species of *Ilex, Mahonia, Quercus, Robinia, Sapindus* and *Ungnadia* (see Table III). Similarly, the Late Tertiary floras of southern California include close relatives of many plants that are typical of that region today. Mixed with them were species whose descendants are distinctive now of 1) the Insular Woodland, such as *Lyonothamnus mohavensis* (*floribundus*), *Prunus* (*Laurocerasus*) *mohavensis* (*lyonii*) and *Quercus declinata* (*tomentella*); 2) the Coastal woodland and chaparral such as *Ceanothus prespinosus* (*spinosus*), *Juglans beaumontii* (*californica*), *Rhus preintegrifolia* (*integrifolia*), *Rhus prelaurina* (*laurina*); 3) the central California digger pine woodland, with *Pinus pieperi* (*sabiniana*) and *Quercus douglasoides* (*douglasii*); and of 4) interior communities that range to the margins of the desert, notably *Cercidium edensis* (*floridanum*), *Condalia coriacea* (*parryi*), *Prosopis mohavensis* (*juliflora*) and *Quercus convexa* (*engelmannii*). Again, they are regularly found with Sierra Madrean Woodland plants, including species of *Arbutus, Juglans, Persea* and *Sapindus.* In this warmer region Arid Subtropical vegetation, including species of *Acacia, Bursera, Condalia, Ficus, Leucanea, Pithecolobium* and *Randia,* lived in closed association (Axelrod, 1939, 1950c, d).

With respect to segregation of modern woodland and chaparral communities from the ancestral Madro-Tertiary vegetation, Sierra Madrean species were restricted southward as summer rains were eliminated during the Pliocene, and only a few relicts are recorded in the Late Pliocene. California oak woodland and chaparral species apparently disappeared from the Great Basin chiefly in response to the development of colder winters over the area in the later Pliocene and during the Pleistocene (Axelrod, 1940b, 1950f). Fossil relatives of modern southern California species were also eliminated from central California late in the Pliocene, apparently as winters became cooler (Axelrod, 1944b: 117). The uplift of the Transverse Ranges during the mid-Pleistocene accounts chiefly for the sharp floral boundary that separates the central and southern California floras today. These mountains regularly block rain-bearing winter storms from entering southern California and result in warmer winters and lower rainfall there as compared with

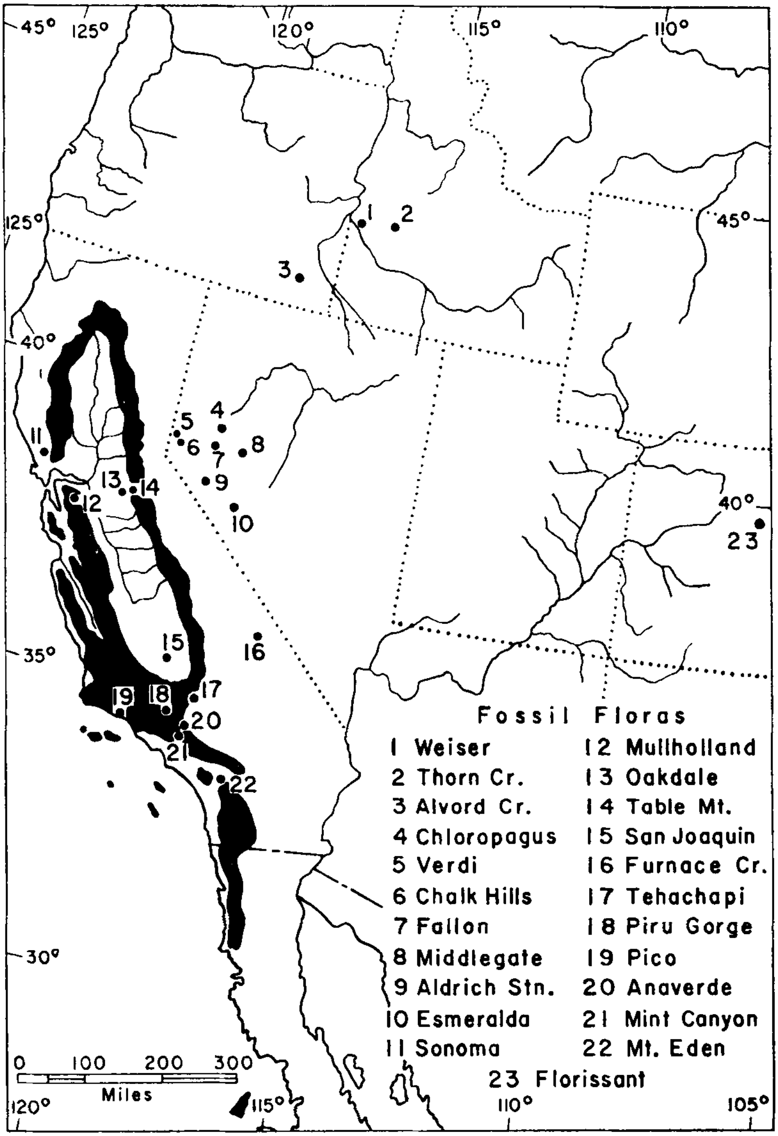

Fig. 7

Occurrence of present California woodland and chaparral (black) and records of related Tertiary vegetation.

central California. Thus differentiation of the woodland and chaparral of these area was due chiefly to recent climatic changes which eliminated from central California species that thrived there into the Late Pliocene under winter climates which were more mild than those that occur there now. That segregation of these floras was taking place as late as the Quaternary is shown by a record of *Juglans californica* in the San Joaquin Valley.

In marked contrast to these communities, the later history of the digger pine woodland appears to have been one chiefly of restriction northward to an area of cooler winter climate. This community now typifies the foothills bordering the Great Valley of California, extending from the flanks of Mount Shasta southward for 400 miles to the edge of the Mojave Desert at Tehachapi Pass and Antelope Valley. Its typical dominants, *Pinus sabiniana* and *Quercus douglasii*, have close counterparts in the Middle Pliocene rocks of southern California (Dorf, 1930; Axelrod, 1937, 1950c), 100 miles south of the present margins of the association, in a region where winter climate is now much milder. The northward restriction of this community was accompanied by the elimination from it of species whose modern derivatives occur in the Sierra Madrean woodland of the southwestern United States, in the Sinaloan thorn scrub of northern Mexico, and in southern California woodland and chaparral vegetation.

Although the floras of central and southern California are largely distinct today, a few typical southern California species have relict occurrences in central California, e.g., *Quercus palmeri* near Paso Robles and *Adenostoma sparsifolium* east of San Luis Obispo (for others, see Axelrod, 1944b: 117). They may be survivors of Pliocene species that were able to persist in favorable sites, though possibly they are relicts of a northward migration during a warm interglacial.

Late Tertiary relatives of species that live now in coastal southern California have been recorded in interior southern California (Axelrod, 1937, 1939, 1950c, 1950d, 1950e). They apparently were restricted coastward as the Peninsular Ranges, Transverse Ranges, Santa Ana Mountains and Puente Hills were elevated in the Middle Pleistocene, and as hotter summers and colder winters developed over the inland region (Axelrod, 1950c, 1950d, 1950e). Differentiation of the modern flora of southern California into coastal and interior sectors is thus quite recent. Hence it is not surprising to find that some coastal species still range inland along major river valleys that have moderating fogs and breezes in summer, and that a few insular endemics still have a foothold in favorable coastal sites. Since this insular flora is a unique one, it seems desirable to review its history in somewhat greater detail than the other California woodland communities.

INSULAR WOODLAND. The flora of the islands off the coast of southern California and northwestern Baja California is rich in species that are known only from this archipelago. Outstanding among the trees and shrubs restricted to this region are:

Ceanothus arboreus
Cercocarpus traskii
Crossosoma californica
Cupressus guadalupensis
Erythea armata
Lyonothamnus floribundus
Hesperelea watsoni
Pinus remorata
Quercus macdonaldii
Quercus tomentella
Rhamnus pirifolia
Salvia brandegei

Several others that are essentially endemic to the insular archipelago have only isolated mainland occurrences:

Ceanothus insularis	Santa Ynez Mountains
Comarostaphylos diversifolia	Santa Ynez Mountains
Lavatera assurgentifolia	Torrey Pines Park
Pinus torreyana	Torrey Pines Park
Prunus (Laurocerasus) lyonii	San Julio Canyon, Baja Calif.

In addition, a number of herbs are known only from these islands of the continental shelf area (for lists, see Munz, 1935). The regular associates of all these endemics are plants that are typical of the southern California flora, including such common trees and shrubs as:

Arctostaphylos glandulosa
Ceanothus cuneatus
Fremontia californica
Platanus racemosa
Populus fremontii
Quercus agrifolia
Quercus dumosa
Quercus englemannii
Rhus laurina
Rhus integrifolia
Salix lasiolepis

The probable history of this insular flora first was outlined by LeConte (1887) who inferred that recent geological changes in southern California chiefly account for its high endemism. His thesis was that the present insular area was colonized from the mainland during the Pliocene, the epoch in which he thought the islands were largely connected with the mainland. LeConte thus considered that the modern insular flora represents in a general way the flora of southern California during the Pliocene and that it retained much of its original composition because of isolation of the insular region by subsidence during the Pleistocene.

