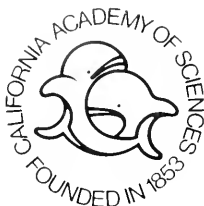# Age and Origin of Sonoran Desert Vegetation

By

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Dedicated to the Memory of

FORREST SHREVE

Foremost Investigator of
North American Desert Vegetation

The most important aim of our work is to keep in view the vast array of influences and circumstances that have determined the history of desert plants and now determine the life and survival of every one of them. . . . Especially do we need to weave together the separate threads of knowledge about the plants and their natural setting into a close fabric of understanding on which it will be possible to see the whole pattern and design of desert life.

Shreve 1936:19

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ABSTRACT

Axelrod, Daniel I. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences*, no. 132, 74 pages, 27 figs., 8 tables, 1979.—Fossil floras now in southern California and adjacent Baja California were transported northward from the region of the present Sonoran Desert by movements on the San Andreas fault system. These floras reveal that from the Late Cretaceous into the Pliocene, the area of the present Sonoran Desert supported a progression of vegetation—savanna, dry tropic forest, short-tree forest, woodland-chaparral, thorn forest. The record shows that local basins supported semidesert vegetation by the early Miocene, and it may be inferred for restricted dry sites by the late Eocene. Thus, the area of the present Sonoran Desert has been accumulating taxa which were preadapted both in form and function to progressively increasing drought during the Tertiary. The taxa are allocated provisionally to several ages, with the oldest containing the most distinct ones. The present regional desert emerged only in the interglacials, and especially after the Wisconsin.

This evidence regarding age and origin leads to a discussion of: *a*) the sources of the Sonoran Desert flora, *b*) the floristic imbalance of the flora, *c*) the great diversity of dominant life forms there as compared with bordering vegetation zones, and *d*) its relations to the Chihuahuan and Hidalgan desert floras.

Age and Origin of Sonoran Desert Vegetation

Daniel I. Axelrod

INTRODUCTION

Recent ecologic and evolutionary studies of modern taxa in desert areas have led to the opinion that the present hot desert environments are ancient. This conclusion has been reached for the Namib Desert of Africa (Zinderen Bakker 1975), the central Australian Desert (Beard 1976, 1977), the Argentine Desert (Solbrig 1976; Blair, Hulse, and Mares 1976), the arid Caribbean vegetation (Sarmiento 1976), and the Sonoran, Chihuahuan and Hidalgan deserts of Mexico and border areas (Johnson 1968; Rzedowski 1962; Blair 1976; Blair, Hulse, and Mares 1976; Halffter 1976; Otte 1976). The evidence for antiquity is based chiefly on modern biotic data that pertain to the degree of endemism, or to the unique morphology, of certain taxa in these desert areas. These investigators call on ancient deserts but have not indicated when they initially appeared (are they "earth-old"?); they have not designated their areas apart from the assumption that they corresponded with present ones; and they also imply that these ancient deserts had climates like the modern ones.

Tentative answers to such problems may be inferred from geologic and paleobotanic evidence of environments that characterized the present desert area during the Late Cretaceous and Tertiary, times when plants ancestral to, and in some cases identical with, those of the present desert and desert-border environments were in existence. Earlier reviews of the fossil plant record have already shown that forests and savannas covered areas of the present subtropical and tropical deserts well into the Eocene, and that dry tropical forest, woodland, and thorn forest covered the modern tropical deserts into the middle and late Tertiary (Axelrod 1950d, 1958, 1970; Axelrod and Raven 1977; Krystofovich 1954; Tankard and Rogers 1978). The evidence also shows that temperate forests composed of conifers and deciduous hardwoods blanketed the areas of the present temperate desert regions into the close of the Miocene, and that they gave way to woodland, grassland, and sage-steppe vegetation with a riparian occur-

rence of trees during the Pliocene. Clearly, the present regional deserts must be more recent. If true, this conclusion raises several related problems that also require consideration. When did semideserts and local deserts initially appear? Where were they situated? What was the nature of their climates: were they like those of the present deserts? If regional deserts do not have great antiquity, how can we explain the origin of the specialized adaptive types (e.g., *Fouquieria, Nolina, Pachycormus*) and the unique monotypic families (e.g., Crossosomataceae, Koeberliniaceae, Simmondsiaceae) that are now in the Sonoran Desert and border areas?

Provisional answers to these questions are provided by a reanalysis of the Cretaceous and Tertiary floras recovered from the region of the present Sonoran Desert and its margins. Some of the older floras have been revised and there are new ones which add important information to the vegetation history of the area. In addition, our knowledge of the geologic history of the region has increased greatly during the past decade. The evidence of plate tectonics which clarifies the history of southern California and Baja California is particularly significant. It shows that fossil floras which represent tropic forest, savanna, and woodland vegetation lived in the present area of the Sonoran Desert, and that they were displaced northward to their present positions by later plate movements. These movements are expressed chiefly by the history of the complex San Andreas fault system and associated sea-floor spreading that opened the Gulf of California during the Miocene and Pliocene (Crowell 1962, 1975; Gastil and Jensky 1973; Gastil, Phillips, and Allison 1975; Karig and Jensky 1972; Matthews 1976; Smith 1976). The progression of fossil floras thus provides incontrovertible evidence which shows that this regional desert developed gradually, and that taxa which were adapted to the progressively drier climate that developed over the region have been accumulating in the Sonoran region since the Late Cretaceous.

The sequence of Cretaceous and Tertiary floras recovered from the present area of the So-

noran Desert region leads to the thesis perceived earlier (Axelrod 1950c, 1958, 1967, 1970, 1972). Forerunners of the present Sonoran Desert taxa *1*) originated in local dry basins and restricted dry sites, *2*) the taxa in the present desert are derivatives of alliances of plant formations that inhabited the area during the Late Cretaceous and Tertiary, before it was a regional desert, *3*) they gradually adapted to increasing and spreading regional drought during the Tertiary, and *4*) the area has only recently emerged as a regional desert of extreme heat and aridity. The present Sonoran Desert region has therefore been a repository for taxa which were preadapted both in life form and function to the trend to progressively increasing aridity during a span of fully 70-odd million years. Hence, it is expectable that the area not only harbors monotypic families of obvious antiquity, but unique genera of both tropical and warm temperate affinity, as well as much younger taxa that are related to those that still live on the borders of the desert, and some that also range far out into the desert. Since the evidence that supports this general conclusion has an important bearing on future evolutionary and systematic studies in this and other tropical deserts, it seems appropriate to outline its history in the light of the data now available.

To aid in understanding the developmental history of the present desert region, the paper begins with a brief review of the general features of the climate and flora of the Sonoran Desert. This is a subtropical desert and is notable because similar taxa are represented in the woodland and chaparral vegetation on its eastern and western margins in slightly wetter areas above the desert. This implies that these taxa probably were distributed more continuously over the region now desert in the past, when rainfall was higher. Next we turn to the geologic and paleontologic evidence that shows that very different terrains, vegetation, and climate characterized the present area of the Sonoran Desert region during Cretaceous and Cenozoic times. The major event in its structural history has been the opening of the Sea of Cortez as the peninsular region was rafted away from the Mexican mainland and then its northward shift some 500 km (about 300 miles) by movement along the San Andreas and allied rifts. During this time there were accompanying changes in relief, with the elevation of the major mountain

ranges of the region. The changes in vegetation and, by inference, the climate of the region that resulted from these topographic and spatial (latitudinal) modifications were accompanied by a general cooling of the ocean that spread southward from high latitudes. This was one of the major factors that led to the spread of progressively drier climates. These changes are reflected in the fossil floras of the region, distributed in time from the Late Cretaceous (70 m.y., million years) into the close of the Pleistocene (12,000 B.P., before the present).

The taxa in the fossil floras recovered from the region are listed because they provide a basis for inferring the nature of the climate under which they lived, and the general type of vegetation to which they contributed. A number of the taxa recur in the listed fossil floras, showing that they persisted from one epoch to the next, much as taxa today may occur in more than one vegetation zone that lives under somewhat different conditions. Indeed, their recurrence provides a thread of continuity for interpreting the sequence of different vegetation zones that have occupied the region, and hence the manner in which desert vegetation has gradually come into existence. Consideration of this evidence makes it clear that the present Sonoran Desert vegetation is made up of taxa that originally belonged to vegetation zones that were adapted to moister climates and to climates with lower ranges of temperature: climates were more equable. Thus, over a span of tens of millions of years some of the woody plants that lived in the region were able to persist and adapt to the progressively drier and less equable climate that culminated in the present conditions. With this as a background, it is then possible to consider some of the evolutionary implications of this general theory to desert evolution in general. The report concludes with a discussion of some of the important features of the present Sonoran Desert flora, notably its sources, the imbalance in the flora, the diversity of life forms, its floristic diversity, and its relation to other desert regions in Mexico chiefly.

GENERAL FEATURES

CLIMATE

The Sonoran Desert (Fig. 1), which has an arid subtropical to tropical climate, finds its counterparts in the warm deserts of Africa,

southwestern Asia, South America, and Australia, deserts whose areas are nicely charted by McGinnies, Goldman, and Laylore (1968:xii–xxviii). The primary cause of all these dry regions is that they coincide with the permanent high pressure cells that now dominate generally between latitudes 23° and 30°. Descending air in these areas is heated adiabatically and arrives at the surface largely devoid of moisture and is therefore incapable of producing rain. Equatorward, the subtropical deserts are replaced gradually by thorn forest, dry tropic forest, and savanna as moist tropical air penetrates more frequently to produce conventional rain during summer. On their poleward margins, subtropical deserts give way to grassland and sclerophyll woodland and brushland. These areas now receive frontal rains in winter regions with a mediterranean-type climate. However, summer rains characterized these present areas of winter rain into the early Pleistocene, and they still occur over the interior in areas with sclerophyll vegetation, as in Arizona-Texas-Tamaulipas, as well as in northern Turkey, southeast Australia, and South Africa.

Two secondary factors also contribute to the aridity of desert regions. First, in areas where subtropical deserts are bordered by a cool ocean on the western side of the continent, a layer of cool, moist air moving inland beneath the descending dry air produces fog, but no precipitation. The resultant very mild climate supports a fog-desert, as along the Pacific coast of northern Baja California, the Chilean coast from near La Serena northward, and in the Namib of southwest Africa. Since the relationship is determined by the regional occurrence of cold water offshore, which has developed largely since 4.0 m.y. (Kennett et al. 1975; Shackelton and Kennett 1975; Kemp 1978), foggy deserts are new in a geologic sense. The second factor that accentuates aridity occurs in areas where air forced over mountains deposits moisture on the windward slope and descends warm and dry to the lee. The severity of dry climate that develops in the "rainshadow" depends on whether moisture comes occasionally from another direction. Since high topography is a relatively young feature in western North America, Chile-Peru, and elsewhere, its development has accentuated both the area and the intensity of drought in the lee of the recently uplifted cordilleras.
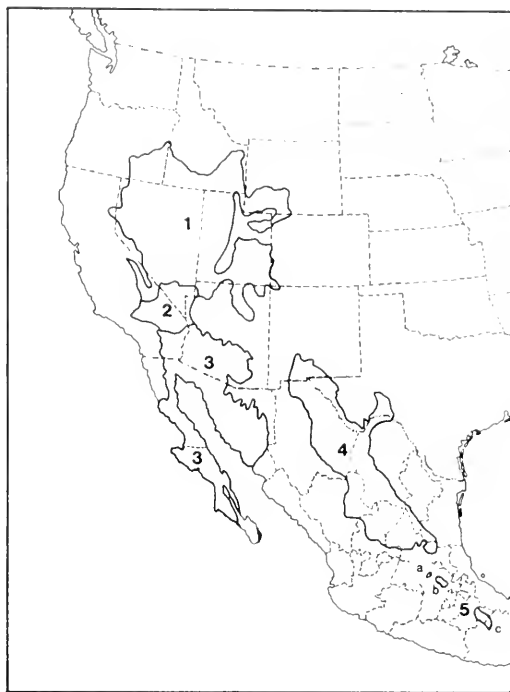

FIGURE 1. Position of Sonoran Desert in relation to other desert regions of North America (Shreve 1942; Rzedowski 1973). 1 = Great Basin, 2 = Mojave, 3 = Sonoran, 4 = Chihuahuan, 5 = Hidalgan, a. Toliman & vic., b. Valle de Mesquital, c. Tehuacán Valley.

The Sonoran Desert is now under the influence of both the primary and secondary factors. Most of its area lies within the subtropical high pressure cell, and its northern arm in California and adjacent Baja California receives little winter precipitation because it is in the lee of the Peninsular Ranges. The summer rains that fall over the Sierra Madre Occidental in western Mexico and adjacent Arizona rapidly decrease to the west, away from their source area which is chiefly the Gulf of Mexico. Those that originate in the tropical eastern Pacific lose strength as they meet the mountains of western Mexico and the colder waters along its north coast. Coastal fog dominates the outer coast of central to northern Baja California in summer, where a rich fog-desert exists.

These conditions that account for the present desert can not be considered "earth-old." The subtropical high pressure system gradually increased in strength during the middle and late Tertiary as the global thermal gradient nearly doubled. The oceans chilled quite rapidly fol-

lowing the Miocene, and the uplift of the ranges to the windward of the present desert is also very recent—chiefly late Pliocene and early to middle Pleistocene. These data imply that climate over the area of the present desert must have been quite different in the recent past. This is apparent from the occurrence in the present desert region of fossil floras which reveal that woodland and other kinds of non-desert vegetation covered the area well into the late Tertiary, and even in the late Quaternary.

Vegetation

The desert region of each continent can be subdivided into a series of deserts. Commencing with those that have rather well developed communities that respond to at least one favorable season for growth, there is a transition to those with slightly less vegetation that results from more unfavorable moisture conditions, to those that are extremely dry and essentially barren. Each major continental desert grades into more favorable regions which are semidesert and then non-desert, but which have taxa that relate them to those in the desert. Thus, a series of deserts displays the same unity as a series of forest- or woodland-types, showing gradual modifications in composition and physiognomy as climate changes progressively over a broad region.

As emphasized earlier by Shreve (1940), the Sonoran Desert is bordered by widely different kinds of vegetation. As sketched in a general way in Figure 2, on its southern, warmer and moister margins the desert gives way to arid tropical scrub and mesquite grassland, both of which are replaced by arid tropical (deciduous) forests in moister areas, as in the Cape Region or in the foothills of southern Sonora and Sinaloa, where it is termed short-tree forest by Gentry (1942). Along its northern borders in Arizona the desert is replaced by grassland in slightly moister areas, and then by an oak-piñon woodland or piñon-juniper woodland along its colder margins in northern Arizona and in eastern California. In its northwestern, coastal sector the desert grades into a denser rich coastal sage near Rosario that extends northward to the San Diego region (Shreve 1936), where it is replaced by another coastal sage community of lower diversity. In the scattered uplands of the Sonoran Desert, as in Baja California and also in western Arizona and southeastern California, there are small patches of oak woodland, piñon, chapar-

ral, or grassland, all clearly relict from other more genial and older climates.