LeConte's major inferences find support in present geological and paleobotanical evidence. The islands lie on broad, shallow marine shelves, but since the area of each island is small, only a minor part of the geologic history of the insular region is available for study. Thus the actual connections between the island areas and the mainland are somewhat uncertain. The most recent evidence suggests that the Santa Barbara Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) probably were connected with the mainland during most of the Pliocene (Corey, 1954), and San Nicholas to the south may have been united with this Pliocene peninsula (Fig. 8). Catalina and Santa Barbara appear to have formed a large island in the Pliocene, but San Clemente may have been isolated. Although some of these islands probably were not connected with the mainland in the Pliocene, this would not have hindered migration, for the distances are not great and paleoclimate was favorable for establishment of migrants (Axelrod, 1952b).

Close ancestors of present insular endemics appear first in the Miocene rocks of southern California (Axelrod, 1939, 1940c; U. C. Mus. Pal.), where species similar to the living *Ceanothus insularis, Cercocarpus traskii, Lyonothamnus floribundus, Prunus lyonii, Quercus tomentella* and *Rhus lentii* are recorded. Their associates comprised many fossil species of the California Woodland and Chaparral Elements, including all of the modern equivalents listed above which occur in both the insular and mainland areas. Additional associates comprised trees and shrubs of the Sinaloan Element of thorn scrub alliance (*Acacia, Bursera, Colubrina, Dodonaea, Erythea, Euphorbia, Ficus, Karwinskia, Pithecolobium, Randia*) that are confined now to northern Mexico.

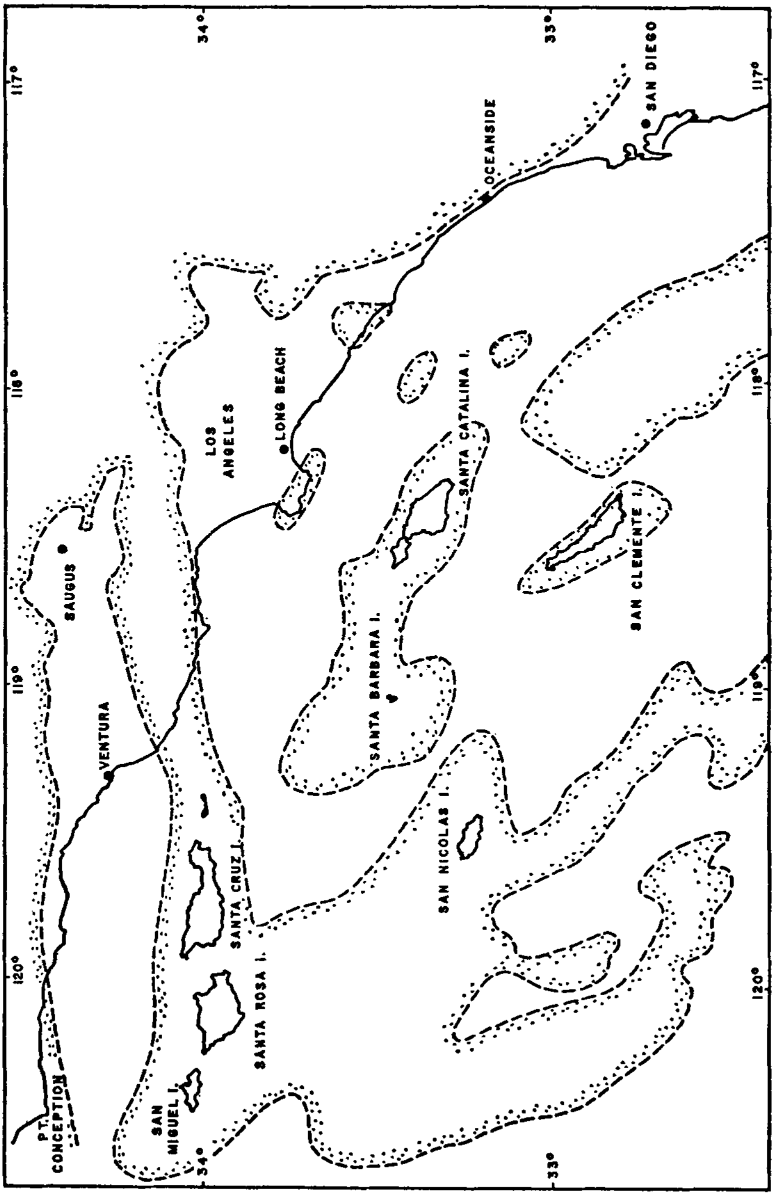

Fig. 8

Generalized Pliocene land-sea relations in southern California (after Corey, 1955).

The Sierra Madrean Woodland Element, with its species of *Arbutus, Celtis, Clethra, Ilex, Mahonia, Persea, Populus, Quercus, Robinia* and *Sapindus,* all represented by related living species in woodland from Arizona eastward to Texas and southward into Mexico, is regularly recorded with fossil relatives of the insular endemics. The same general association of floristic elements persisted into the Pliocene of the region. Clearly, the Insular Woodland is an integral part of the Madro-Tertiary Geoflora.

A few species of the Insular Woodland Component also occur with members of the Madro-Tertiary Geoflora in areas to northward, as in central California, demonstrating that close relatives of these insular species had a wider range on the continent in the recent past. *Lyonothamnus,* one of the most distinctive genera known anywhere in the record, has a related fossil species in two central California floras (Axelrod, 1944b, 1944e:218), as does *Quercus tomentella* (Axelrod, 1944b, 1944d).

The Madro-Tertiary Geoflora, of which these insular species were a part, was differentiated into floristic regions during the later Cenozoic in response to climatic change. Disappearance of summer rain and lowering of winter temperature apparently account for the restriction southward to Mexico of arid subtropic vegetation. The Sierra Madrean Woodland Element also disappeared from California as summer showers were reduced in amount and in frequence. Significantly, a few of these types still persist with the insular endemics on Cedros and Guadalupe Islands, as well as with *Prunus lyonii* at its only known mainland station in southern Baja California, all areas of milder winters and more frequent summer showers than southern California.

Thus by the close of the Pliocene only a generalized California flora was left over the region from central California southward into Baja California. As colder winters developed in central California in the Late Pliocene, relatives of insular endemics were eliminated there. Some of the present endemics persisted on the mainland in southern California into the Pleistocene, as shown by the Plio-Pleistocene occurrence of *Pinus remorata* at Potrero Canyon near Santa Monica, and by its Pleistocene record at Carpinteria (Chaney and Mason, 1933), when the Santa Monica Mountains still extended seaward to include the Santa Barbara Islands. Although a few insular species occur at isolated mainland localities close to the coast, most of them presumably disappeared from the mainland in response to colder Pleistocene climates. They survive now only under the milder climate of the continental shelf islands, a region they probably have occupied continuously since the Late Tertiary, as suggested by LeConte.

CONIFER WOODLAND ELEMENT. A piñon-juniper woodland now ranges from the east front of the southern Cascade-Sierra Nevada-Peninsular Ranges to the Front Range in Colorado, northward to the Oregon-Idaho-Wyoming border, and southward to central Arizona and New Mexico. In the Great Basin it is dominated by *Pinus monophylla* and *Juniperus utahensis*, but at the east chiefly by *P. edulis and J. monosperma*. The community comprises small trees which are usually well scattered. Whereas grasses make up an important ground cover in the eastern community, the western association has chiefly a dense matrix of *Artemisia tridentata*, *Purshia tridentata* and their usual associates[6]. Evergreen oaks, which are so characteristic of the pine-oak woodland of the southwestern United States and adjacent Mexico, are absent. With respect to its evolutionary history, we shall discuss first the western or Nevadan community, and then the eastern or Coloradan.

The Madro-Tertiary Geoflora gradually invaded the central and northern Great Basin during the Late Miocene and assumed dominance over the lowlands in the Early Pliocene (Axelrod, 1940a, 1940b, 1950f, 1956). The fossil floras of this region contain plants whose modern derivatives now comprise the Nevadan pinon-juniper association, including *Amelanchier apiculata* (*utahensis*), *Cercocarpus linearifolius* (*ledifolius*), *Juniperus nevadensis* (*utahensis*), *Pinus lindgreni* (*monophylla*), *Prunus preandersonii* (*andersonii*), *Purshia* n. sp. (*tridentata*) and *Symphoricarpos oreophiloides* (*oreophilus*). Shrubs that occurred with them in western Nevada but whose modern relatives are now characteristic of the Coloradan association include *Cercocarpus holmesii* (*paucidentatus*) and *Fraxinus millsiana* (*anomala*). Other typical cordilleran species in the region at this time were *Acer arida* (*grandidentatum*) *and Populus payettensis* (*angustifolia*).