The Sonoran is an arboreal desert, characterized by numerous small trees of diverse genera (Shreve 1942, 1951). The dominant plants represent a wide variety of life forms which give the vegetation its distinctive physiognomy. These notably include arborescent yuccas, barrel cacti, arborescent columnar cacti, evergreen trees and shrubs, leafless trees and shrubs, diverse perennials, deciduous to semideciduous shrubs and small trees, shadowless plants, leafless succulents, and many others (see Shreve 1951:34). The dominants differ markedly in height; in bulk; in manner and amount of branching; in the nature of the stem; in the size, duration, and seasonal behavior of the leaves; in the degree of succulence; in the time of flowering; and in other features as well. The habitats that support the largest number of growth forms are on the hill- and mountain-slopes and upper bajadas where rainfall is greater (230–300 mm; ~9–12 inches) and where temperatures are more moderate than at lower levels. Whereas such areas frequently have 20 or more life forms, the drier plains and lower bajadas may have only 3 or 4. Meteorological data for stations in these areas demonstrate that the lower and drier *Larrea-Franseria* zone has a hotter, less equable climate (Axelrod 1965:fig. 7). Yang and Lowe (1956) report that the *Larrea-Franseria* desert, which dominates the lower flats where the finer soil has a considerable clay fraction, has a higher moisture content than the slopes covered by the cactus savanna which requires more adequate drainage (cf. Spalding 1909:124).

Shreve (1951) mapped several subdivisions of the Sonoran Desert based on changes in the composition of the dominant vegetation. As judged from a number of representative stations (*in* U.S. Dept. Commerce, *Climatography of the United States*; Garcia 1973), the general thermal conditions under which the Sonoran and other western deserts now live are shown in Figure 3. Note that the stations along the northern border of the Sonoran Desert, such as Phoenix and Palm Springs, are regularly subject to light frost, and that the climate at the south is arid tropical and frost free. Precipitation over these areas varies from dominant summer rainfall in the tropical deserts of Mexico, to a biseasonal rainfall in areas near the international boundary, to chiefly winter precipitation in the Mohave and
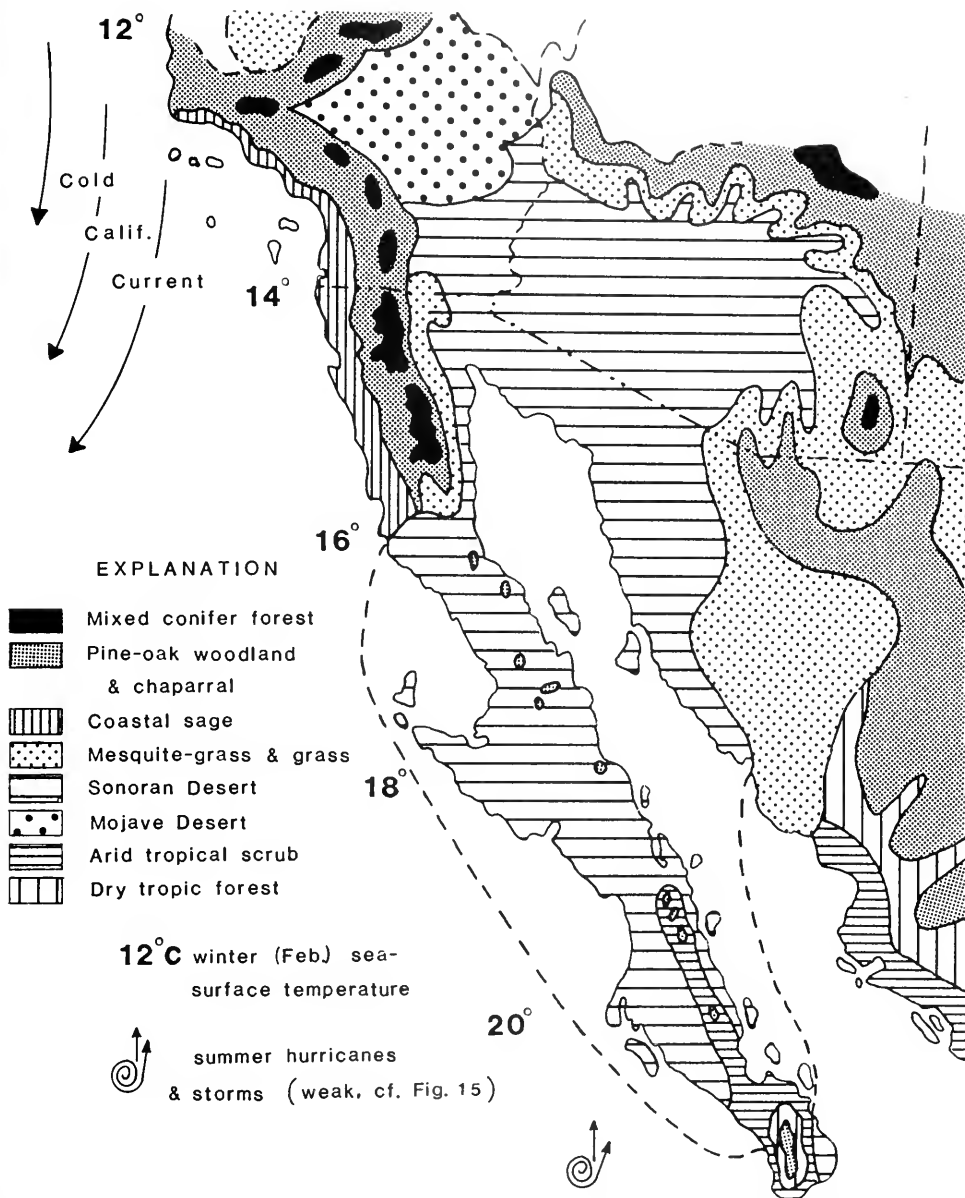
FIGURE 2. General distribution of vegetation bordering the Sonoran Desert region (from Shreve 1937; Nicol 1937; Leopold 1950; and personal observation).

Great Basin desert areas, which frequently (Mohave) or regularly (Great Basin) have snow.

FLORA

The area of the Sonoran Desert is similar to that of the California floristic province, yet these areas differ importantly in numbers of taxa and the degree of endemism (Raven and Axelrod 1978:table 1). Both have a similar number of genera (746 in the Sonoran, 795 in California floristic province) of which 20 (2.7%) are endemic to the Sonoran Desert and 50 (6.3%) to the California floristic province. Whereas 2,441 species are in the Sonoran Desert, the California floristic province has 4,452. Of these, 650 species (26.6%) are endemic to the Sonoran province.
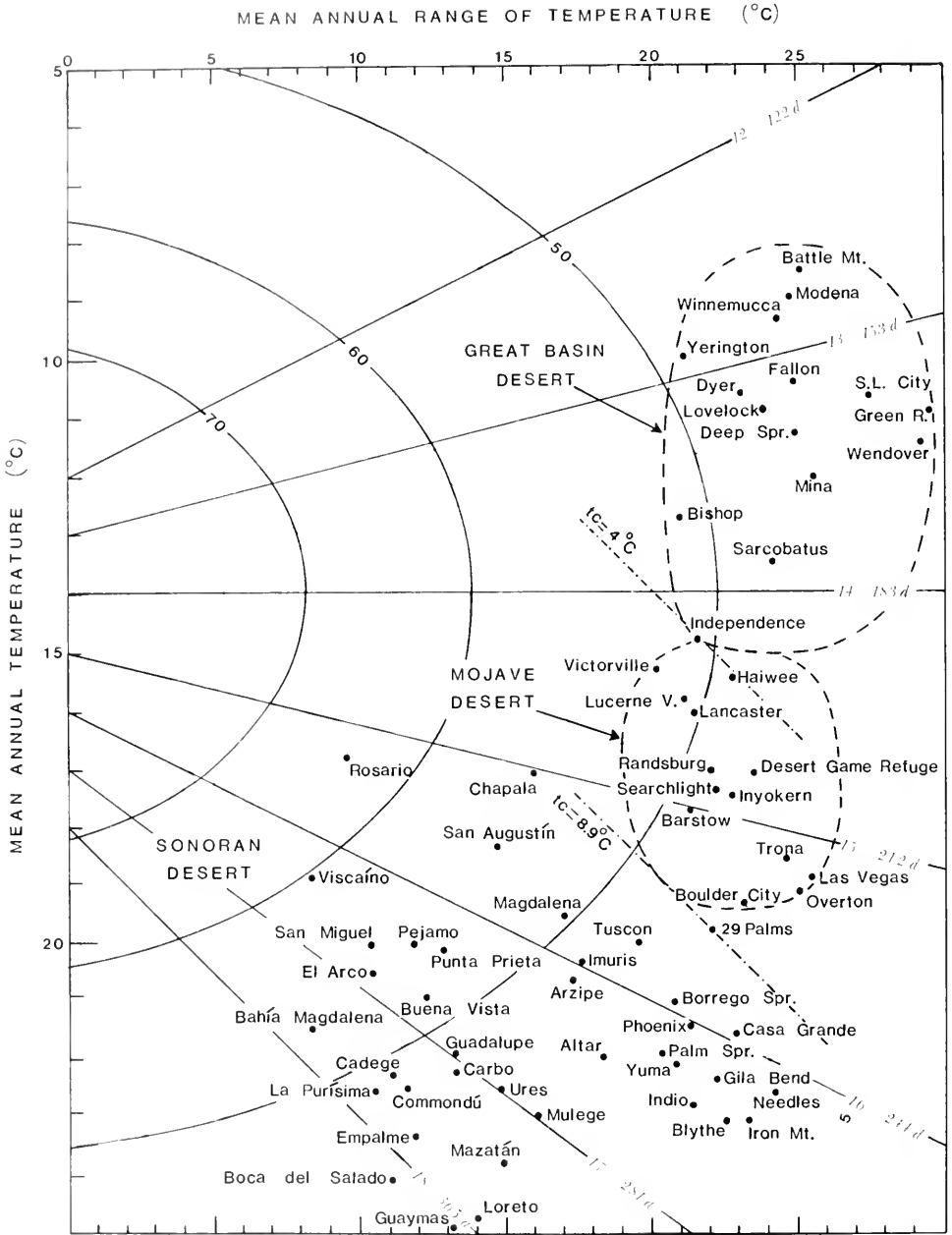
FIGURE 3. Thermal relations of representative stations in the North American deserts, plotted in a Bailey nomogram (Bailey 1960, 1971). Recall that the radians represent a measure of warmth of climate and indicate the number of days (*d*) in the year in which the mean temperature rises above the stipulated level. The arcs provide a measure of the temperateness or equability of climate and indicate departure from an ideal mean temperature of 14 C and a mean annual range of 0 C. (Data from U.S. Dept. Commerce.)

are 2,125 species (47.7%) are restricted to the California floristic province. The richest part of the Sonoran Desert is up in mountains and on the upper bajada slopes where moisture is higher

and temperatures are not so extreme as in the lowlands.

The desert flora is regarded here as the culmination of the development of a truly arid

PRESENT LINKS ACROSS THE DESERT

CHAPARRAL

Arctostaphylos pringleii
Arctostaphylos pungens
Ceanothus greggii
Cercis occidentalis
Cercocarpus montanus
Fremontodendron californicum
Garrya flavescens
Quercus dunnii
Quercus turbinella
Rhamnus californica
Rhamnus ilicifolia
Rhus ovata
Rhus trilobata

FIGURE 4. The occurrence of 13 woody species that contribute to the disjunct chaparral vegetation of California and Arizona demands an earlier continuum across the area presently desert. (CH = Chihuahuan; GB = Great Basin; M = Mohave; S = Sonoran.)
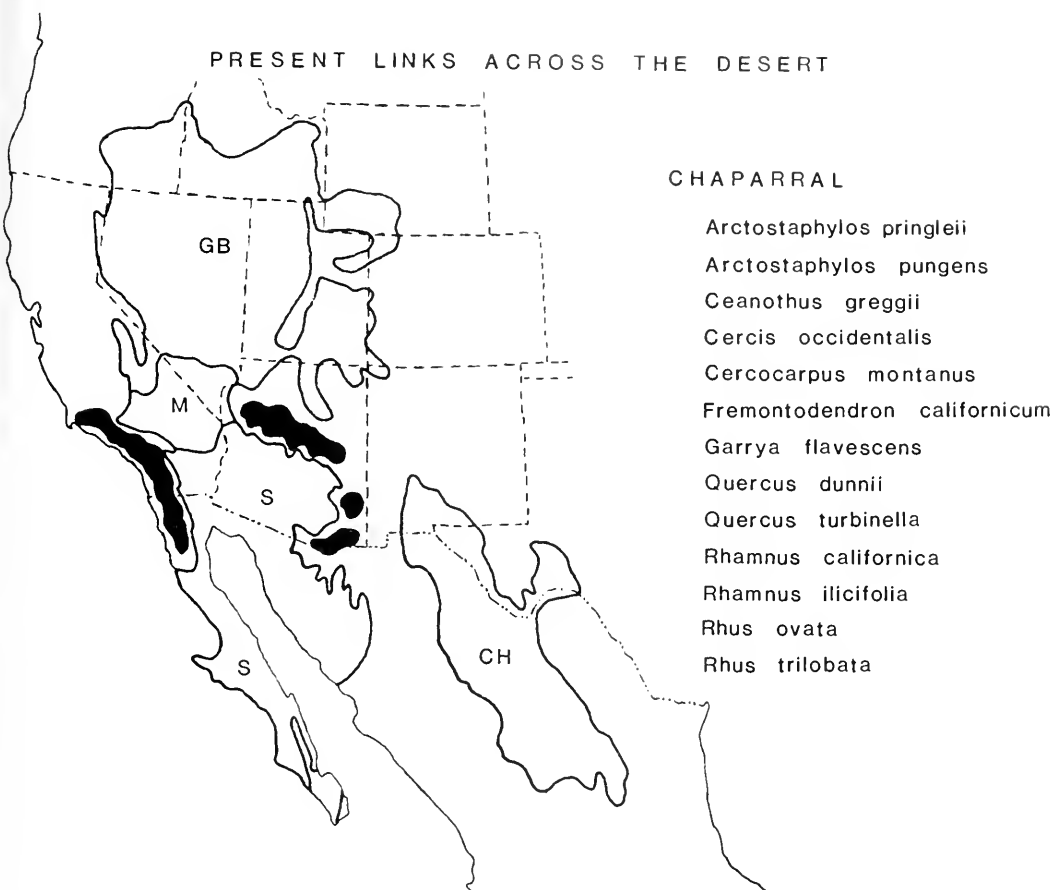
adaptive zone which developed gradually during the Late Cretaceous and Tertiary. The spreading dry belt in which drought has been increasing is a zone into which species have moved and evolved continuously for over 80 million years. Most were not able to adapt to the progressively more severe conditions. They have either become extinct in the northern hemisphere (e.g., *Araucaria*), or their descendants (e.g., *Persea, Quercus, Thouinia*) now live in moister regions, in derived dry tropic forest or in oak woodland vegetation. Although the richest part of the Sonoran flora is now up in the desert ranges, the low desert is now almost a "vacuum" so far as plants are concerned, which is consistent with the low diversity of its flora.

PRESENT LINKS ACROSS THE DESERT

The area of the Sonoran Desert is bordered now by different kinds of vegetation, notably grassland, sage, oak-juniper woodland, and thorn forest. Clements (1936) noted that the taxa of these vegetation zones, and at times the zones themselves, have relict occurrences up in the desert ranges where moisture is greater and temperature more moderate. He effectively used this relation to show that the origin of the Coloradan sector of the Sonoran Desert is related to the disappearance of grass dominants from the region of desiccation. In particular he noted that grasses and associated forbs that are now dominant or subdominant in grasslands on both sides of the Mohave-Coloradan deserts occur at

TABLE 1. SIMILAR AND RELATED WOODY SPECIES IN THE WOODLAND AND CHAPARRAL OF SOUTHERN CALIFORNIA AND CENTRAL ARIZONA.

Californian taxa	Arizonan taxa
Pinaceae	
Pinus monophylla	P. monophylla; edulis; cembroides
Cupressaceae	
Cupressus nevadensis	C. arizonica
Juniperus californica	J. osteosperma
Agavaceae	
Nolina bigelovii	N. bigelovii
Nolina parryii	N. parryii
Yucca brevifolia	Y. brevifolia
Yucca schidigera	Y. schidigera
Salicaceae	
Populus fremontii	P. fremontii
Salix gooddingii	S. gooddingii
Salix lasiolepis	S. lasiolepis
Salix laevigata	S. laevigata
Betulaceae	
Alnus rhombifolia	A. oblongifolia
Fagaceae	
Quercus chrysolepis	Q. chrysolepis
Quercus dunnii (=palmeri)	Q. dunnii (=palmeri)
Quercus engelmannii	Q. oblongifolia
Quercus turbinella	Q. turbinella
Quercus wislizenii	Q. emoryii
Moraceae	
Celtis reticulata	C. reticulata
Berberidaceae	
Mahonia dictyota	M. wilcoxii
Mahonia fremontii	M. fremontii
Saxifragaceae	
Fendlerella utahensis	F. utahensis
Ribes quercetorum	R. quercetorum
Crossosomataceae	
Crossosoma bigelovii	C. bigelovii
Rosaceae	
Amelanchier florida	A. oreophila
Cercocarpus betuloides	C. montanus
Cercocarpus ledifolius	C. ledifolius
Chamaebatiaria millefolium	C. millefolium
Cowania mexicanum	C. mexicanum
Holodiscus glabrescens	H. dumosus
Prunus fasciculata	P. fasciculata
Purshia tridentata	P. tridentata
Caesalpiniaceae	
Cercis occidentalis	C. occidentalis
Fabaceae	
Amorpha californica	A. californica
Rutaceae	
Ptelea trifoliata	P. angustifolia

TABLE 1. CONTINUED.

Californian taxa	Arizonan taxa
Anacardiaceae	
Rhus glabra	R. glabra
Rhus ovata	R. ovata
Rhus trilobata	R. trilobata
Aceraceae	
Acer negundo	A. negundo
Rhamnaceae	
Ceanothus greggii	C. greggii
Ceanothus integerrimus	C. integerrimus
Condalia lycioides	C. lycioides
Rhamnus californica	R. ursina
Rhamnus crocea	R. crocea
Rhamnus ilicifolia	R. ilicifolia
Sterculiaceae	
Fremontodendron californicum	F. californicum
Ericaceae	
Arbutus menziesii	A. arizonica
Arctostaphylos pringleii	A. pringleii
Arctostaphylos pungens	A. pungens
Oleaceae	
Forestiera neomexicana	F. neomexicana
Fraxinus anomala	F. anomala
Fraxinus velutina	F. velutina
Hydrophyllaceae	
Eriodictyon californicum	E. angustifolium
Solanaceae	
Lycium andersonii	L. andersonii
Lycium californicum	L. californicum
Lycium pallidum	L. pallidum
Bignoniaceae	
Chilopsis linearis	C. linearis
Caprifoliaceae	
Lonicera interrupta	L. interrupta
Sambucus mexicana	S. mexicana
Symphoricarpos longiflorus	S. longiflorus
Cucurbitaceae	
Cucurbita foetidissima	C. foetidissima
Cucurbita palmata	C. palmata

moderate levels in the mountains of the present desert. The rainfall requirements of grassland suggest that patches probably extended across the present desert region when the effective yearly rainfall over the lowlands was about 250–300 mm (10–12 inches). Clements also noted that woodland and associated chaparral taxa now have similar or related taxa on opposite sides of the present desert, implying continuity over the area at a time when rainfall was near 500 mm
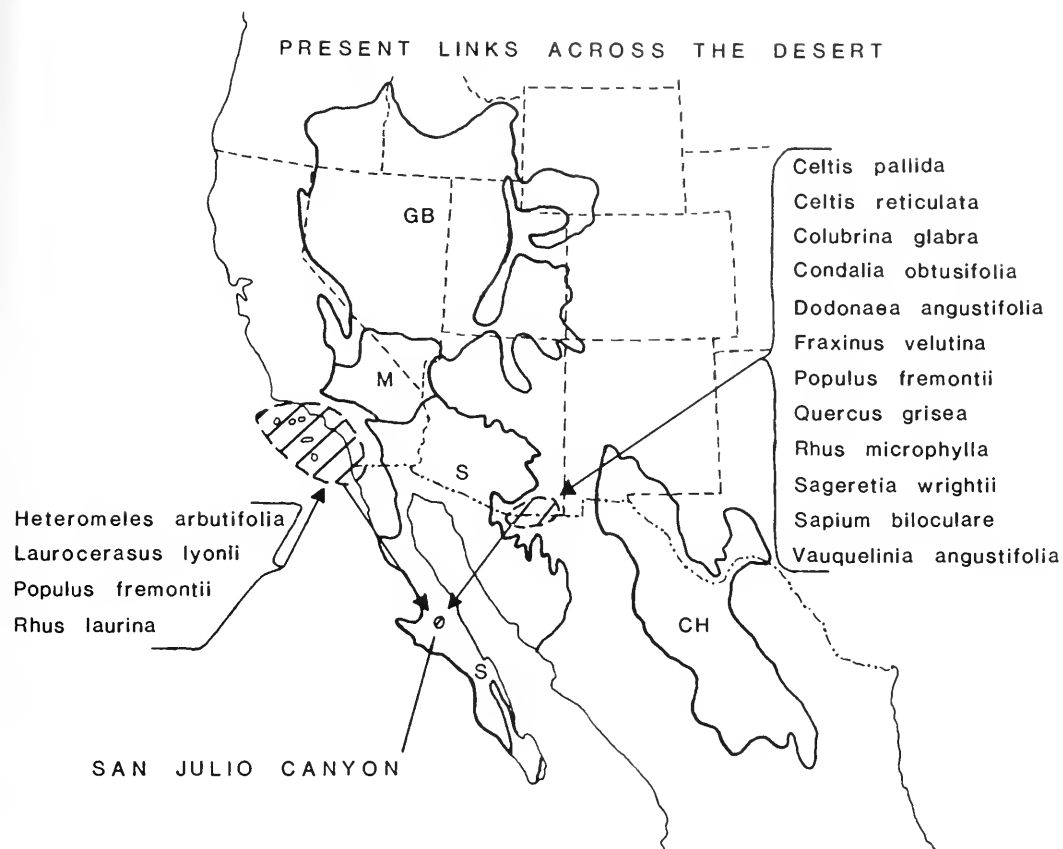
FIGURE 5. Many species in San Júlio Canyon in mountainous central Baja California are largely disjunct either to southern Arizona or to southern California. Their present intermingling at San Júlio parallels the composition of Neogene floras.

(20 inches) at a minimum, and when temperatures were much milder. Clements pointed out that if a sustained trend toward increased precipitation were to commence, these vegetation zones would successively move down from the surrounding mountains and plains out onto the present desert area.

However, it is apparent now from the late Pleistocene record of woodrat middens recovered at numerous localities (see Wells 1976b) that juniper-piñon woodland inhabited the southern Mohave lowlands (Wells and Jorgensen 1964; Wells and Berger 1967; T. J. King, Jr. 1976), that oak-conifer woodland covered much of the Sonoran Desert in Arizona (van Devender and King 1971; Lanner and van Devender 1974; van Devender 1976), and also the northern Chihuahuan Desert (Wells 1966, 1976a; van Devender et al. 1976). Since woodland covered the

present desert area as recently as 10,000–12,000 years ago, it is understandable that the taxa that now border the desert often have relict occurrences up in the desert ranges, having retreated into the mountains as precipitation decreased following the last major pluvial. The absence of regional grassland is implied also by the pollen record, though grasses were present. These were dispersed in openings of the formerly more continuous woodland, and persisted in sites below the present woodlands and as local patches in moister sites in the desert. The grassland that now covers the slopes above the desert in western Arizona appears to be a vegetation type of post-Wisconsin age, formed by the increase and spread of grasses as the woodland retreated to higher, moister levels.

Among the links that are in the chaparral of southern California and in central Arizona from

TABLE 2. TRANSADS ACROSS THE SEMIARID PARTS OF NORTH AMERICA THAT INDICATE PAST LINKS ACROSS THE AREA NOW DESERT.

Taxa	California	Arizona-Texas	Eastern Mexico	Western Mexico	Baja California
Pinus	subsect. *Cembroides* *monophylla* *quadrifolia* *[*](cembroides)	*edulis*	*cembroides* *cembroides* *nelsonii*	*cembroides*	*cembroides*
Platanus	*racemosa*	*wrightii*		*racemosa*	*racemosa*
Quercus	*chrysolepis* *dunnii*	*chrysolepis* *dunnii*			[1]*chrysolepis* [1]*cedrosensis*
Quercus	*wislizenii* *[*](emoryii)	*emoryii*		*emoryii*	[2]*devia* [1]*peninsularis*
Quercus	*[*](virginiana, brandegeii)	[3]*fusiformis*	*virginiana*		[2]*brandegeii*
Populus	*fremontii* *[*](palmerii)	*fremontii-arizonica-palmerii*	*mexicana*	*fremontii*	*fremontii*
Arbutus	*menziesii*	*arizonica*	*xalapensis*	*xalapensis*	[2]*peninsularis*
Garrya	*flavescens*; *elliptica*	*flavescens*; *ovata*	*ovata*	*flavescens*; *laurifolia*	[2]*salicifolia*
Cercis	*occidentalis*	*occidentalis reniformis*	*canadensis*		

[1] Northern Baja California.

[2] Cape Region only.

[3] Edwards Plateau only.

[*] Fossil records, Miocene.

the Mogollon Rim eastward to the Hualpai Mountains are a good dozen species (Fig. 4). Some of them still have outposts in the desert ranges today, or did in the recent past, for instance *Quercus dunnii* (=*palmeri*) in the Newberry Mountains south of Las Vegas (Leskinien, 1975). Apart from the taxa that are confined primarily to chaparral, there are a number of additional identical and related species in the bordering woodland of each region that also indicate links across the desert in the past; the entire group is listed in Table 1. In addition, Clements noted that a number of transads now link woodland vegetation in different parts of the western United States and Mexico, implying a greater extent for their precursors at times of higher rainfall, before there was a regional desert climate. Although some of his groupings are too broad and unnatural for acceptance today, there are a number of examples of related species that are now widely separated by the desert and live under different climatic regimes (Table 2). The distribution of these clusters of related species implies continuity of an ancestral alliance over the region by the late Eocene-Oligocene because some of them (*Pinus* cf. *cembroides*; *Quercus* cf. *brandegeii*) were already present then. Of special interest is the fact that some of the taxa—notably the oaks—have fossil records in California but their nearest descendants are no longer there, being confined now to regions with summer rainfall.

Apart from the ties between California and Arizona woodland-chaparral vegetation, there are taxa in coastal southern California that occur in the mountains of central Baja California, associated there with trees and shrubs that are now in southern Arizona (Fig. 5). They point to connections in the past, at a time when precipitation was at least 380 mm (15 inches) higher than at present, and when temperatures were more moderate. Furthermore, there are taxa in the California insular and coastal woodland that are closely allied to those now in the woodland of central Mexico (Fig. 6). They also imply that there were earlier connections across the area of the present desert, probably at a time when rainfall was near 635–760 mm (25–30 inches) at

PRESENT LINKS ACROSS THE DESERT

ALLIED LIVING SPECIES

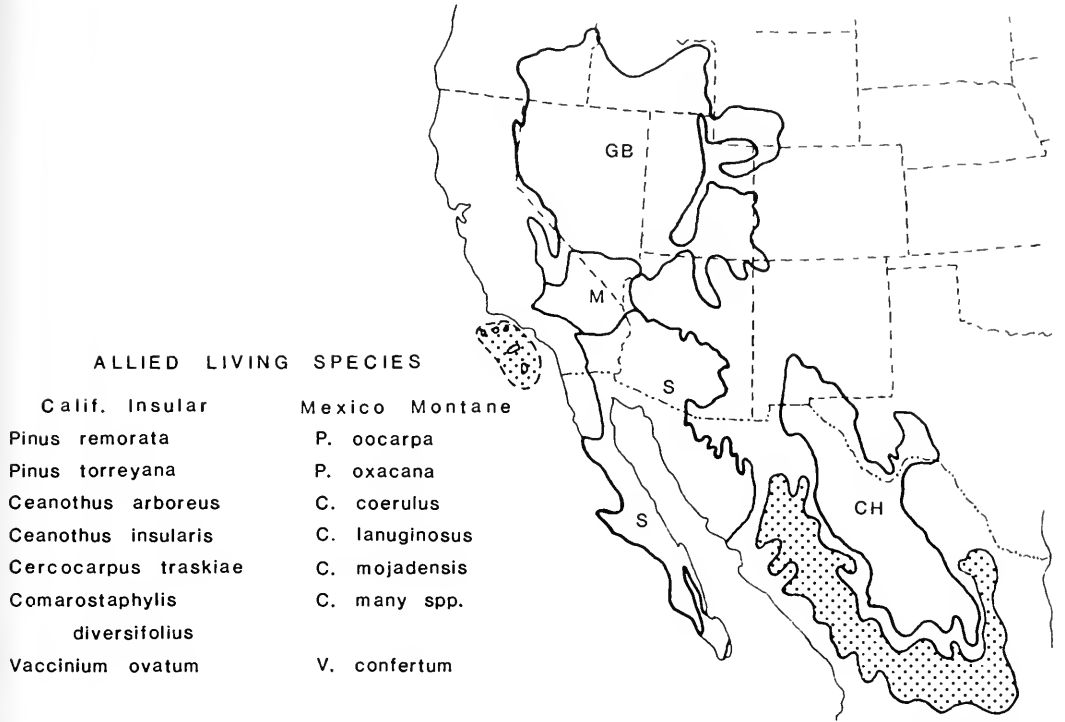| Calif. Insular	Mexico Montane
Pinus remorata	P. oocarpa
Pinus torreyana	P. oxacana
Ceanothus arboreus	C. coerulus
Ceanothus insularis	C. lanuginosus
Cercocarpus traskiae	C. mojadensis
Comarostaphylis diversifolius	C. many spp.
Vaccinium ovatum	V. confertum

FIGURE 6. Some unique taxa in the insular and maritime flora of southern California have their nearest allies in the Sierra Madre of Mexico, indicating a former continuum between these areas now isolated by desert climate.

a minimum, and when temperatures were moderate (see below).

These additional data lead to the inescapable conclusion reached earlier by Clements (1936): the area of the present desert was subject to a *progressive trend* toward gradual desiccation during the Tertiary, changing gradually from a well-watered area to the present region of extreme drought. The emergence of the desert as a broad regional environment is clearly an event of the latest Cenozoic.