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[6] This may be due in part to overgrazing in a region of summer-dry climate.

Their regular associates were plants whose modern relatives now comprise two other woodland communities. As listed in Table II, some of these species find their close descendants in the present woodland and chaparral communities of central and southern California. Others were typical Sierra Madrean Woodland plants, including species of *Arbutus, Populus, Quercus, Rhus* and *Robinia* (see Table III).

It is evident that during the Early Pliocene the Madro-Tertiary Woodland in the Great Basin was of generalized composition, for representatives of all these floristic units occurred in association. As precipitation gradually decreased during the Pliocene, due in part to secular climatic change and in part to the Late Cenozoic elevation of the Sierra Nevada (Axelrod, 1957), steppe environments came into existence over the lowlands, and woodland and chaparral gradually were confined to the moister basin ranges. With the disappearance of summer rains, Sierra Madrean species were restricted to summer-rain areas to the southeast where winters are comparatively mild. Representatives of the Coloradan piñon-juniper community were confined eastward to the central cordilleran area of biseasonal precipitation and cold winters. Lowered winter temperatures seem to account for the elimination of species of the California Woodland and Chaparral Elements from the region, though a few of their derivatives persist as relicts on the west margin of the province: *Quercus chrysolepis* occurs near Woodfords on the east front of the Sierra Nevada; *Ceanothus greggii* has a relict station near Reno; and *Quercus wislizenii* and *Fraxinus velutina* are near Independence. Clearly, the surviving piñon-juniper woodland of the Great Basin, which lacks those species that occur now in California, or the southwestern United States, or the central cordilleran area, but whose fossil relatives were associated with it in the Great Basin into Middle Pliocene time, is an impoverished, derivative community that has become adapted to the colder climate of post-Middle Pliocene time. Today the surviving Nevadan conifer woodland ranges southward to the Transverse and Peninsular Ranges of southern California, where it meets many species whose fossil relatives occurred with its Pliocene counterpart in Nevada. It also extends southeastward where it mingles with derivatives of the Sierra Madrean Woodland in southern Utah and adjacent Arizona, a region of summer rain, and to the east it meets the Coloradan conifer woodland in central Utah.

Comparatively few floras are now available to assist in an analsis of the history of the Coloradan association. The best records of it are provided by the Creede flora of south-central Colorado, where it interfingered with montane forest in the Creede basin (Knowlton, 1923; Stewart, 1940). Juniper is well represented, together with species of *Chamaebataria, Holodiscus* and *Philadelphus*, whose derivatives are in the association today. Madro-Tertiary plants at Creede which have related species that now live in regions of milder winter climate to southward include species of *Arbutus, Ceanothus, Cercocarpus, Mahonia* and *Rhus.* Other floras in the nearby region, such as the Antero (U. S. Nat. Mus.), Florissant (MacGinitie, 1953) and Silver Cliff (Lesquereux, 1887), also include members of this group.They appear to have been confined southward at the close of the Tertiary as the area was elevated several thousand feet, and a colder winter climate developed over the region. Thus the surviving conifer woodland is an impoverished community, comprising hardier types that became adapted to a climate of lower winter temperature.

SIERRA MADREAN WOODLAND ELEMENT. The Sierra Madrean Woodland, which now ranges across northern Mexico from the Cape Region of Baja California to the Sierra Madre Oriental in Nuevo and Tamaulipas, and northward into southern Arizona, New Mexico and western Texas, is typified by evergreen oaks and conifers (piñon and juniper). Some of its more characteristic and widely distributed species are:

Arbutus arizonica
Juniperus pachyphloea
Pinus edulis
Quercus arizonica
Quercus emoryi
Quercus grisea
Quercus oblongifolia
Quercus hypoleucoides

Regularly associated with them along stream courses are species of *Celtis, Condalia, Fraxinus, Juglans, Morus, Platanus, Populus, Robinia* and *Sapindus.* Diverse shrubs are scattered through the woodland, and in some areas contribute to chaparral. Among these are species of *Arctostaphylos, Ceanothus, Cercocarpus, Condalia, Garrya, Mahonia, Rhus* and *Vauquelinia.* Throughout the region a sprinkling of dry tropic types often is scattered in the association, including species of *Acacia*, *Agave*, *Brickellia*, *Calliandra*, *Nolina* and *Yucca*.

Important changes occur in the composition of woodland vegetation across this broad region. Distinctive associations characterize the area from *a*) the Edwards Plateau southward into Nuevo Leon, *b*) in the Sierra Madre Oriental farther south, notably in the region of San Luis Potosi, *c*) in the area of southern Arizona-New Mexico-west Texas, and adjacent Sonora and Chihuahua, *d*) in the Sierra Madre from Sinaloa into Durango, and *e*) in the Cape Region of Baja California. Fossil plants representing close ancestors of species now characterizing these associations have been recorded at many localities in the western United States. They correspond to the Coahuilan, Potosian, Arizonan, Durangan and Lagunan Woodland Components, respectively (Axelrod, 1950a). The more important occurrences of Sierra Madrean fossil plants in areas north of the ranges of their present living analogues are listed in Table III and plotted in Figure 9.

Some of the Sierra Madrean species recorded in California are represented by plants that live now chiefly in the region from west-central Texas into northeastern Mexico. The occurrence of representatives of typically eastern plants on the west coast during the Tertiary is shown also by species of other communities. Members of subtropical forests in the coastal Eocene and Early Oligocene floras of California have many of their surviving equivalents in the Sierra Madre of Mexico south of Monterrey (Potbury, 1935; MacGinitie, 1941). The deciduous hardwood forests of eastern North America have a large generic representation in the middle Tertiary floras in the far West (Chaney, 1938, 1947, 1957). And certain members of the arid subtropic scrub on the east coast of Mexico also have close counterparts in the Miocene of southern California. The relationships of species of five types of vegetation in the fossil record—subtropical forest, deciduous hardwood forest, woodland, chaparral, arid subtropic scrub—thus unite to indicate that throughout the Tertiary there was a greater degree of simlarity between the floras of the east and west coasts than exists today.

We have noted that species of the Sierra Madrean Woodland Element regularly lived with plants comprising the California

TABLE III

Components of the Sierra Madrean Woodland Element and Their Distribution

Fossil Species; Similar Living Plants in Parentheses	COMPONENTS					Fossil Records
	Lagunan	Arizonan	Durangan	Coahuilan	Potosian	
Arbutus mohavensis (peninsularis)	x					Tehachapi
Arbutus prexalapensis (xalapensis)			x	x	x	Mount Eden; Middlegate
Arctostaphylos prepungens (pungens)		x	x			Clarendon
Bumelia beaverana (lanuginosa)		x	x	x		Aldrich Station; Anaverde
Cercocarpus holmesii (paucidentatus)		x	x	x		Sonoma; Alvord Cr.; Middlegate; Silver Cliff
Cercocarpus myricaefolius (macrophyllus)				x	x	Florissant
Cercocarpus n. sp. (montanus)		x				Mint Canyon
Clethra petolaris (lanata)			x			Tehachapi
Condalia mohavensis (lycioides)		x		x		Tehachapi; Laverne
Colubrina lanceolata (arborea)	x					Tehachapi
Colubrina spiraeafolia (glomerata)				x	x	Florissant
Forestiera sp. (*reticulata*)				x		Tehachapi
Ilex sonomensis (brandegaena)	x					Sonoma; Mint Canyon
Juglans beaumontii (rupestris)		x				Mount Eden

TABLE III (Continued)

COMPONENTS OF THE SIERRA MADREAN WOODLAND ELEMENT AND THEIR DISTRIBUTION.

Fossil Species; Similar Living Plants in Parentheses	COMPONENTS					Fossil Records
	Lagunan	Arizonan	Durangan	Coahuilan	Potosian	
Leucanea californica (microcarpa)				x		Tehachapi
Mahonia prelanceolata (lanceolata)			x			Table Mountain, Sonoma
Mahonia obliqua (trifoliata)		x				Florissant
Morus symmetrica (microphylla)		x				Florissant
Myrica mohavensis (mexicana)					x	Tehachapi
Persea florissanti (podadenia)			x			Florissant
Platanus florissanti (wrightii)		x				Florissant
Quercus convexa (oblongifolia)		x				Tehachapi; Table Mountain
Quercus mohavensis (brandegei)	x					Tehachapi; Florissant
Quercus orindensis (vaseyana)				x		Mulholland
Quercus peritula (incarnata)			x	x	x	Florissant
Quercus turneri (arizonica)		x				Esmeralda
Populus sonorensis (brandegei)	x					Tehachapi; Mount Eden; Anaverde; Aldrich Station

TABLE III (Continued)