PALEOENVIRONMENTS OF THE SONORAN DESERT REGION

Earlier analyses of the fossil floras known from areas in or marginal to the present Sonoran Desert have revealed that *1)* forests and savannas dominated over the region into the early Eocene, *2)* woodland and thorn scrub had appeared by the middle Eocene, *3)* semidesert tracts evidently were present in local edaphic sites and restricted rainshadows and dry valleys in the Oligocene and Miocene, though the taxa

also contributed then to grassland, short-tree forest, woodland, and thorn scrub, *4)* the semidesert taxa were preadapted both in form and function to the secular trend to increased aridity, and *5)* the present desert vegetation only appeared as a broad regional environment in post-Pleistocene time (Axelrod 1950d, 1958).

The notion that regional desert environments developed gradually and are comparatively new has not been accepted by most investigators. They argue that desert vegetation is of ancient origin and, by their inference, presumably occupied wide tracts throughout angiosperm history. They appear to hold this opinion chiefly because the unique adaptive types and morphologic novelties, which no doubt originated early, appear to give these floras the aspect of great age: since they live in deserts, deserts must be ancient. However, this view does not take into account that the distinctive adaptive types and most of the unique genera of the desert also contribute to vegetation zones that border the desert. Hence, these taxa need not indicate antiq-
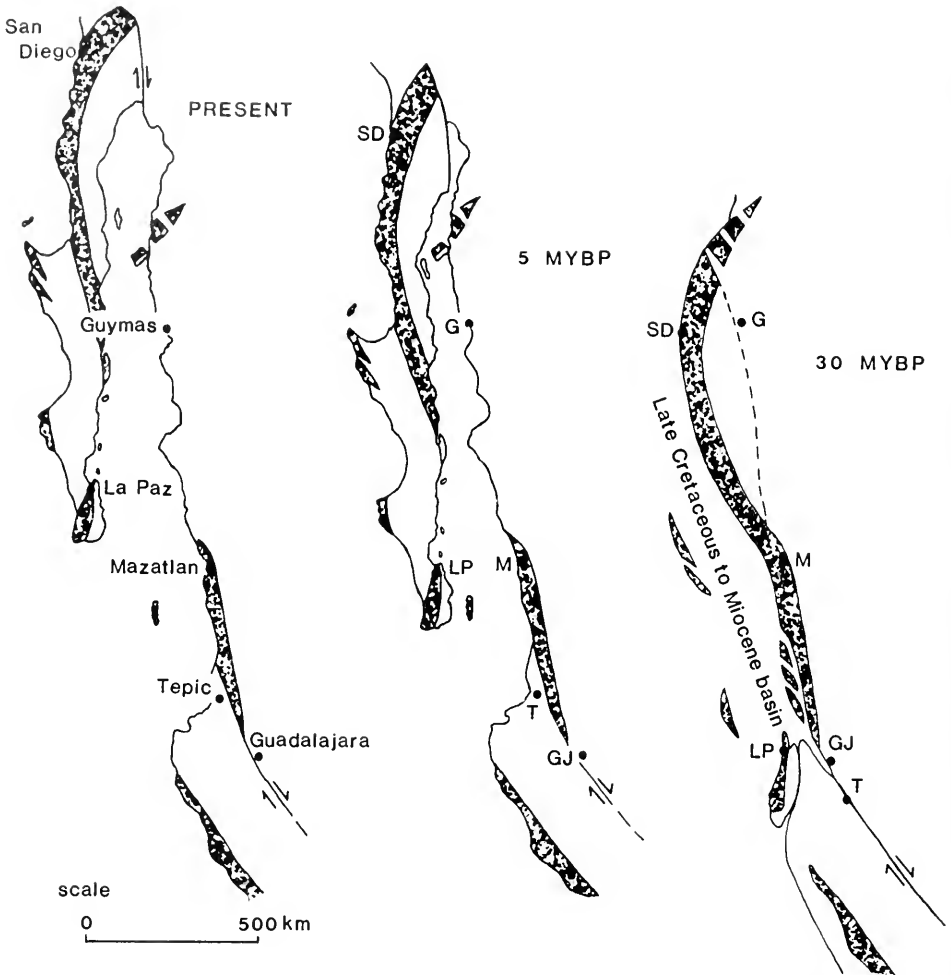
FIGURE 7. Reconstruction of the Pacific coastal sector of Greater California before rifting, after Gastil and Jensky (1973).

uity for regional desert climate, but rather an origin in dry sites and an ability to adapt to increasing and spreading drought, and to radiate with it later in their history.

This is consistent with evidence that *Fouquieria* is not confined to desert regions, but ranges into more mesic vegetation belts in central Mexico (Hendrickson 1972), including dry tropic forest where annual rainfall totals 1,000 mm (40 inches). Furthermore, *Beaucarnea* and *Yucca* (arborescent) are other unique adaptive types that range from the desert into dry tropic forest in the former case, and into oak-juniper woodland in the latter. *Canotia* is another distinctive isolate in its family (Celastraceae) that ranges up into the woodland belt, as do palms

(*Brahea, Sabal, Washingtonia*) and numerous arborescent cacti (*Lemaireocereus, Pachycereus*) which contribute to thorn forest and dry tropic forest. This is paralleled by *Welwitschia*, long regarded as an indicator of the antiquity of desert environment in South Africa. Typical desert adaptations (e.g., thick cuticle, deeply sunken stomata, small or reduced leaves, leaves often rolled or deciduous) are not present in *Welwitschia*. Actually it has the longest-lived leaves of any plant, as well as an enormous surface area (Bornman 1972, 1974; Bornman et al. 1972). Germination is controlled by an inhibitor which is only leached by sufficient rain. Young plants are most abundant not in the desert, but in wetter regions to the north. *Welwitschia* has

acquired crassulacean acid metabolism or CAM photosynthesis, a secondary characteristic adapting it to increasing aridity (Bornman 1977). (CAM photosynthesis involves the nocturnal opening of stomata and uptake of CO_2 and results in a greatly enhanced water-use efficiency.) Many succulent plants that inhabit arid areas also have CAM photosynthesis. Bornman concludes that *Welwitschia* probably originated in a subtropical climate, that it adapted to increasing and spreading aridity, and that the Namib Desert is not ancient, but youthful. In this regard, Krystofovich (1954) pointed out that if the report of *Welwitschia* pollen (Chiguryaev 1951) in the Eocene of Kazakhstan is confirmed, it would indicate that the taxon did not migrate to Kazakhstan from southwestern Africa, but rather that it has found its last refuge there. This interpretation is consistent with a recent analysis of the history of African vegetation during the Late Cretaceous and Tertiary (Axelrod and Raven 1977).

On this basis, the plants which were adapted to seasonally dry climates in border-tropical and tropical regions have been evolving continuously in local dry areas from the Late Cretaceous down to the present (*see* Axelrod 1958:fig. 2). As these local sites became progressively drier they represented the loci for the continuing origin of new taxa adapted to the ever-drier climates that spread over the lowlands (Axelrod 1967:fig. 1). This leads to the conclusion that the present area of the Sonoran Desert has been amassing taxa which were adapted to the drier climates that spread over the region. Those that originated in the Cretaceous, or the Eocene, or later, were preadapted to the increasingly drier conditions that spread over the region and have persisted there with little or only moderate change. As the trend to aridity increased, dry tracts spread and coalesced into a regional desert only during the interglacial ages, and especially after the last glacial. The evidence that supports this conclusion is based on the geologic history of the region, which not only includes its changing spatial and structural features, but also the evidence of environment provided by the sediments, and by the fossil plants and vertebrates that are preserved in them.

Geologic Setting

The geologic history of the Sonoran province provides critical evidence for interpreting the age and origin of desert vegetation. The data involve *a*) the shifting spatial relations of the coastal strip west of the San Andreas fault system, with the northward displacement of fossil floras from more southerly areas where they originally lived, *b*) the evidence of environments under which the sedimentary rocks associated with the fossil floras were formed, and *c*) the age of the development of the high relief in the area today.

Baja California–Gulf Province

The California batholith of mid-Cretaceous age and allied metamorphic rocks extend southward to form the basement of Baja California, southwestern Arizona, northwestern Sonora, and the coast of mainland Mexico southward into Jalisco. The Gulf of California, which now bisects this crystalline belt longitudinally, is sliced by several major transform faults. As outlined in recent critical papers (Gastil and Jensky 1973; Gastil and Krummenacher 1977; Gastil, Phillips, and Rodriquez-Torres 1972), in mid-Cretaceous time Alta and Baja California south of the Transverse Ranges lay against the present east coast of the Gulf of California between Guaymas and Cabo Corrientes, northern Jalisco. The Salinia–West Franciscan–Transverse–Orocopia–Tiburon blocks lay along Sonora and southeast California between the Tehachapi Mountains and Guaymas (Fig. 7). Active subduction in the mid-Cretaceous resulted in andesitic volcanism along a belt extending southward through southern Arizona, the states of Sonora, Baja California, and Sinaloa, accompanied by deeper granitic plutonism. The volcanic belt marked the western edge of the epicontinental sea which opened into the Atlantic.

As the positions of the Pacific spreading centers changed, subduction became localized and strike-slip motion was initiated. Evidence of movement is provided by the exotic clasts in the Cretaceous–Eocene–Oligocene conglomerates of southern California, derived apparently from source areas in Sonora and southern Arizona (Merriam 1968; Woodford, Welday, and Merriam 1968; Sage 1973; Doyle and Gorsline 1977). Minch (1971) showed that the streams that flowed westerly in both Sonora and the Peninsular Ranges fix the relations of the source and depositional areas and suggest rifting of up to 300–350 km northwest from the Mexican mainland. This interpretation is consistent with the
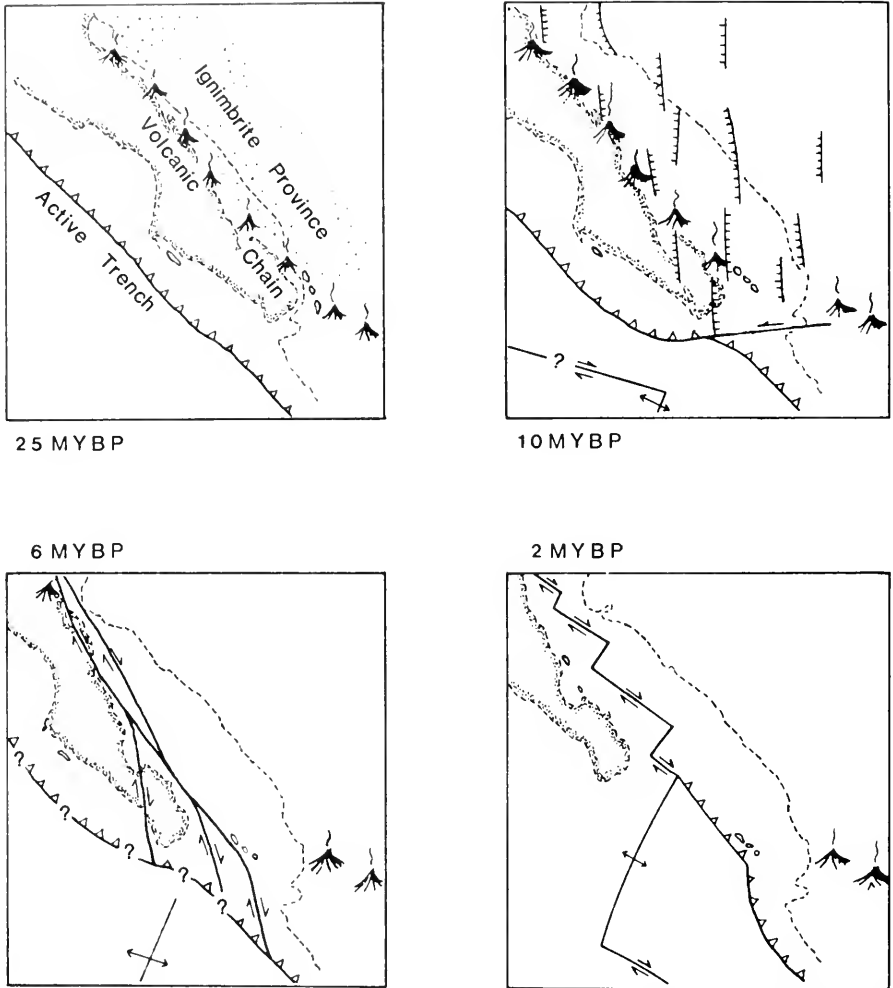
FIGURE 8.   Diagrammatic representation of the history of the Gulf and Peninsula of Baja California, after Karig and Jensky (1972).

late Mesozoic reconstruction of the blocks of the San Andreas rift zone as restored by Gastil and his associates (1972, 1973, 1977), and shown in Figure 7. Abbott and Smith (1978) add further convincing evidence.

Peninsular California first separated from continental Mexico in the middle Miocene, opening a shallow proto-Gulf of California (Karig and Jensky 1972; Christiansen and Lipman 1972; Moore 1973; Smith 1976). To the northwest, Peninsular California collided with and underthrust the more northerly blocks, producing the transverse structures. Middle Tertiary deposits filled the early depressions of the southern Gulf

and southern peninsular region. In late Tertiary time, all of mobile California moved northwest, producing the modern San Andreas fault and the deep basins of the Gulf of California.

Karig and Jensky (1972) note that the geology of the Gulf of California and the bordering areas to the east and west indicates that a trench, an andesite chain, and an ignimbrite province coexisted in the middle to late Tertiary in a tectonic pattern similar to that observed in other trench-arc systems. Extension and formation of the broad tectono-rift zone of the proto-Gulf of California occurred in mid to late Miocene time, creating a zone of weakness subsequently used

for strike-slip faulting and interplate extension. The model reconstructed by Karig and Jensky (1972) is reproduced here (Fig. 8) and agrees with that of Moore (1973) and Smith (1976). Baja California was about 300 km to the southeast, lying along the present coast of Sonora–Sinaloa–Nayarit and with the Cape Region tucked into the present bulge of northern Jalisco (also see Hamilton 1961; Rusnak, Fisher, and Shepard 1953). The Gulf of California is a pull-apart feature caused chiefly by Pliocene strike-slip displacement plus sea-floor spreading which adds up to 160 km (100 miles) of cross-strike separation of the continental plate, and with subcontinental magma having welled up into the rift during the late Pliocene (since 4 m.y.).

Thus, the development of the area chiefly involves events of the last 15-odd million years, starting with a simple marginal trench-arc system along the west coast of Mexico (Fig. 8a). A volcanic chain near the future site of the proto-Gulf spread andesitic and basaltic debris westward into Baja California and eastward into Sonora, Sinaloa, and Nayarit. The first sign of change is correlated with the eruption of ignimbrite (ash-flow) sheets in the Sierra Madre from centers close to, but east of, the andesite centers. Major extension probably began near the end of the main ignimbrite eruptions, between 10 to 15 m.y. ago (Fig. 8b). Up to this time, the area was one of relatively low relief as shown by the widespread ignimbrites, though there was a chain of volcanism down the eastern peninsular axis. The duration of extension within the proto-Gulf is inferred to have been from Miocene into early Pliocene, with faulting producing low ranges (Fig. 8c). Cessation of spreading in the Pliocene is suggested by small-scale faulting in the onshore and offshore sediments of this age, and by the rapid change in sediment thickness near the center of the Gulf where younger tectonic features were activated.