COMPONENTS OF THE SIERRA MADREAN WOODLAND ELEMENT AND THEIR DISTRIBUTION

Fossil Species; Similar Living Plants in Parentheses	COMPONENTS Lagunan	Arizonan	Durangan	Coahuilan	Potosian	Fossil Records
Rhus stellariaefolia (lanceolata)				x		Florissant; Hazen
Rhus sonorensis (virens)		x	x			Tehachapi
Rhus tehachapiensis (chondroloma)		x	x			Tehachapi
Rhus n. sp. (*microphylla*)		x				Mint Canyon
Robinia californica (neomexicana)		x				Tehachapi; Mint Canyon; Table Mtn; Middlegate
Sapindus oklahomensis (drummondii)		x	x			Mount Eden; Mulholland
Sabal mohavensis (uresana)						Tehachapi; Piru Gorge
Sabal n. sp. (*mexicana*)			x	x		Clarendon
Ungnadia clarki (speciosa)			x	x		Table Mtn.
Vauquelinia coloradense (californica)		x				Florissant; Elko
Vauquelinia linaria (angustifolia)		x				Florissant; Elko
Zanthoxylon n. sp. (*pterota*)		x		x		Mint Canyon
Zizyphus florissanti (obtusifolia)		x				Florissant

Woodland and Conifer Woodland Elements during the Middle and Late Tertiary, and that their southward restriction was in response to different factors in different areas: *a*) in the far West they appear to have disappeared as summer rains were reduced; *b*) in the Great Basin both elimination of regular summer rain and development of colder winter climate seem to have been responsible; and *c*) in the central Rocky Mountains and on the High Plains lowered winter temperature apparently was the critical factor. As Sierra Madrean species were confined to more southerly areas, surviving members of the California Woodland and Conifer Woodland associations persisted and adapted to the new climates that typify the regions their descendants now occupy.

Segregation of the Sierra Madrean Woodland into its major associations probably took place chiefly in response to the evolution of the distinctive semiarid climates that now characterize their areas. Until fossil floras containing relatives of these plants are discovered in the southwestern United States and adjacent Mexico, we shall not be able to outline the Late Cenozoic evolution of these communities. In the far West, however, there are important records of one of these distinctive, derivative Sierran Madrean associations—the Lagunan woodland of the Cape Region of Baja California and adjacent areas to northward. Thus it seems appropriate to sketch briefly the history of this endemic community.

LAGUNAN WOODLAND. The Lagunan woodland is isolated from the California woodland to northward by nearly 600 miles of desert, and from the Arizonan and Durangan woodlands by the Gulf of California and the desert plains of Sonora. It attains optimum development at altitudes of 4000 to nearly 8000 feet in the Sierra Laguna south of La Paz, but remnants of it are scattered northward along the summit of the Sierra Gigantea to the vicinity of Commondu at Lat. 26°N. Many of its characteristic woody species are endemic, including *Arbutus peninsularis, Garrya salicifolia, Populus brandegeei, Quercus brandegei, Q. devia* and *Q. idonea.* Some of its distinctive species, for instance, *Ilex brandegaena, Quercus albocincta* and *Rhus hartmannii,* have a discontinuous distribution, occurring also in the mountains of southern Sonora and adjacent Sinaloa where they contribute to oak woodland communities. Numerous herbs are also known only from this region. Among the usual associates of the Lagunan woodland are

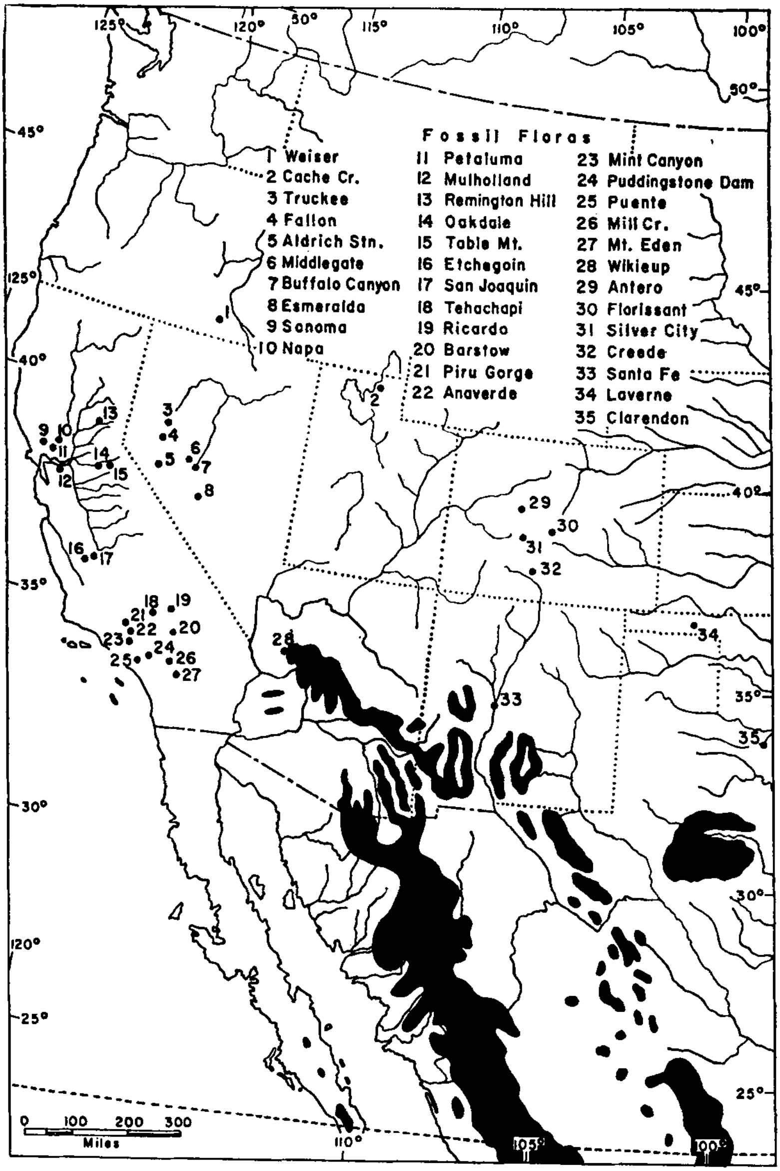


Fig. 9

Occurrence of present Sierra Madrean Woodland (black) and records of related Tertiary vegetation.

species of *Celtis, Platanus, Pinus,* (piñon), *Populus* and *Salix,* all of which range widely through areas of woodland vegetation in southwestern North America. The Lagunan woodland commonly extends down the canyons to warmer levels, to interfinger with arid subtropical vegetation characterized by *Acacia, Albizzia, Bursera, Cassia,* numerous cacti, *Erythea, Ficus, Lysiloma, Karwinskia, Pithecolobium, Randia* and many others (Nelson, 1921; Shreve, 1938).

Fossil species closely related to modern Lagunan woodland species occur in several floras in the western United States, as shown in Fig. 10 and listed in Table IV.

TABLE IV

DISTRIBUTION OF FOSSIL SPECIES OF LAGUNAN WOODLAND COMPONENT

Flora and Region	Fossil Species of Lagunan Woodland	Similar living Species
Southern California		
Anaverde	*Populus sonorensis*	*P. brandegeei*
Mill Creek	*Populus sonorensis*	*P. brandegeei*
Mint Canyon	*Ilex sonomensis* *Quercus mohavensis*	*I. brandegaena* *Q. brandegei*
Mount Eden	*Populus sonorensis*	*P. brandegeei*
Tehachapi	*Populus sonorensis* *Arbutus mohavensis* *Quercus mohavensis*	*A. peninsularis* *P. brandegeei* *Q. brandegei*
Central California		
Sonoma	*Ilex sonomensis*	*I. brandegaena*
Central Nevada		
Aldrich Station	*Populus sonorensis*	*P. brandegeei*
Colorado		
Florissant	*Quercus mohavensis*	*Q. brandegei*

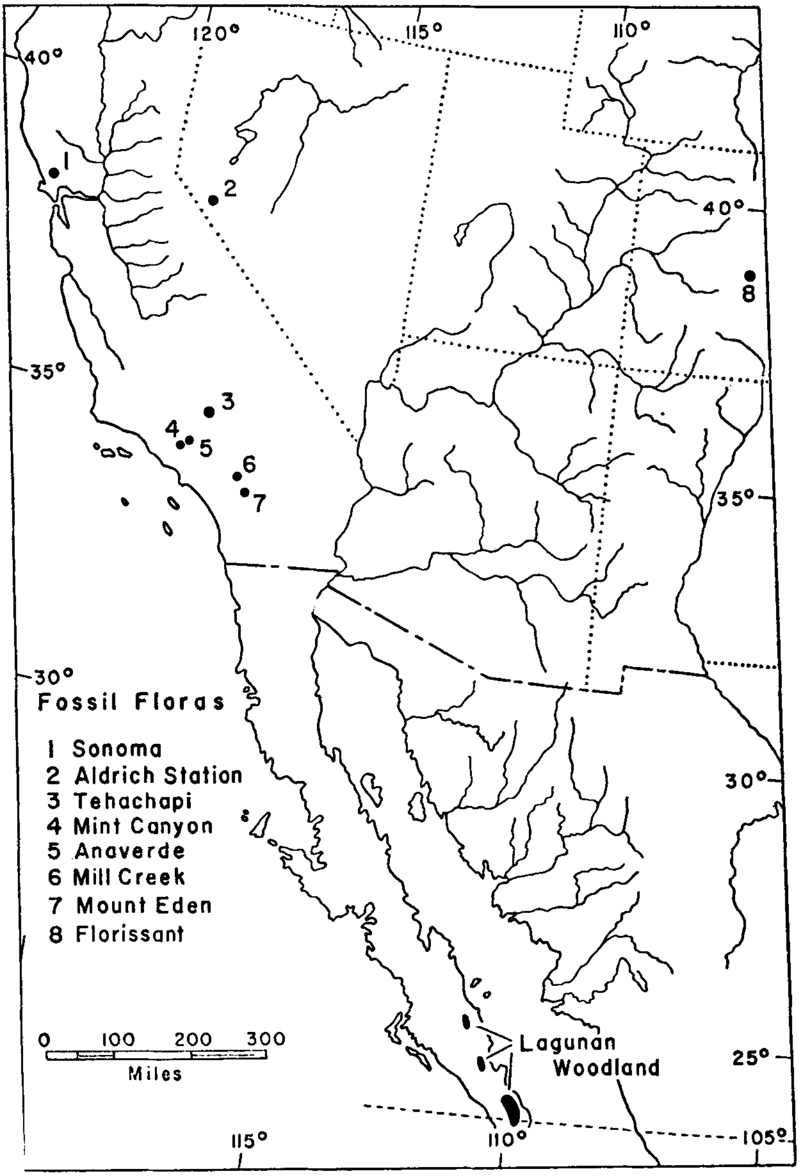


Fig. 10

Occurrence of present Lagunan woodland (black) and records of related Tertiary vegetation.

Their associates included fossil plants whose nearest modern relatives characterize woodland communities elsewhere in western North America. For example, the Miocene floras of southern California include such Lagunan woodland species as *Arbutus mohavensis* (*peninsularis*), *Ilex sonomensis* (*brandegaena*), *Populus sonorensis* (*brandegeei*) and *Quercus mohavensis* (*brandegei*), together with the following plants whose living representatives now typify the California flora:

Ceanothus precuneatus (*cuneatus*)
Ceanothus precrassifolius (*crassifolius*)
Cercocarpus antiquus (*betuloides*)
Lyonothamnus mohavensis (*floribundus*)
Prunus prefremontii (*fremontii*)
Prunus mohavensis (*lyonii*)
Quercus dispersa (*turbinella*)
Quercus hannibali (*chrysolepis*)
Quercus convexa (*engelmannii*)
Quercus pliopalmeri (*palmeri*)
Rhamnus precalifornica (*californica*)
Umbellularia salicifolia (*californica*)

Fossil species of other components of the Sierra Madrean Woodland, whose nearest relatives occur now in the southwestern United States and adjacent Mexico, are also recorded with them:

Arbutus prexalapensis (*xalapensis*)
Cupressus mohavensis (*arizonica*)
Myrica mohavensis (*mexicana*)
Quercus n. sp. (*emoryi*)
Quercus turneri (*grisea*)
Quercus n. sp. (*potosiana*)
Rhus tehachapiensis (*chondroloma*)
Rhus sonorensis (*virens*)
Zanthoxylon n. sp. (*clava-herculis*)

The occurrence of fossil representatives of Lagunan woodland endemics with species whose nearest relatives now form woodland associations in California, Arizona to Texas, and northern Mexico indicates that the Lagunan Woodland is a segregate of the Madro-

Tertiary Geoflora. That its general ecological relations have persisted since Miocene (and earlier) time is shown by the occurrence of arid subtropic scrub with these plants. Species of *Acacia*, *Bursera*, *Cardiospermum*, *Condalia*, *Dodonaea*, *Erythea*, *Ficus*, *Karwinskia*, *Lysiloma*, *Morus*, *Passiflora* and *Pithecolobium* regularly are recorded with these woodland species in the Miocene and Pliocene floras of southern California. And as noted above, woodland is also associated with subtropic plants in the Florissant and Green River floras. In all these instances, arid subtropic communities probably occupied the lower, warmer levels, with woodland on bordering slopes, relations of a type which occur widely in northern Mexico, including southern Baja California, today.

Available evidence suggests that the Madro-Tertiary Geoflora invaded the present region of Baja California during the Late Miocene. Geological data (Anderson, 1950) indicate that most of the peninsular region was a lowland area from the Cretaceous into the Miocene, with much of the southern half still inundated by the sea during the Middle Miocene. This was followed by volcanic activity (Commondu formation) in the Late Miocene, which formed a series of volcanoes extending along the present east coast of Baja California from the southern San Pedro Martir Range in the north to the Cape Region at the south.

The Madro-Tertiary Geoflora may have ranged southward from California, where it was well developed in the Miocene, along the middle and upper flanks of these volcanoes into southern Baja California. Migration over the lowlands from the north or east seems unlikely at that time, for arid subtropic scrub and patches of subtropical forest, both of which were well developed in the lowlands of southern California, probably dominated at these lower, warmer levels in northern Mexico. With subtropic communities in the lowlands, and woodland in the mountains, we find a close parallel with the present relations in Sonora and Sinaloa, as well as in the Cape Region, all areas where the Madro-Tertiary Geoflora shows relationship to modern vegetation.

Owing to the subsidence in the present area of the Gulf of California in the Early Pliocene, the sea extended northward from near Lat. 26° in the Gulf area to Banning in southern California, thus forming the peninsula of Baja California and isolating it from the mainland at the east. As drier climates developed in the later

Tertiary, the surviving woodland in the peninsula probably was confined gradually to higher altitudes and to successively more localized moister upland sites. The persistence of isolated patches of woodland along the crest of the Sierra Gigantea in the southern peninsula may be due to the fact that as precipitation was being reduced in the Late Tertiary, the present east scarp of the peninsula was elevated by large-scale faulting. Likewise, the occurrence of woodland in the Cape Region apparently is due chiefly to the elevation of that granitic highland several thousand feet by faulting in the Late Cenozoic, bringing into existence an area of cooler and moister climate above the dry subtropic vegetation that dominates the lower levels.

Several typical California species, including *Photinia arbutifolia* and *Rhus laurina*, still occur in the Lagunan woodland but a large number are not known from it. In proceeding northward to the middle peninsula region, where winter rains gradually increase, an important floral boundary is encountered near Commondu, north of which California plants are met with increasing frequence. In San Julio Canyon (alt. 3000 ft.), a few miles northwest of Commondu, are several relicts of the California flora that are not known from the Cape Region 200 miles southward. Outstanding among these is *Prunus lyonii* which is known elsewhere only from the Channel Islands off the coast of southern California. Additional plants at San Julio Canyon and in the nearby region include (Brandegee, 1889):

Celtis pallida
Celtis reticulata
* *Condalia brandegei*
Condalia obtusifolia
Colubrina glabra
Dodonaea viscosa
Fraxinus velutina
Populus fremontii
** *Quercus grisea*
Rhus laurina
Rhus microphylla
Sageretia wrightii
Sapium biloculare
Vauquelinia angustifolia
Viscainoa geniculata

* Recorded by Brandegee as *Condalia mexicana?*
** Recorded by Brandegee as *Quercus pungens?*

A botanist might well describe this community as a western outpost of the southern Arizona flora intermingling with California species, for associated here with typical California plants are an oak and a number of shrubs known elsewhere only from the southwestern United States and adjacent Mexico. Significantly, the same floristic relationship existed in southern California during Miocene and Pliocene times. This modern community in the central peninsula region thus appears to be a surviving relict of the Madro-Tertiary Geoflora that earlier extended southward into the Cape Region, together with species of the Lagunan woodland which have persisted in the moister, summer-rain upland areas farther south.

CHAPARRAL

In discussing woodland vegetation, chaparral was considered chiefly from a distributional standpoint. We noted that the community had a wider range in the past than it does today, that it included mixtures of species whose descendants now comprise different associations, and that its present areas are chiefly refugia where it has been able to persist under favorable environment. From a distributional standpoint the following points were made:

1. Ancestors of California chaparral species recorded in the Late Tertiary floras of the Great Basin probably disappeared there in the later Pliocene as winter temperatures were lowered.

2. Close relatives of typical southern California species were eliminated from central California in the later Pliocene, presumably as winter temperatures decreased.

3. Fossil counterparts of present day coastal southern California chaparral species which are recorded in interior southern California gradually were confined coastward during the late Cenozoic as hotter summers and colder winters developed over the interior in response to major topographic-climatic changes.