From about 7 m.y. to 4 m.y. ago, there was little or no extension in the Gulf, and up to several km of marine sediments accumulated there. There probably was strike-slip faulting within the Gulf along faults more nearly parallel to the peninsula than are those presently active (Fig. 8c). Motion on the southern California segments of the San Andreas fault zone since 10–12 m.y. is postulated to total 260–280 km (Crowell 1975), and it may be 300 km (Howell 1975; Matthews 1976; Sage 1973). During the past 4 m.y. the

history of the southern Gulf has been one of further interplate extension (Fig. 8d). This was accompanied by major uplift of the peninsula and the appearance of a drier climate within the Gulf and its margins.

Peninsular Ranges

The area of crystalline basement from the San Jacinto Mountains southward through the Agua Tibia and Cuyamaca mountains into the Sierra Juárez and Sierra San Pedro Mártir of northern Baja California is sliced by major faults that have important vertical as well as lateral components of movement (Jahns 1954; Gastil, Phillips, and Allison 1975). Although the absence of Neogene marine sedimentary rocks from most of the area indicates that the region was above sea level, structural and geomorphic evidence imply that much of its present elevation is quite recent. This has been inferred from the displaced young basalts in the hills west of the Elsinore fault near Murrietta-Temecula (Jahns 1954:fig. 10), and from the highly deformed Mount Eden (8–7 m.y.) and Bautista (2–1.5 m.y.) formations in the San Jacinto Mountains. In addition, there are thick, folded and faulted fanglomerates (Canebrake, Palm Springs, Ocotillo formations) of Pliocene and Pleistocene age along the front of the Santa Rosa Mountains southward through the Anza-Borrego Desert region (Jahns 1954:fig. 8). Since the Miocene and older Pliocene rocks of the same area are finer grained for the most part (see Dibblee 1954:fig. 2; Sylvester and Smith 1976:fig. 3), uplift in the later Pliocene and Pleistocene is implied. To the south in northern Baja California, Gastil, Phillips, and Allison (1975) present convincing evidence (especially Chap. 8, pls. 4, 6) for the late Pliocene and Pleistocene deformation and uplift of the extensive Cretaceous peneplaned bedrock surface, with its low relief and thin veneer of sedimentary and volcanic rocks.

Transverse Ranges

Recent detailed geologic studies in southern California have provided additional evidence that the Transverse Ranges are the result of very young uplifts accompanied by severe deformation (Dibblee 1968, 1975; Jahns 1973; Crowell 1973, 1975). The Plio-Pleistocene sedimentary units throughout the entire region of the Transverse Ranges are folded, faulted, and now elevated, a deformation that was captioned the

"Pasadenan Orogeny" (Reed and Hollister 1936). During the middle Tertiary and earlier, southern California was dominated by east-west–trending structural basins bounded by normal faults. Studies of the sedimentary sequences in these basins show that the coarse clasts were transported westward from the interior (Bohannon 1975; Minch 1971; Woodford, Welday, and Merriam 1968). Subsequent right-slip movements on the San Andreas and San Gabriel faults have displaced the structural basins and their sedimentary sections to their present positions. That the westward transport of sediment from the interior ceased recently is now clear from studies along the desert slopes of the Transverse Ranges.

Woodburne (1975) notes that formations of diverse ages in the area from western Antelope Valley at the west corner of the Mohave Desert southward to Cajon Valley had westward-flowing drainage systems during most of the Tertiary. The trend ceased only after the San Gabriel and San Bernardino mountains were uplifted in the late Pliocene, though local episodes of uplift may have temporarily interrupted formerly through-going drainage systems prior to Hemphillian time (5–8 m.y.). In the San Bernardino Mountains, the Mill Creek beds (=Potato Sandstone) of upper Miocene age evidently were deposited by west-flowing streams. However, the formation is now isolated from the interior by the uplifted block of the San Bernardino Mountains north of the Mill Creek fault (the north branch of the San Andreas), a block that is a part of the Mohave province (Dibblee 1975). This block is broken into several northward-tilted fault blocks that contain remnants of north-dipping Pliocene (?) fluviatile sedimentary rocks (Crowder Formation, Santa Ana Sandstone), indicating that they were laid down in a valley that probably drained coastward from the Mohave region in the Pliocene (Dibblee 1975). Clearly, the local relief in the region was quite low in the Pliocene, but at times hills were present adjacent to sedimentary basins now aligned along the major fault systems and contributed to distinctly different clastics deposits in them. The broad structural picture is thus the late Pliocene and Pleistocene uplift of the San Gabriel and San Bernardino mountains blocking the previous east to west transport of clastic sediments. The elevation of the mountains brought a drier climate and also greater ranges and extremes of

temperature, to the interior area where the desert presently occurs.

Summarizing, in California, movement on the San Andreas fault system has been about 300 km (190 miles) since the late Miocene (10–15 m.y.), as judged from displaced volcanic sequences (Huffman, Turner, and Jack 1973; Matthews 1976; Ehlig, Ehlert, and Crowe 1975; Joseph and Davis 1977), from displaced basins (Blake et al. 1978), and from unique plutonic rocks (Ehlert and Ehlig 1977; Farley and Ehlig 1977). Evidence also suggests that there may have been major right-slip in offshore southern California, displacing San Miguel, San Nicolas, and southern Santa Cruz islands 120–160 km (75–100 miles) northwesterly since the middle Miocene (Howell, Stuart, Platt, and Hill 1974; Abbott and Smith, 1978). Other segments of the system, such as the San Jacinto, San Gabriel, and other faults, evidently have moved at least 150 km (Blake et al. 1978). Earlier, pre-Miocene movements are recorded in Baja California–Jalisco (Gastil and Jensky 1973) and also in central to northern California (Clarke and Nielsen 1973). Miocene sea-floor spreading as well as right-slip movements have displaced the Cape Region fully 500 km (300 miles) northward from Cabo Corrientes (Gastil, Phillips, and Rodriquez-Torres 1972). This corresponds closely with the results reached in Alta California. The spatial relations as presently understood are indicated in Figures 7, 8, and 9.

VEGETATION SEQUENCE

The preceding summary of available geologic evidence provides a reliable basis for assessing changing environments over the area of the present Sonoran Desert from the Late Cretaceous down to the present. It is amply clear that all of the fossil floras in southern California and Baja California that lie west of the San Andreas fault system lived well south of their present areas, and that a number of them lived in areas that now correspond to the central part of the Sonoran Desert. A more precise reconstruction of the positions of these floras must await further geologic studies. Figure 9 pictorializes the displacement of about 500 km since the middle Miocene, a separation that places San Diego at the general latitude of Guaymas (Fig. 7). The estimated positions of the fossil floras are outlined in Figure 9. It is therefore appropriate to consider the nature of the changing environments

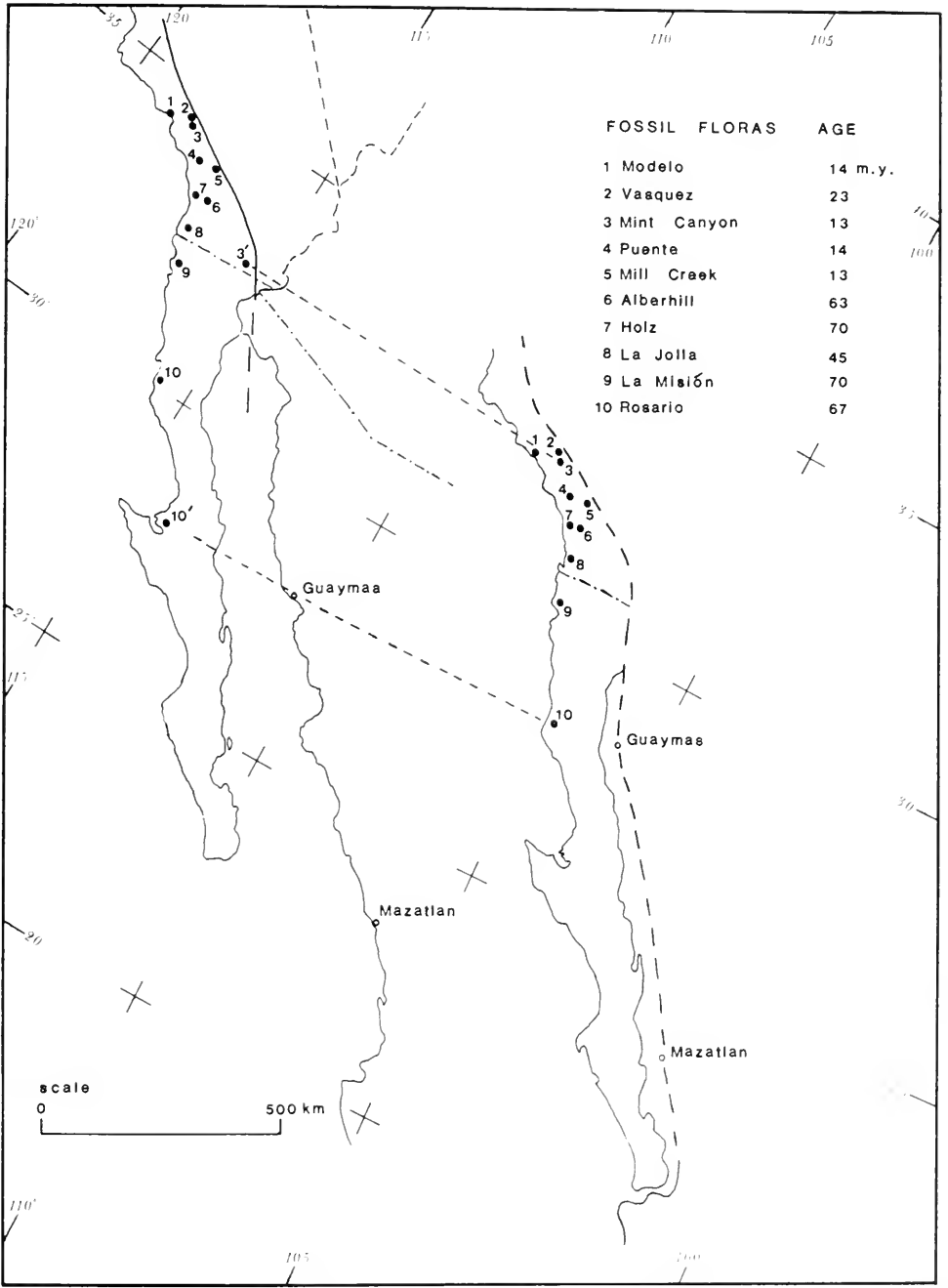| FOSSIL FLORAS	AGE
1 Modelo	14 m.y.
2 Vasquez	23
3 Mint Canyon	13
4 Puente	14
5 Mill Creek	13
6 Alberhill	63
7 Holz	70
8 La Jolla	45
9 La Misión	70
10 Rosario	67

FIGURE 9. Reconstructed positions of fossil floras that lie west of the San Andreas rift zone. Maximum possible distance (500 km) is shown. Note that most of the floras. which have been transported north by complex plate movements. were situated in areas presently occupied by the Sonoran Desert flora (see Fig. 10).
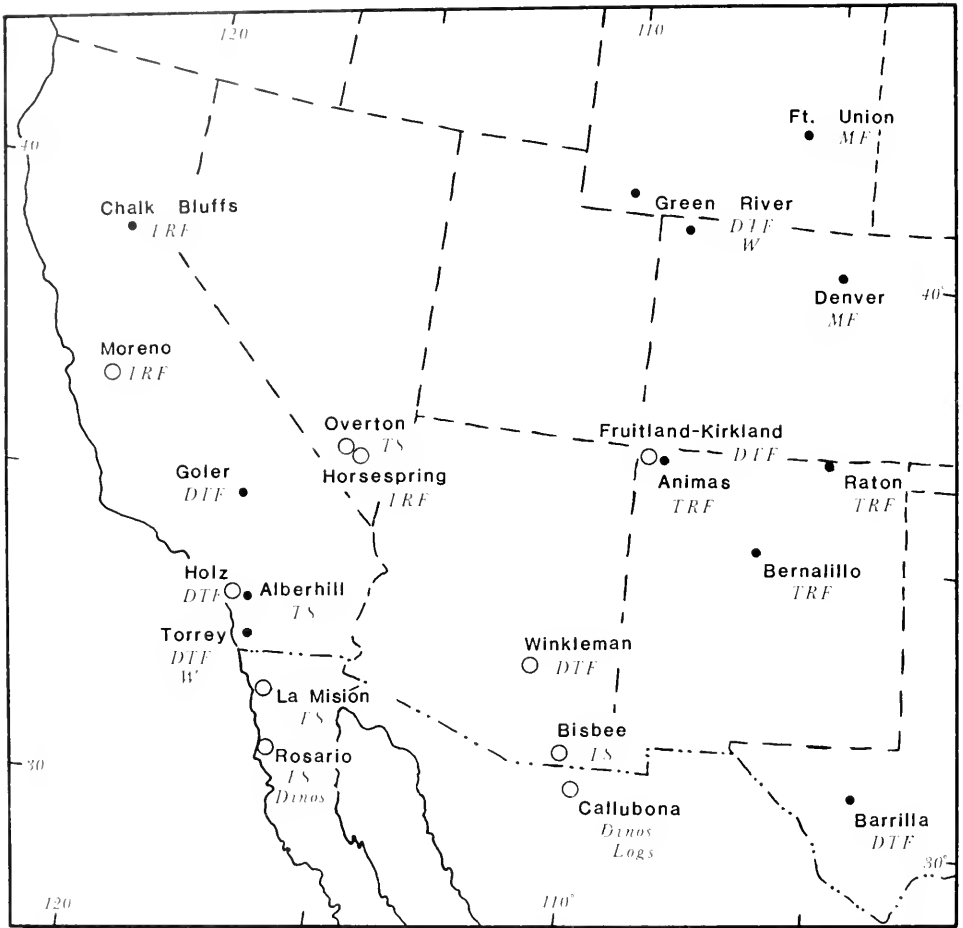
FIGURE 10.   Some Late Cretaceous (open circles) and early Paleogene (closed circles) floras that provide evidence of vegetation and climate. *TS* = tropic savanna, *DTF* = dry tropic forest, *TRF* = temperate rainforest, *DTF* = dry tropic forest, *W* = woodland and tropic scrub, *Dinos* = large dinosaurs, *Logs*, identity not known (see Fig. 9, for earlier positions).

indicated by them and by fossil floras elsewhere in the Sonoran province and its border areas, for they provide indubitable evidence concerning both the age and origin of desert vegetation. The location of the Cretaceous and older Paleogene floras is presented in Figure 10.

Cretaceous

Dry Tropic Forest and Savanna

In southern California, leaves representing a number of taxa have been recovered from the marine Holz Shale Member of the Ladd Formation. exposed in the central Santa Ana Mountains. Collected by Mr. and Mrs. Frank Grouard and presented to the Geology Department,

Chapman College, the flora is from beds that appear to correlate with those that contain *Turritella chicoensis* which is of early Campanian age (W. P. Popenoe and L. Saul, written comm.). *Araucaria*, the commonest plant, is represented by numerous branchlets, cone scales, and a cone. Also present are leaves of the conifer *Podozamites* and twigs that seem to be *Taxodium*. Ferns are represented by fronds that are similar to *Anemia* and *Osmunda*. Most of the dicot leaves are relatively small, chiefly in the size of microphyll and smaller. They include a lanceolate leaf similar to those of *Quercus*, a possible *Salix*, and *Litsea*. Smaller specimens of nanophyll size suggest such taxa as *Forestiera*, *Cercocarpus* and *Tephrosia*. Larger

leaves are less common, but include a complete *Magnolia* leaf 14 cm long, a fragment allied to *Credneria*, and a broken leaf of notophyll size that may be an araloid. The assemblage suggests that *Araucaria*, *Taxodium*, *Magnolia*, and *Credneria* formed a dense forest along water courses, and with dry tropic forest and associated shrubs on well-drained, drier slopes. The occurrence of deeply weathered red conglomerates of non-marine origin in the underlying section supports the inference of a warm, dry season, probably in winter.