During the Tertiary, trees probably were mixed in with chaparral far more than they are today in the derivative California community. Such relations now exist in areas of summer rain, and which more nearly approximate the Tertiary environment. For example, in northeastern Mexico chaparral is a diversified community, comprising species of *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Garrya*, *Quercus* (scrub oak) and *Rhus*. But it commonly contains a scattering of piñon, juniper, oak and madrone of the woodland which is prominent at higher levels, as well as leguminous shrubs and other arid subtropic plants of the lower, drier elevations (Muller, 1939). Similar relations also occur on the Edwards Plateau, in southern Arizona and locally on the slopes of the desert ranges in southern California where fire has not been recently active.

In California, segregation of the sclerophylls to form the dominants of the chaparral probably took place during the later Pliocene in response to several factors. With the elimination of summer rains and the lowering of winter temperature, shrubs from the thorn scrub community in southern California which probably were mixed in the chaparral at lower, warmer levels were eliminated from the region. A few relict colonies of this type still persist on the slopes of the desert ranges from the San Jacinto Mountains southward, where species of *Acacia*, *Condalia*, *Fouquieria* and other genera are scattered in the community. The disappearance of summer rain eliminated a number of Sierra Madrean woodland trees which may also have been scattered in the Tertiary chaparral in California. The surviving California chaparral thus includes shrubs well adapted to summer drought.

As the summer-wet woodland and thorn scrub types were eliminated in the Late Pliocene, new habitats were rapidly formed by the rising mountains which attained essentially their present heights in the Middle Pleistocene. The surviving sclerophyllous shrubs were better adapted than woodland trees to survive on these exposed, steep, well-drained slopes subject to recurrent scorching fires and long periods of drought; in fact, fire commonly is necessary for chaparral seed germination, and in some species fire initiates rejuvenation by sprouting. Clearly, chaparral species in California have adapted to a new environment and have assumed new habits, a regular feature of all evolution.

A close relation exists between the chaparral of southern California and that in central Arizona. A number of species are common to the two communities, including:

Arctostaphylos pungens
Ceanothus greggii
Ceanothus integerrimus
Cercocarpus betuloides
Quercus Palmeri
Quercus Turbinella
Rhamnus Ilicifolia
Rhus Ovata
Ribes Quercetorum

Furthermore, certain common California chaparral species are known elsewhere only as relicts in the central Arizona community, including *Fremontia californica* and *Dendromecon rigida.* In the same way, some common Arizona species, e.g., *Mahonia fremontii,* are relict in California. The following species-pairs also link these two chaparral areas: *Mahonia nevinii-haematocarpa, Rhamnus californica-ursina, Arctostaphylos drupacea-pringlei.* The Arizona chaparral also embraces species of *Acacia, Agave, Mahonia, Nolina, Fallugia, Mimosa* and other genera that are not in the California community.

These interrelations clearly imply an historical connection. From the preceding discussion it is apparent that chaparral ranged across the present desert area in the Middle and Late Tertiary, closely associated with woodland and arid subtropic scrub communities, some of whose species entered the matrix of chaparral. Although the Arizona and California communities were closely similar into the Pliocene, ancestors of a number of typical Arizona types were eliminated from California as summer rains were reduced, and the two communities became more nearly separate entities. Connections across the desert presumably were severed in the latest Cenozoic as continued desiccation eliminated relict communites from most of the desert ranges.

Chaparral occurs also on the western flanks of the Sierra Madre Oriental in Nuevo Leon, Coahuila and Tamaulipas in northeastern Mexico (Pringle, 1888, 1890; Muller, 1939). Many of the dominant genera in the western associations typify the Coahuilan, and there are several species common to all communities. The greater degree of similarity between the Arizona and Coahuila chaparral, as compared with the California, is due chiefly to the occurrence of summer rain in the former regions, and winter precipitation in the latter.

Typical members of the Coahuila chaparral include

Arctostaphylos pungens
Berberis trifoliata
Ceanothus greggii
Garrya wrightii
Cercocarpus mojadensis
Microrhamnus ericoides
Quercus cordifolia
Quercus invaginata
Quercus intricata
Quercus hypoxantha
Quercus pringlei
Rhus microphylla
Rhus trilobata
Rhus (*Schmaltzia*) *virens*

Of these, *Arctostaphylos prepungens* (*pungens*), *Ceanothus* n. sp. (*greggii*), *Rhus* n. sp. (*microphylla*) and *Rhus* (*Schmaltzia*) *sonorensis* (*virens*) are now known in the Miocene and Pliocene floras of California. Others may be discovered there as new floras are found, for the modern species range today to west-central Arizona except for the more localized oaks and mountain mahogany, the woodland bordering the Coahuila chaparral has a number of close relatives in the Miocene of the far West, and the piñon-juniper woodland meets chaparral in both areas.

CLIMAX AND CLIMATE

Depending on climate, Madro-Tertiary communities attained dominance in different areas at different times during the history of the geoflora. The role that climate had in determining the time certain communities attained dominance has been outlined in the preceding pages, or elsewhere, and need only be summarized here.

WOODLAND

Live-oak woodland dominated the lowlands of the western Mojave region by the Early Miocene, and it probably was established there in the Oligocene, if not earlier. Woodland also typified the lowlands of western Nevada, but not until the Early Pliocene, for climate was sufficiently temperate there into the later Miocene to support the Arcto-Tertiary Geoflora. Oak woodland no longer occurs in this region which has winters much colder than those in areas where live oaks survive today. Live oak woodland did not become established over the lowlands of west-central

California until the Middle Pliocene, the driest part of the Tertiary. Earlier in the epoch temperate forests characterized the area, and today live oak woodland is generally subordinate to border-redwood (oak-madrone) forest of cooler and moister aspect. Live oak woodland is also recorded in central Colorado where it is well represented in the Oligocene. Late Cenozoic elevation of the region, which brought to it a colder climate, confined this vegetation type several hundred miles farther south.

In contrast to live oak woodland, conifer (piñon-juniper) woodland is a comparatively recent plant community. Close relatives of the conifers and associated shrubs that comprise the modern community were part of a generalized Madro-Tertiary woodland in the Middle and Late Tertiary. By becoming adapted to a cold-winter climate as live oaks and their associates were confined to milder areas to the south and west in the later Pliocene, a unique conifer-woodland came into existence over the area from the Great Basin eastward to the High Plains, with regional differences imposed by summer rain at the east and summer drought to the west.

CHAPARRAL

The Late Miocene Mint Canyon flora of southern California includes approximately 20 chaparral species, and some of them were among the subdominants of the flora. They undoubtedly formed an important association near the site of deposition, and probably dominated slopes bordering the dominant oak woodland and savanna and thorn scrub vegetation of the lowlands. The Middle Pliocene Mount Eden flora of southern California includes 17 chaparral species, which also formed a dominant association on adjacent slopes there, marginal to oak woodland and savanna communities of the lowlands. In both these areas, and elsewhere in southern California, chaparral has apparently expanded under the influence of a drier post-Pleistocene climate, aided materially by recurring fires, to supplant woodland, savanna and other lowland associations that are now relict in these areas. Thus chaparral seems to be even more prominent here today than it was in the Late Tertiary.

The Middle Pliocene Mulholland flora of west-central California has a dozen chaparral species which lived on slopes bordering the dominant oak woodland of the lowlands. At that time chaparral was more diverse in composition, and more prominently developed over the lowlands of central California than it is today. Since the climate of central California was drier in the Middle Pliocene than at any other time in the Tertiary, chaparral formed a more important association there than it does now.

Chaparral is moderately represented in the Late Tertiary floras of the western Great Basin, which include species that ally it to the modern chaparral of central and southern California. Chaparral no longer occurs in the region, owing to the cold winter climate.

ARID SUBTROPIC SCRUB

This plant formation was common along the river valleys and drier plains of interior southern California from Early Miocene (or earlier) well into Middle Pliocene time. It included species similar to those dominating the living communities in Sonora, Sinaloa and Tamaulipas, suggesting that during this interval southern California had mild frostless winter and ample summer rain. In response to increasing cold and reduction of summer precipitation in the later Pliocene, the formation was confined to more southerly regions. A few of its species nonetheless have isolated occurrences in the Mojave area, and larger numbers are encountered in the warmer Sonoran Desert. Apparently they were able to adapt to increased aridity in this mild-winter region, and now contribute to desert vegetation as well. In any event, they clearly are relicts of the thorn forest that dominated southeastern California at an earlier date, when climate was more favorable for its optimum development.

Records of the community are also known from the Oligocene Florissant flora of Colorado. Climate is clearly too cold there today for such an association, which find its closest parallel in the subtropic scrub and mesquite grassland of northeastern Mexico.

DESERT

The present desert vegetation of western North America, including the Great Basin, Mojave and Sonoran Deserts, is a new plant formation in terms of regional occurrence (Axelrod, 1950f). In the Early Pliocene the present area of the northern Great Basin Desert was dominated by conifer forest representing part of the Arcto-Tertiary Geoflora. At the same time the central Great

Basin area was typified by live-oak woodland over the lowlands with montane forest on the bordering slopes, a relation typical of the ecotone between the Arcto-Tertiary and Madro-Tertiary Geofloras. To southward the region of the Mojave and Sonoran Deserts was characterized by oak woodland, chaparral and thorn scrub vegetation. By the Middle Pliocene, in response to the continued secular trend toward aridity, forest and woodland were restricted largely to moister upland sites over the present desert area, and only a few hardier types persisted over the lowlands along stream banks and lake borders. Grasslands appear to have largely characterized the lowlands of the Great Basin at this time, but the Mojave region was typified by semidesert scrub, scattered thorn forest and mesquite grassland.

Late Pliocene and Quaternary elevation of the Sierra Nevada-Cascade axis and the Peninsular Ranges of southern California rapidly brought drier climates into existence over the lowlands to the east. Only then did the present regional desert climax come into existence, its species being derived from those represented in the geofloras which earlier had dominated over the lowlands. This, of course, would not preclude the existence of local subdesert tracts to the lee of the low ranges, especially in the southern sector, during the Pliocene.

The preceding data indicate that each of these plant formations —woodland, chaparral, thorn scrub, desert—attained climax status in different regions at different times. The stage during which dominance was attained was determined chiefly by climate. In some areas a given plant formation has been in existence since the Early Miocene (or earlier), though composition in terms of genera and species has been altered (i.e., southern California: live oak woodland, chaparral). In other regions the communities are still represented, but they no longer are as prominent as they were in the Pliocene (i.e., west-central California: live oak woodland. chaparral). Some areas no longer have climaxes that were represented in the Pliocene (i.e., central Nevada: live oak woodland, chaparral; Southern California: arid subtropic scrub; central Colorado: live oak woodland, chaparral). And in one case we appear to be dealing with a wholly new climax in terms of present day regional environment (i.e., southwestern North America: desert).

SUMMARY

1. The Madro-Tertiary Geoflora comprises semiarid live oak-conifer woodland, chaparral, arid subtropic scrub, plains (desert) grassland, and subdesert to desert vegetation.

2. The taxonomic and adaptive relations of its plants suggest that it was derived chiefly from subtropical to warm temperate groups that evolved in response to the expansion of a new adaptive zone—dry climate.

3. The geoflora seems to have had an origin in southwestern North America because (*a*) types that appear to be ancestral to Madro-Tertiary lineages are represented in the Cretaceous and Paleocene floras of that region, (*b*) they are not known from the temperate Arcto-Tertiary Geoflora to northward, and (*c*) they are not recorded in the humid phases of the Neotropical-Tertiary Geoflora.

4. Geologic and paleoclimatic data suggest that southwestern North America was generally a lowland region, characterized by tropic savanna climate during the Cretaceous and Early Tertiary.

5. During this interval, ancestral Madro-Tertiary phylads probably were evolving chiefly in sites away from the moist lowland floodplains, in drier areas provided by local edaphic and climatic conditions.

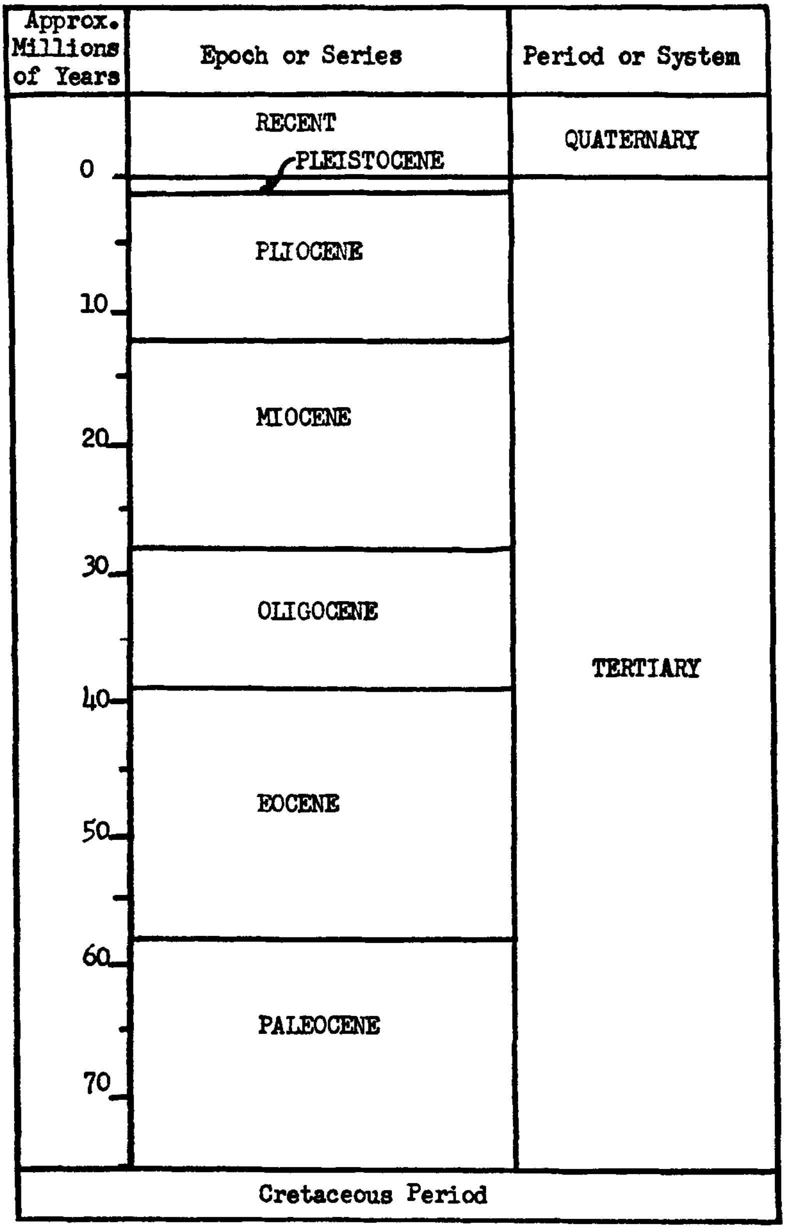
6. With a strong linear component to selection imposed by a gradual trend toward increased aridity, these scattered, isolated phylads of subtropic to warm temperate affinities may have been undergoing megaevolution during the Cretaceous and Paleocene, giving rise to numerous, highly specialized taxonomic and adaptive types.

7. When first recorded in moderate numbers in the Eocene and early Oligocene, they are closely similar to modern species.

8. As dry climates continued to expand in area and to increase in severity, the Madro-Tertiary Geoflora migrated widely over southwestern North America. The stage during which it attained dominance in each province was governed chiefly by geographic position and time.

APPENDIX

Cenozoic Time Scale



9. In response to the evolution of new dry climates in the later Cenozoic, each of the generalized Madro-Tertiary communities was differentiated into a number of modern associations that are adapted now to more localized dry environments.

BIBLIOGRAPHY

ANDERSON, C. A .1950. Geology of islands and neighboring land areas. *In*: 1940 E. W. Scripps Cruise to the Gulf of California. Geol. Soc. Amer., Mem. 43: 1-53.

AXELROD, D. I., 1934. A Pliocene flora from the Eden beds. Amer. Mus. Nov. 729: 1-4.

————, 1937. A Pliocene flora from the Mount Eden beds, southern California. Carnegie Inst. Wash., Pub. 476: 125-183.

————, 1938. The stratigraphic significance of a southern element in later Tertiary floras of western America. Jour. Wash. Acad. Sci. **28**: 314-322.

————, 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash., Pub. 516: 1-129.

————, 1940a. The Pliocene Esmeralda flora of west-central Nevada. Jour. Wash. Acad. Sci. **30**: 163-174.

————, 1940b. Late Tertiary floras of the Great Basin and border areas. Bull. Torrey Bot. Club **67**: 477-487.

————, 1940c. The Mint Canyon flora of southern California: a preliminary statement. Amer. Jour. Sci. **238**: 577-585.

————, 1944a. The Black Hawk Ranch flora (California). Carnegie Inst. Wash., Pub. 553: 91-101.

————, 1944b. The Mulholland flora (California). Carnegie Inst. Wash., Pub. 553: 102-146.

————, 1944c. The Oakdale flora (California). Carnegie Inst. Wash., Pub. 553: 147-165.

————, 1944d. The Sonoma flora (California). Carnegie Inst. Wash., Pub. 553: 166-206.

————, 1944e. The Pliocene sequence in central California. Carnegie Inst. Wash., Pub. 553: 207-224.

————, 1944f. The Alvord Creek flora (Oregon). Carnegie Inst. Wash., Pub. 553: 225-262.

————, 1944g. The Alturas flora (California). Carnegie Inst. Wash., Pub. 553: 263-284.

————, 1948. Climate and evolution in western North America during Middle Pliocene time. Evolution **2**: 127-144.

————, 1950a. Classification of the Madro-Tertiary Flora. Carnegie Inst. Wash., Pub. 590: 1-22.

————, 1950b. A Sonoma florule from Napa, California, Carnegie Inst. Wash., Pub. 590: 23-71.

————, 1950c. Further studies of the Mount Eden flora, southern California. Carnegie Inst. Wash., Pub. 590: 73-117.