Records from Baja California include twigs of *Araucaria* and *Brachyphyllum* in the Late Cretaceous (Campanian) rocks on the cliffs above La Misión, now situated about 100 km south of Tijuana. In addition, a cone of *Araucaria* and leaves of a laurel, similar to *Persea*, and other broadleaved dicots, and large logs (13 m long) are in the Late Cretaceous (Campanian) rocks near Rosario (Kilmer 1963; Morris 1967; Schile 1974). Remains of large terrestrial dinosaurs (Morris 1967) also occur in this area which is now in the northern Sonoran Desert (Shreve 1936, 1951). Farther south, large fossil logs are reported in the Middle Cretaceous (late Albian–Cenomanian) rocks of southern Baja California (Mina 1956:17–18).

Lower Cretaceous (Aptian-Albian) rocks near Bisbee, Arizona, yield in situ logs of *Araucaria* that are up to one meter in diameter (Stoyanow 1949). They imply a well-watered tropical savanna climate with mild (equable) temperature, probably not greatly unlike that in southern Brazil today. In the nearby Callubona basin of Sonora, fossil logs are common in Upper Cretaceous rocks, and remains of a duckbill dinosaur indicate permanent water bodies and ample precipitation (Taliaferro 1933). On the east side of the Santa Rita Mountains, southern Arizona, Upper Cretaceous rocks in Adobe Canyon have yielded remains of the large carnivorous dinosaur *Gorgosaurus* (Stoyanow 1949:59). It presumably preyed on animals that required ample vegetation for food, and hence a climate of adequate precipitation is implied. These inferences are consistent with the occurrence of a Late Cretaceous broadleaved forest, reportedly containing *Cinnamomum*, *Myrica*, *Platanus*, *Sabal*, and *Viburnum* near Winkleman, Arizona (*in* Campbell 1904). This locality is now dominated by *Carnegiea*, *Cercidium*, *Fouquieria*, *Ferocactus*, *Larrea*, and other typical members of the Sonoran Desert flora. The Late Cretaceous Overton and Horsetank formations near Las Vegas, southern Nevada, situated close to the present northern margin of the Sonoran Desert, have yielded tree fern (*Temskya*), cycad, and several large-leaved (mesophyll) dicots (Read and Brown 1937; UC Mus. Pal. [University of California, Museum of Paleontology, Berkeley]).

Reconstruction of the positions of these Late Cretaceous plants, as suggested by structural evidence (Hill and Dibblee 1953; Crowell 1962, 1975; Gastil and Jensky 1973; Huffman, Turner, and Jack 1973), indicates that they lived in the area that now corresponds to the middle of the Sonoran Desert (Fig. 9). The plants from the Holz Shale were then situated near the present latitude of Viscaino Bay, and the taxa in the Late Cretaceous deposits at La Misión and near Rosario were then at the general latitude of Loreto-Commondú in the southern third of the present Sonoran Desert. From a regional climatic standpoint this area (lat. 25–30°N) may certainly be judged to have been the driest part of the continent at any time in the Late Cretaceous or early Tertiary. The data therefore indicate that the central part of the present Sonoran Desert region did not support an ancient desert of broad regional extent; there was sufficient rainfall for tropic savanna and dry tropic forest.

That a large desert region could not have occupied northwestern Mexico during the Cretaceous is apparent also if one attempts to draw a map of isohyets for a regional desert (Fig. 11a), a reconstruction that seems highly improbable. In the first place, the gradient could not have been steep—as required by a regional desert—because it would place the Late Cretaceous floras in areas of less than 200 mm (8 inches) rainfall, yet they probably required fully 1,140–1,270 mm (45–50 inches) at a *minimum*. Secondly, there was only a gentle temperature gradient northward during the Late Cretaceous (Lowenstam 1963), as well as in the early Tertiary (Frakes and Kemp 1973). Hence, there is no dynamic climatological basis for assuming a large region of extreme drought. Since the area in the latitude of central Baja California–Sonora was located under a subtropical high pressure system, seasonal drought is indicated. However, it was not a strong system because the floras indicate conditions suitable for savanna and dry tropic forest (Fig. 11b). That somewhat drier tracts had local, highly restricted occurrences
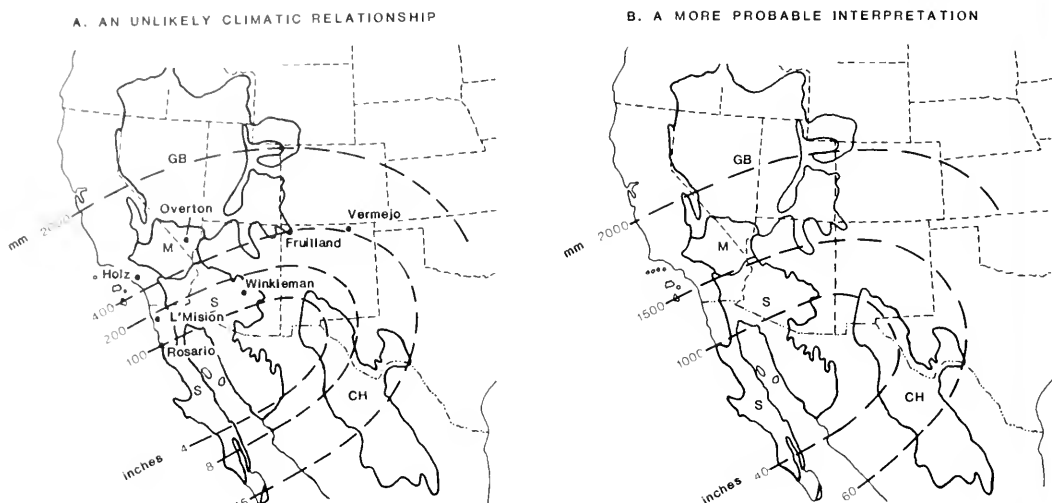
FIGURE 11.   Interpretations of paleoclimate. *A*. Reconstruction such as required by adherents of a regional desert climate in the Cretaceous and early Tertiary. *B*. A more probable interpretation suggests a broad savanna region with local dry sites in the lee of low ranges and on rocky exposures with thin soil.

over the region during the Late Cretaceous can scarcely be doubted.

Tertiary

Tropic Savanna

The Paleocene Elsinore flora, from the east side of the Santa Ana Mountains in southern California, reflects a wetter climate than that indicated by the flora from the Holz Shale Member of the Ladd Formation 29 km (18 miles) west. The Elsinore plants have much larger leaves, ranging in size from notophyll to mesophyll. They appear to include taxa in common with the Raton flora of the western interior. Large fronds of ferns are especially abundant, and the collection also includes feather-palm and fan-palm. The flora indicates ample rainfall, probably in the range of 1,200–1,500 mm (50–60 inches) at a minimum. A dry season probably was present, but not of great intensity or duration to judge from the abundant tree ferns. The inference of high rainfall and intense leaching under warm climate is supported by the mineralogy of the Alberhill Clay Member of the Silverado Formation in which the Alberhill flora is preserved (Sutherland 1935). It is a rich refractory clay and fine glass sand of the type that develops under intense chemical weathering in warm regions of high rainfall. Similar conditions are also recorded in the early Eocene of central California,

where the Ione Formation is composed of quartz sand, anauxite-bearing clays, and a thick residual iron-crust that developed there (Allen 1929).

The Elsinore flora (UC Mus. Pal.), which indicates a denser, richer vegetation than that represented by the Late Cretaceous flora of the Holz Shale, probably represents a savanna forest on a broad, well-watered floodplain near the coast. The flora, which lived near the present site of Viscaino Bay during the Paleocene, again demonstrates that a regional desert (or arid) climate could not have existed at the latitude of the present central Sonoran region at that time (see Fig. 9).

Temperate Rainforest

Paleocene to early Oligocene floras from central California northward (e.g., Brown 1962; Drugg 1967; MacGinitie 1941; Potbury 1935; Chaney and Sanborn 1933; Sanborn 1935) and eastward contain numerous plants allied to those that now contribute to the temperate rainforest (cloud forest) and dry tropic forest of southern Mexico and central America (Fig. 12), and to the similar forests of southern China. Taxa in these floras that occur in the temperate rainforest now in southern Mexico are distributed among the following alliances: Cycadaceae (*Dioon, Zamia*); Arecaceae (*Chamaedorea, Sabal*); Fagaceae (*Oreomunnea, Quercus*); Ulma-
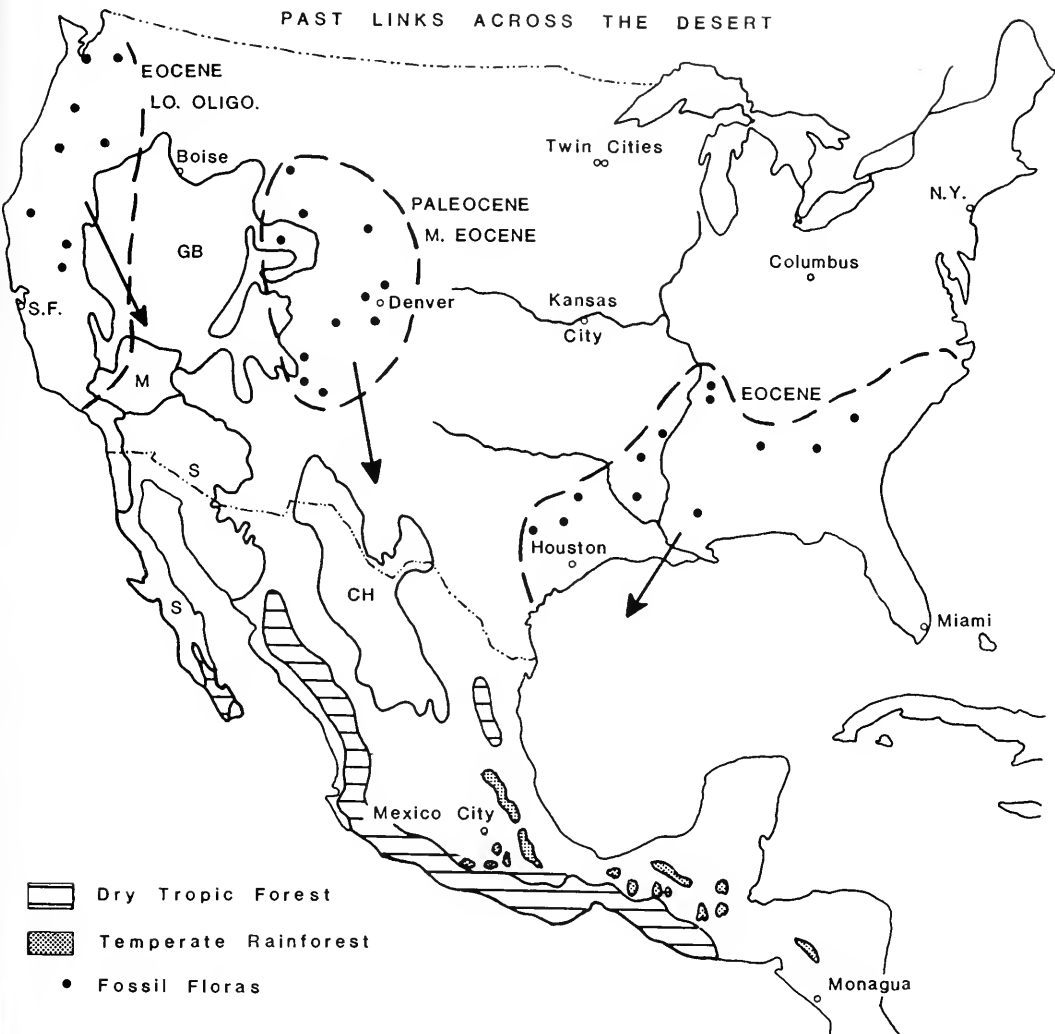
FIGURE 12. Taxa in the early Paleogene floras of the western United States have their nearest allies in the cloud forest (= temperate rainforest) and dry tropic forests of Mexico. They indicate past links over the present desert area, probably via uplands in western Mexico and prior to the late Eocene.

ceae (*Chaetoptelea*); Moraceae (*Ficus*); Papaveraceae (*Bocconia* [recorded as *Artocarpus*]); Menispermaceae (*Hyperbaena*); Magnoliaceae (*Magnolia*); Lauraceae (*Nectandra, Persea, Ocotea*); Hamamelidaceae (*Liquidambar*); Platanaceae (*Platanus*); Caesalpinaceae (*Cassia*); Fabaceae (*Dalbergia*); Mimosaceae (*Inga, Pithecellobium*); Meliaceae (*Cedrela*); Sapindaceae (*Allophyllus, Cupania*); Rhamnaceae (*Rhamnidium*); Dilleniaceae (*Tetracera*); Vitaceae (*Cissus*); Myrtaceae (*Calyptranthes*); Boraginaceae (*Cordia*); Styracaceae (*Styrax*); Apocynaceae (*Tabernaemontana*).

As judged from the present requirements of these plants, the fossil floras indicate ample precipitation (+1,500 mm; +60 inches), there probably was a brief dry season in the cooler months and a low range of mean monthly temperature, probably on the order of 5–8 C (10–15F) between the warmest and coldest months. The past occurrence of closely similar temperate rainforest taxa on opposite sides of the present desert region indicates former links across the area. The date of the connection is uncertain because of the lack of a known fossil record in Mexico. However, the nature of the Paleocene and

Eocene floras of the central and southern Rocky Mountains imply that any connections must have taken place prior to the middle Eocene (Axelrod 1939:76–78; 1975:317–320). The pathway probably was down the Sierra Madre axis in western Mexico because the eastern Sierra Madre had not yet been elevated (Schuchert 1935; de Cserna 1960, 1961). The western cordillera would have received ample rain from the expanded Gulf of Mexico and the Interior Embayment. Thus, climate probably was favorable for the continuity of rainforest into the Mexican uplands into the early Eocene and through the area now covered by desert, woodland, and grassland vegetation, and their respective climates (Fig. 12).

Previously known samples of this forest, as represented by the Paleocene–early Eocene floras of the Rocky Mountain province (Brown 1962; MacGinitie 1974; Leopold and MacGinitie 1972) and by those from central California northward, are supplemented now by a small flora from the Goler Formation in the western Mohave Desert. Taxa provisionally identified in it are *Anemia, Celastrus, Combretum, Ficus, Juglans, Magnolia, Myrica, Parathesis, Persea, Platanus, Sapindus,* and *Symplocos*. Associated with coal (Fairbanks 1896) that accumulated in a local swamp, it represents a broadleaved dicot forest rich in tree ferns (*Anemia*). The leaves of most of its species have a size (notophyll and larger) like many of those in the Raton, Animas, and allied floras of the central Rocky Mountain province (Knowlton 1917, 1924; Brown 1962). The Goler plants clearly indicate a region of high rainfall, and red beds in the basal part of the formation imply a dry season, probably in winter. The moist, equable climate indicated for the area is consistent with its position on the western slope of a crystalline upland region inland from the coast, in an area of moderate relief that probably had an elevation on the order of 305 m (~ 1,000 ft) above sea level.

Comparison of the moist forest climate indicated by the Goler flora with that in the central and southern Rocky Mountains demonstrates that regional differences in vegetation and climate were not marked, and that the present cordilleran axis had not yet been elevated. Furthermore, the general similarity of the Goler vegetation to that represented by the contemporaneous Elsinore flora, which has been transported northward from the latitude of central Baja California where it originally lived, demonstrates that widespread forests living under adequate rainfall characterized the present area of the Sonoran and Mojave deserts into Paleocene time.

Dry Tropic Forest

The trees that contribute to this vegetation regularly are of moderate stature and many of the taxa drop their leaves in the dry winter season. The vegetation grades southward into tropical savanna, and to the north where rainfall is lower, it gives way to a forest of lower stature, termed short-tree forest by Gentry (1942) in his admirable treatment of the vegetation of the Rio Mayo. As he notes, in that area the short-tree forest is composed of two major associations, the deciduous uniform forest of the slopes and the partially evergreen forest of the moister canyon bottoms and arroyo margins. The vegetation forms a continuous, unbroken forest canopy that is 9–15 m (30–50 ft) above the ground. At lower, warmer, and drier levels short-tree forest grades into arid tropical thorn forest, and at higher elevations it is replaced by oak woodland. As precipitation increases to the south, it gives way to a tropical semideciduous forest of richer composition and greater stature, as described notably by Rzedowski and McVaugh (1966).

As for the fossil record of dry tropic forest in the Sonoran region, a coaly seam in the basal part of the middle Eocene Torrey Sandstone in La Zanja Canyon, coastal San Diego County (Hanna 1926; Kennedy and Moore 1971), yields abundant pollen that appears to largely represent taxa of a dry tropic forest that lived near the shore area, about 3–5 km (2–3 miles) from the granitic basement hills to the east. The record provides an indication of the general environment of the area which was then situated near the present central part of the Sonoran Desert in Baja California. The following taxa have been recognized by Dr. William S. Ting in his preliminary study: Cycadaceae (*Dioon*); Pinaceae (*Pinus* subsect. *Ponderosae*; *Pinus* subsect. *Cembroides*); Juglandaceae (*Carya*); Fagaceae (*Quercus*); Ulmaceae (*Celtis*); Moraceae (*Ficus*); Caesalpiniaceae (*Bauhinia, Cercidium*); Aquifoliaceae (*Ilex*); Aceraceae (*Acer*); Simaroubaceae (*Suriana*); Bombacaceae (*Bombacopsis, Pachira*); Sterculiaceae (*Fremontodendron, Guazuma*); Rhamnaceae (*Gouania*); Vitaceae (*Cissus*); Fouquieriaceae (*Fouquieria*);

Oleaceae (*Forestiera*); Apocynaceae (*Cuphea*); Acanthaceae (*Ruellia*).

Many others are present though their generic identity is not yet established. Among those that appear to be present are: Arecaceae (3 different palms); Euphorbiaceae (cf. *Phyllanthus*); Sapotaceae (cf. *Bumelia*); Rhamnaceae (cf. *Ceanothus*); Rhizophoraceae (cf. *Rhizophora*). The structures of the sedimentary rocks and the nature of the clasts in the associated conglomerate indicate that most of the flora was derived from granitic hills nearby to the east. They apparently were clothed with vegetation like that now in Sinaloa and southward as judged from the descriptions of that region by Gentry (1942, 1946a, b), and Rzedowski and McVaugh (1966). In the Sierra Tachichamona southeast of Culicán and in the Sierra Madre to the north, there are transitions from short-tree forest or tropical deciduous forest to oak woodland which appear to parallel the record implied by the Torrey Sandstone sample. The shore area evidently supported mangrove swamps, and the higher hills to the east were covered with a pine-oak woodland, including *Pinus* (subsect. *Cembroides*), *Ceanothus, Celtis, Fremontodendron, Ilex,* and *Quercus.*

Mammals occur in the middle Eocene Ardath Shale of the La Jolla Group which is in part equivalent in age to the Torrey Sandstone. They are also in the immediately overlying formations of the La Jolla Group, as described by Golz (1976). These faunas, which are middle Eocene and late Eocene in age, imply a well-wooded region, with ample browse for the dominant, large artiodactyla. Clearly, the fauna could not have existed in a large regional desert.

Taxa that represent short-tree forest also appear to be in the Oligocene La Porte flora of the northern Sierra Nevada (Potbury 1935), as judged from the numerous taxa represented by small leaves and leaflets in the collection (UC Mus. Pal.) which are still undescribed. They apparently formed a drier forest on slopes bordering the dry evergreen forest whose taxa had larger leaves and were mesic in their requirements.

Species that represent a relict dry tropic (short-tree) forest evidently are also in the middle Miocene Tehachapi flora of southern California, where they lived chiefly on moister slopes bordering the semiarid basin. Among the taxa that may be assigned to short-tree forest are species of: *Acacia, Bursera, Cedrela, Cleth-*ra, Colubrina, Conzattia, Euphorbia, Dodonaea, Ficus, Persea, Platanus, Rhus, Schmaltzia, Trichilia.

The late Miocene Mint Canyon flora, which was then situated in the present area west of the Salton Sea (*see* Fig. 9), has only a few taxa that can be referred marginally to short-tree forest. These are in the following genera: *Cardiospermum, Cassia, Laurocerasus, Persea, Robinia, Sapindus* and *Thouinia*. Their rarity in the flora is not surprising, for the basin was in the lee of hills which gave it a drier climate over the lowlands which were dominated by semidesert (see below), woodland, and thorn forest vegetation.

To the east, the middle and late Eocene floras of south-central Texas (Ball 1931, 1939) represent a dry tropic forest that lived along the shores of the retreating Eocene seaway. They demonstrate that the present dry areas of the northern Chihuahuan Desert and the semiarid mesquite-grassland of southwestern Texas were not yet in existence. At a minimum, rainfall over the region probably totalled at least 127 mm (50 inches), with a dry, frostless winter season. In addition, the small late Eocene (38–39 m.y.) Barrilla flora of western Texas (Berry 1919), which is farther in the interior, represents a dry subtropic forest rich in laurels, palms, and other taxa that lived in a region that is now semidesert (Axelrod and Bailey 1976:237). A late Eocene (40 m.y.) pollen flora from the Galisteo Formation near Bernalillo, New Mexico, is now situated at the north edge of the Chihuahuan Desert in the Rio Grande trough (Leopold and MacGinitie 1972). Living at a higher elevation than the Barrilla flora, it indicates a moist, equable climate sufficient to support mixed evergreen-deciduous hardwood forest of warm temperature requirements, as implied by its species of *Acer, Alnus, Bombacopsis, Carya, Castanopsis, Engelhardtia-Alfaroa, Jatropha, Morus,* Palmae, *Pterocarya, Thouinia,* and others (Axelrod and Bailey 1976:236).

Sclerophyll Woodland

This vegetation, composed of evergreen and deciduous oaks, piñon, juniper, and their frequent associates (e.g., *Arbutus, Bumelia, Clethra, Garrya, Ilex, Mahonia, Rhus, Robinia, Sapindus*) now inhabits the mountains across the southwestern United States, the Sierra Madre of eastern and western Mexico, and the higher ranges of Baja California. Several very distinct

associations contribute to the modern wood-
land, each of which has a number of restricted
endemics. The modern communities are segre-
gates of the richer, more diverse, more gener-
alized Madro-Tertiary Geoflora. Species allied
to those that make up the Madrean woodlands
now in northern Mexico occur in middle Eocene
and younger floras scattered from California to
the High Plains and northward into Colorado-
Utah. They clearly demand a former continuum
across the region now desert.

As noted earlier (Axelrod 1939, 1950c), the
oldest known records of woodland vegetation
are in the interior, in the Green River and Flo-
rissant floras (MacGinitie 1953, 1969). By late
Eocene time, taxa allied to living species of *Pi-
nus* (subsect. *Cembroides*), *Arbutus*, *Clethra*,
Cercocarpus, *Mahonia*, *Morus*, *Quercus* (sev-
eral), *Prosopis*, *Robinia*, *Rhus (Schmaltzia)*,
Sapindus, and others were already established.
Taxa that represent oak woodland appear to oc-
cur also in the middle Eocene Torrey Sandstone
pollen flora near San Diego (see above). The
occurrence there of *Agave*, *Bauhinia*, *Ceano-
thus-Rhamnus*, *Celtis*, *Cercidium*, *Gouania*, *Fo-
restiera*, *Fremontodendron*, and *Quercus* indi-
cates that a seasonally dry climate was well
developed south of the Eocene temperate rain-
forest represented by the early Eocene Chalk
Bluffs (MacGinitie 1941) and late Eocene Com-
stock (Sanborn 1935) floras of central California
and Oregon.

That dry tropic scrub as well as sclerophyllous
taxa were already present in the Torrey Sand-
stone area is not surprising. Ecologically com-
parable taxa are in the middle Eocene Green
River flora of Colorado-Wyoming (MacGinitie
1969), including species of *Pinus* (subsect. *Cem-
broides*), *Bursera*, *Cardiospermum*, *Oreopanax*,
Platanus, *Populus*, *Quercus*, *Rhus*, *Sapindus*,
Thouinia, *Vauquelinia*, and numerous leaflets of
taxa that represent Caesalpineae and Mimoseae.
These relations support the opinion that the Tor-
rey Sandstone taxa originated earlier, in dry lo-
cal sites provided by exposed slopes and rocky
ridges with thin soil when the area was situated
farther south, near the center of the Eocene high
pressure system which was much weaker than
the present one (see Axelrod 1958:fig. 2).

That oak woodland with sclerophyllous
shrubs occupied the lowlands of the Sonoran
region in the middle and late Tertiary is apparent
from the nature of Vasquez, Tehachapi, and

Mint Canyon floras. Included in the small Vas-
quez flora, which was then situated near the
present California–Baja California border, are
species representing oak woodland and thorn
forest. Short-tree forest probably was also in the
area, for there are records of it in the younger
floras in the interior, in the Tehachapi and Mint
Canyon. On this basis, the region had about 635–
760 mm (25–30 inches) rainfall, or about 254–380
mm (10–15 inches) less than that inferred for the
coastal strip (see below). To judge from rainfall
distribution patterns, somewhat drier climate no
doubt was in existence farther south, near the
present center of the Sonoran Desert. If the av-
erage rainfall over the lowlands of that region
was near 380–500 mm (15–20 inches), then local
dry slopes, deep sheltered canyons, and inter-
range valleys must have been drier and would
have supported a rich semidesert flora. It may
have resembled that which may be seen at the
upper edge of the desert today in the foothills of
Sonora, in southern Baja California, on the
flanks of the mountains in southern Arizona, and
in central Mexico, all regions where semidesert
vegetation interfingers with grassland, oak
woodland, or thorn forest.

The large Tehachapi flora (Axelrod 1939) is
composed of species representing oak-conifer
woodland, thorn forest, and short-tree forest
(*Arbutus*, *Clethra*, *Myrica*, *Persea*, *Pithecello-
bium*, *Trichilia*), as well as local semidesert
patches (see below) on dry sites. The flora in-
dicates a frostless climate during the middle
Miocene (17 m.y.), with rainfall near 635 mm
(25 inches), distributed chiefly in the warm sea-
son. This flora was situated near the northern
edge of the Miocene Madrean province which
has been a major floristic boundary since Oli-
gocene time at least (Axelrod 1950c). Oligocene
and Miocene floras to the north are composed
primarily of plants allied to those that are now
in the forests of the western United States, east-
ern United States, and eastern Asia, all of which
contributed to the rich Arcto-Tertiary Geoflora
that lived under moist, temperate climate. The
marked differences between these provinces is
attributed to a rapid rise in elevation northward
during the Miocene to a plateau near 760–915 m
(2,500–3,000 ft) where climate was cooler and
moister (Axelrod 1956, 1968), as sketched in Fig.
13 for the late Miocene.

Inasmuch as the Tehachapi flora is situated
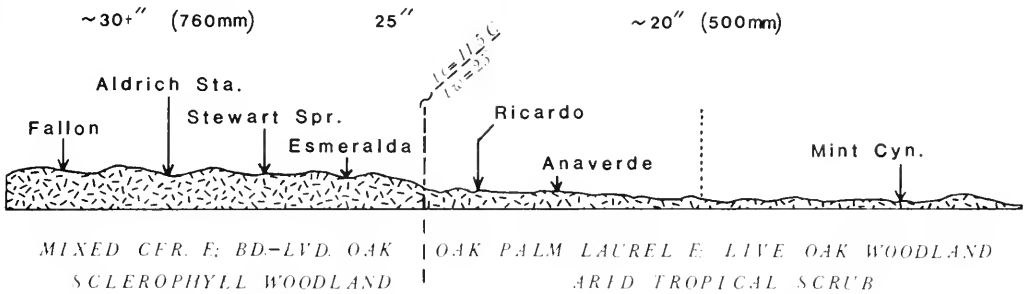near the north margin of the Tertiary Sonoran
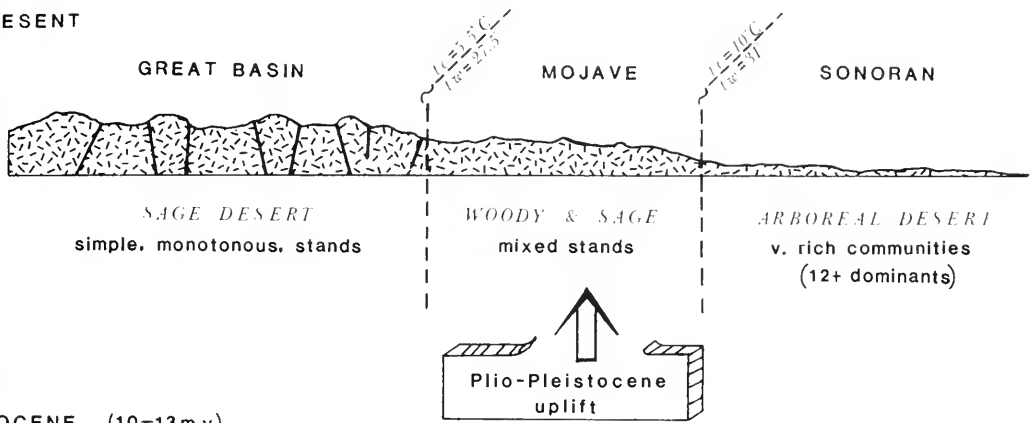
FIGURE 13. Transect from western Nevada southward into southeastern California today and in the late Miocene. Uplift of the Mohave block brought to it a colder climate and restricted taxa southward to the warmer Sonoran province and enabled more temperate alliances to invade the area from the north. tc and tw are mean temperatures, real and estimated, at the boundaries of the major biotic regions today and in the late Miocene, respectively.

province, the region farther south no doubt was somewhat drier, especially in the lee of Baja California which was covered with low volcanic hills at this time (Gastil, Phillips, and Allison 1975). The relations suggest that a rich semidesert (to desert?) flora probably occupied local discontinuous dry areas wherever effective rainfall was near 300 mm (12 inches). The actual extent of such areas and the composition of the flora are indicated by the nature of the late Miocene (13 m.y.) Mint Canyon flora, which was then situated west of the present area of the Salton Sea near the Mexican border. This particularly rich flora (over 100 species) is dominated by live oaks, numerous sclerophyllous shrubs, many legumes, and associated thorn forest taxa. The nature of the flora implies a dry basin, probably with about 500 mm (20 inches) rainfall in its drier parts. Precipitation was distributed chiefly in the warm season as judged from the numerous plants in it that are allied to species now in

northern Mexico. Among the taxa recorded are species of: Palmaceae (*Brahea*); Typhaceae (*Typha*); Cyperaceae (*Dichromena*); Salicaceae (*Populus, Salix*); Fagaceae (*Quercus* [7 spp.]); Ulmaceae (*Celtis* [2 spp.]); Juglandaceae (*Juglans*); Berberidaceae (*Mahonia* [2 spp.]); Lauraceae (*Persea*); Platanaceae (*Platanus*); Saxifragaceae (*Fendlera*); Crossosomataceae (*Crossosoma*); Rosaceae (*Cercocarpus* [2 spp.], *Holodiscus, Laurocerasus, Lyonothamnus, Prunus*); Leguminosae (*Acacia, Caesalpinia, Dalea, Eysenhardtia, Lysiloma, Piscidia, Pithecellobium, Robinia*); Euphorbiaceae (*Acalypha, Euphorbia*); Burseraceae (*Bursera* [3 spp.]); Anacardiaceae (*Pachycormus, Pistacia, Rhus* [4 spp.], *Tapirira*); Aquifoliaceae (*Ilex*); Celastraceae (*Schaefferia*); Hippocastanaceae (*Aesculus*); Rhamnaceae (*Ceanothus* [6 spp.], *Condalia* [3 spp.], *Colubrina, Rhamnus* [2 spp.]); Sapindaceae (*Cardiospermum, Dodonaea, Sapindus, Thouinia*); Vitaceae (*Vitis*); Passifloraceae (*Pas-*

siflora); Sterculiaceae (*Fremontodendron*); Fouquieriaceae (*Fouquieria*); Ebenaceae (*Diospyros*); Ericaceae (*Arctostaphylos, Comarostaphylis*); Oleaceae (*Forestiera, Fraxinus*); Verbenaceae (*Lippia*); Rubiaceae (*Chiococca*); Asteraceae (*Baccharis, Brickellia*).