————, 1950d. The Anaverde flora of southern California. Carnegie Inst. Wash., Pub. 590: 119-158.

————, 1950e. The Piru Gorge flora of southern California. Carnegie Inst. Wash., Pub. 590: 161-214.

————, 1950f. Evolution of desert vegetation in western North America. Carnegie Inst. Wash., Pub. 590: 215-360.

————, 1952a. A theory of angiosperm evolution. Evolution **6**: 29-60.

————, 1952b. Variables affecting the probabilities of dispersal in geologic time. Bull. Amer. Mus Nat. Hist. **99**: 177-188.

————, 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif., Publ. Geol. Sci. **33**: 1-322.

————, 1957. Late Tertiary floras and the Sierra Nevadan uplift. Bull. Geol. Soc. Amer. **68**: 19-46.

BAILEY, I. W., and E. W. SINNOTT, 1915. A botanical index of Cretaceous and Tertiary climates. Science, n. s. **41**: 832-833.

————, 1916. Investigations on the phylogeny of the angiosperms. 6: The climatic distribution of certain types of angiosperm leaves. Amer. Jour. Bot. **3**: 23-39.

BALL, O. M., 1931. A contribution to the paleobotany of the Eocene of Texas. Bull. Agr. & Mech. College Texas. IV. **2**: 1-172.

BERRY, E. W., 1916. The Lower Eocene floras of southeastern North America. U. S. Geol. Survey, Prof. Paper 91: 21-353.

————, 1919. An Eocene flora from Trans-Pecos Texas. U. S. Geol. Surveys, Prof. Paper 125: 1-9.

————, 1930. Revision of the Lower Eocene Wilcox flora of the Southeastern United States, with descriptions of new species, chiefly from Tennessee and Kentucky. U. S. Geol. Survey, Prof. Paper 156: 1-196.

BEWS, J. W. 1927. Studies in the ecological evolution of angiosperms. New Phytol. **26**: 1-21, 65-84, 129-148, 209-248, 273-294.

BRADLEY, W. H., 1929. The varves and climate of the Green River epoch. U. S. Geol. Survey, Prof. Paper 158: 87-110.

BRANDEGEE, T. S., 1889. A collection of plants from Baja California. Proc. Cal. Acad. Sci., II., **2**: 117-216.

BROWN, R. W., 1934. Recognizable species of the Green River flora. U. S. Geol. Survey, Prof. Paper 185: 45-77.

CAIN, S. A., 1944. Foundation of plant geography. 556 pp. Harper & Bros., N. Y.

CHANEY, R. W., 1938. Paleoecological interpretations of Cenozoic plants in western North America. Bot. Rev. **4**: 371-396.

————, 1944a. Introduction (*to* Pliocene floras of California and Oregon). Carnegie Inst. Wash., Pub. 553: 1-19.

————, 1944b. Summary and Conclusions (*to* Pliocene floras of California and Oregon). Carnegie Inst. Wash., Pub. 553: 353-373.

————, 1944c. A fossil cactus from the Eocene of Utah. Amer. Jour. Bot. **31**: 507-528.

————, 1947. Tertiary centers and migration routes. Ecol. Monog. **17**: 139-148.

————, 1958. Miocene forests of the Columbia Plateau. Carnegie Inst. Wash., Pub. 617.

————, and H. L. MASON, 1934. A Pleistocene flora from the asphalt deposits at Carpenteria, California. Carnegie Inst. Wash., Pub. 415: 47-79.

————, and E. I. SANBORN, 1933. The Goshen flora of west-central Oregon. Carnegie Inst. Wash., Pub. 439: 1-103.

CLEMENTS, F. E., 1920. Plant indicators. Carnegie Inst. Wash., Pub. 290: 1-388.

————, 1936. The origin of the desert climax and climate, *In*: Essays in geobotany in honor of William Albert Setchell. [T. H. Goodspeed, ed.] Univ. Calif. Press: 87-140.

CONDIT, C., 1944a. The Remington Hill flora (California). Carnegie Inst. Wash., Pub. 553: 21-55.

————, 1944b. The Table Mountain flora (California). Carnegie Inst. Wash., Pub. 553: 57-90.

COREY, W. H., 1955. Tertiary basins of southern California. *In*: Historical Geology: 73-83. Geology of Southern California, State of California, Dept. of Natural Resources, Div. of Mines, Bull. 170.

DORF, E., 1930. Pliocene floras of California. Carnegie Inst. Wash., Pub. 412: 1-112.

————, 1942. Upper Cretaceous floras of the Rocky Mountain region. Carnegie Inst. Wash., Pub. 508: 1-168.

ELIAS, M. K., 1942. Tertiary prairie grasses and other herbs from the High Plains. Geol. Soc. Amer., Spec. Pap. 41: 1-176.

GRAY, ASA, 1878. Forest geography and archaeology. Amer. Jour. Sci. & Arts. III. **16**: 85-95.

————, 1884. Characteristics of the North American flora. Amer. Jour. Sci. & Arts. III. **28**: 323-340.

GREGORY, H. E., 1917. Geology of the Navajo country. U. S. Geol. Survey, Prof. Paper 93: 1-161.

HARSHBERGER, J. W., 1912. Phytogeographic survey of North America. *In*: Engler and Drude, Vegetation der Erde. Vol. 13.

HEMSLEY, W. B., 1888. Biologia centrali-americana; or contributions to the knowledge of the fauna and flora of Mexico and Central America . . . Botany **4**: 306-314.

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

JOHNSTON, I. M., 1940. The floristic significance of shrubs common to North and South American deserts. Jour. Arn. Arb. **21**: 356-363.

KNOWLTON, F. H., 1917. Fossil floras of the Vermejo and Raton formations of Colorado and New Mexico. U. S. Geol. Survey. Prof. Paper 101: 223-450.

————, 1922. The Laramie flora of the Denver basin. U. S. Geol. Survey, Prof. Paper 130: 1-168.

————, 1923. Fossil plants from the Tertiary lake beds of south-central Colorado. U. S. Geol. Survey, Prof. Paper 131: 183-197.

————, 1924. Flora of the Animas formation. U. S. Geol. Survey, Prof. Paper 134: 71-117.

————, 1930. The flora of the Denver and associated formations of Colorado. U. S. Geol. Survey, Prof. Paper 155: 1-142.

LECONTE, J., 1887. The flora of the coast islands of California in relation to recent changes of physical geography. Bull. Calif. Acad. Sci. **2**: 515-520.

LESQUEREUX, L., 1887. List of recently identified fossil plants belonging to the U. S. National Museum with descriptions of several new species. Proc. U. S. Nat. Mus. **10**: 21-46.

MASON, H. L., 1947. Evolution of certain floristic associations in western North America. Ecol. Monog. **17**: 201-210.

MACGINITIE, H. D., 1937. The flora of the Weaverville beds of Trinity County, California. Carnegie Inst. Wash., Pub. 465: 83-151.

————, 1941. A Middle Eocene flora from the central Sierra Nevada. Carnegie Inst. Wash., Pub. 1-178.

————, 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash., Pub. 599: 1-188.

MUNZ, P. A., 1935. A manual of southern California botany. 642 pp. Claremont, Calif.

MULLER, C. H., 1939. Relations of the vegetation and climatic types in Nuevo Leon, Mexico. Amer. Mid. Nat. **21**: 687-729.

NELSON, E. W., 1921. Lower California and its natural resources. Mem. Nat. Acad. Sci. **16**.

POTBURY, S. S., 1935. The LaPorte flora of Plumas County, California. Carnegie Inst. Wash., Pub. 465: 29-81.

PRINGLE, C. G., 1888. The vegetation of northern Mexico. Garden & Forest **1**: 117, 141-142.

————, 1890. Notes on the ligneous vegetation of the Sierra Madre of Nuevo Leon. Garden & Forest **3**: 337-338, 362-363.

SHREVE, F., 1937. The vegetation of the Cape Region of Baja California. Madroño **4**: 105-113.

————, 1951. Vegetation of the Sonoran Desert. Carnegie Inst. Wash., Pub. 591, vol. 1: 1-192.

SIMPSON, G. G., 1953. The major features of evolution. 434 pp. Columbia.

STEBBINS, Jr., G. L., 1947. Evidence on rates of evolution from the distribution of existing and fossil plant species. Ecol. Monog. **17**: 149-158.

————, 1950. Variation and evolution in plants. 643 pp. Columbia.

————, 1952. Aridity as a stimulus to plant evolution. Amer. Nat. **86**: 33-44.

STEWART, B. K., 1940. Plant ecology and paleo-ecology of the Creede Valley, Colorado. Univ. Col., Ph.D. thesis.

WODEHOUSE, R. P., 1932. Tertiary pollen. I. Pollen of the living representatives of the Green River flora. Bull. Torrey Bot. Club **59**: 313-340.

————, 1933. Tertiary pollen. II. The oil shales of the Green River formation. Bull. Torrey Bot. Club **60**: 479-521.