The relatively low rainfall indicated by the Mint Canyon flora is consistent with its setting in a fault-controlled basin largely enclosed by hills of older crystalline rocks, Cretaceous sedimentary formations, and older Miocene sedimentary rocks of the Vasquez and Tick Canyon formations (Jahns 1954). Judging from the frequent occurrence of fanglomerates in the basin-margin sediments, hills lay in all directions with a major river entering the area from the east (see Ehlig, Ehlert, and Crowe 1975:fig. 3). To the west, the basin was separated from the coast by hills which have since been displaced northwest by movement on the San Gabriel fault (Crowell 1952, 1975).

That the Mint Canyon flora inhabited an interior basin is apparent also from the composition of the middle Miocene Topanga and Modelo floras now situated 37 km (23 miles) south of the Mint Canyon area, and the nature of Puente flora situated 72 km (45 miles) southeast of it, all in coastal southern California. These floras, which were situated near the present latitude of Ensenada–Santo Tomas in the Miocene, show that the coastal strip had a higher rainfall and supported a rich evergreen oak-laurel woodland with sclerophyllous shrubs, and with short-tree forest in moister sites. Among the taxa represented in these coastal floras which lived in an area that is presently semidesert are: Arecaceae (*Sabal miocenica* Axelrod); Pinaceae (*Pinus* [closed-cone]); Juglandaceae (*Juglans beaumontii* Axelrod); Fagaceae (*Quercus dispersa* [Lesq.] Axelrod, **Quercus* aff. *potosiana,* ** Quercus* aff. *virginiana*); Magnoliaceae (**Magnolia* aff. *schiedeana*); Annonaceae (**Annona* aff. *ampla*); Lauraceae (*Persea mioamericana* Berry); Rosaceae (*Cercocarpus antiquus* Lesquereux, **Lyonothamnus* aff. *floribundus*); Sterculiaceae (*Fremontodendron lobata* Axelrod).

Inasmuch as Oligocene floras regularly indicate a moister climate than do Miocene floras from the same area, we may infer that Oligocene

precipitation in the coastal strip probably was near 890–1,015 mm (35–40 inches), as compared with 760–890 mm (30–35 inches) in the middle Miocene. The early Miocene Vasquez flora from the eastern Soledad basin probably had no more than 635–760 mm (25–30 inches) as judged from the small sample now available. The composition of the Miocene floras thus suggests that the coastal slope of Baja California, then situated along the mainland coast farther south (see Fig. 8), probably was covered with short-tree forest, closed-cone pine forest, oak woodland, and numerous sclerophyllous shrubs during the later Oligocene and Miocene. Winters were frostless and there was a moderate period of drought in the cooler part of the year, as implied by the red beds of the Sespe, Vasquez, and lower Tick Canyon formations.

In this regard, attention is directed to a small, undescribed flora from the highest part of the Mill Creek beds (=Potato Sandstone) east of Redlands, California. The flora is preserved in fine sandstone associated with coarse conglomeratic sandstone and shaly interbeds on the crest of the ridge south of Mill Creek at an elevation close to 1,525 m (5,000 ft). The formation coarsens to the east where conglomerates increase in frequency, the clasts become larger, and the sandstones become more massive and conglomeratic, indicating that their source lay farther east. On the basis of about 300-km movement since the late Miocene, this flora lived in the area of the present international boundary in the heart of one of the driest parts of the present Sonoran Desert. Among the taxa tentatively recognized in this flora are: Pinaceae (**Pinus* cf. *cembroides*); Cupressaceae (*Cupressus preforbesii* Axelrod); Salicaceae (*Populus prefremontii* Dorf, *Populus sonorensis* Axelrod, *Salix edenensis* Axelrod, *Salix hesperia* [Kn.] Condit, *Salix laevigatoides* Axelrod); Fagaceae (*Quercus pliopalmeri* Axelrod, **Quercus* cf. *turbinella, Quercus wislizenoides* Axelrod); Berberidaceae (**Mahonia* cf. *fremontii*); Magnoliaceae (**Magnolia* cf. *schiedeana*); Platanaceae (*Platanus paucidentata* Dorf); Leguminosae (**Acacia* cf. *anisophylla, pringlei, Eysenhardtia anaverdiana* Axelrod, **Lysiloma* cf. *candida*); Rosaceae (*Cercocarpus antiquus* Lesquereux); Sapindaceae (**Cardiospermum* cf. *halicaca-*

Species compared with modern taxa are provisional determinations.

* Species referred to living taxa are provisional determinations.

PAST LINKS ACROSS THE DESERT

MIOCENE & PLIOCENE

MADREAN WOODLAND

Arbutus	Persea
Bumelia	Quercus
Clethra	Rhus
● Ilex	Robinia
Juglans	Sabal
Mahonia	Sapindus
Morus	Ungnadia
Myrica	Vauquelinia

● Fossil Localities

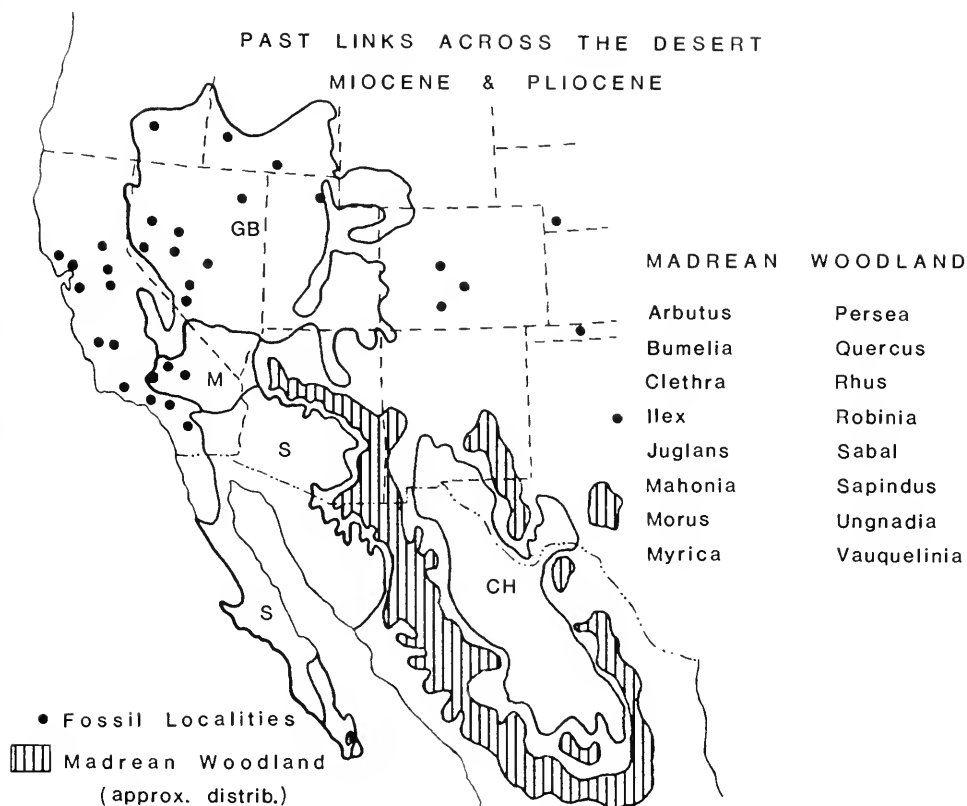▥ Madrean Woodland
(approx. distrib.)

FIGURE 14. Past connections across the present desert region are indicated by woodland taxa that have fossil records at localities well north of areas of their present occurrence.

bum, **Thouinia* cf. *pringlei*); Burseraceae (**Bursera* cf. *laxiflora*); Rhamnaceae (*Ceanothus*).

These taxa represent a piñon-oak-cypress woodland with scattered evergreen shrubs and with thorn forest in nearby drier sites. It suggests that rainfall was near 585–635 mm (23–25 inches) and that mild, frostless winters typified the area. As presently understood, it appears to be slightly older than the Mint Canyon flora. The differences may be ascribed chiefly to its somewhat higher elevation where it received more moisture and had somewhat more moderate temperatures, and thus supported a more mesic flora. Geologic evidence indicates that in the late Miocene this flora was situated in Sonora, near the present head of the Gulf of California (Fig. 9). This area is now pronounced desert, averaging only 50 mm (2 inches) precipitation annually. The present period of long drought is intensified by the very hot summers, with mean

monthly temperatures of from 30 to 33 C (86 to 91 F) in June, July, August, and September, and with *mean daily* temperatures regularly exceeding 38 C (100 F) during these four months.

The early Pliocene Ricardo (Webber 1933; Axelrod 1939:79–80) and the Anaverde (Axelrod 1950b) floras from the western Mohave area also contain species assigned to oak-conifer woodland and thorn forest vegetation. Since woodland and thorn scrub appear to be more impoverished as compared with that of the Miocene Tehachapi and Mint Canyon floras, and short-tree forest apparently was absent, precipitation is inferred to have been lower. This agrees with evidence in the bordering region which shows that rainfall decreased from the middle to late Tertiary. An early Pliocene pollen flora recovered from sediments near Prescott, Arizona, is composed of genera that contribute to oak-conifer woodland and associated sclerophyllous shrubs (Gray 1960). A number of unidentified
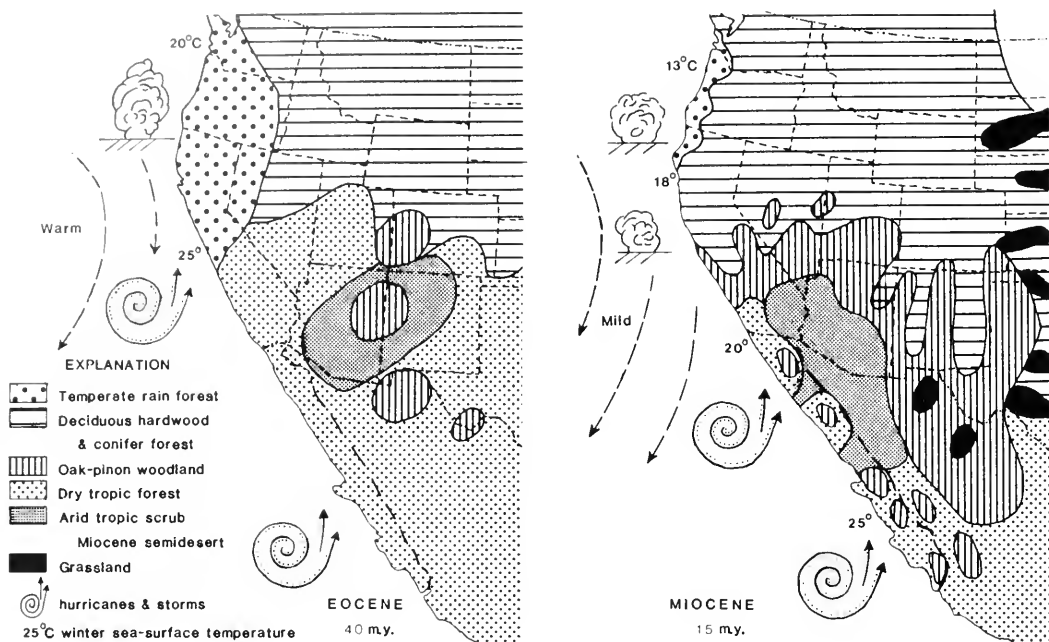
FIGURE 15.   General distribution of vegetation during Eocene and Miocene times. Note cooling sea-surface temperatures and resultant inferred southward restriction of hurricanes in the eastern Pacific (compare with Fig. 2).

grains in the sample may represent thorn scrub taxa, genera which largely occur today in Sonora. Inasmuch as the fossil site has been uplifted from the general level of the Sonoran Desert flora which now lies below it, widespread desert climate evidently was not present there. Rainfall probably was near 500–630 mm (20–25 inches). Since this region and the western Mohave area had not much more than 500 mm (20 inches) precipitation, we may raise the question as to the nature of the Pliocene environment farther south, in the middle of the present Sonoran region. Did it then support local desert vegetation, with woodland, thorn forest, and grassland confined chiefly to streamways and moister valleys and hillslopes with cooler (northerly) exposure?

An answer to this question depends on whether there is evidence that a drier climate was present farther south, in the area of the central Sonoran region, in the middle of the high pressure system. It seems certain that warm-season rainfall was more frequent and more effective over the entire region than it is at present. This follows for two reasons. First, the topographic features that now block the ingress of moist marine air from the tropics, notably the southern

Rocky Mountains and the entire plateau region of Mexico and its fringing mountains, were uplifted chiefly during and after the Pliocene. Second, as the oceans gradually chilled during the Tertiary, the California Current was becoming colder and increasing in strength. As a result, it formed a progressively more important factor that controlled the warm-season hurricanes and convectional summer rain. We may infer that as hurricanes encountered increasingly colder waters during the middle Tertiary they would gradually lose strength and their effect would be reduced at middle latitudes. As a result, during the later Cenozoic they were confined to successively lower latitudes, as sketched in Figures 2 & 15. Their restriction southward, together with the decrease in convectional summer storms, was a significant factor contributing to the rise and spread of semidesert and (later) desert vegetation.

On this basis, the principal areas of semidesert and desert during the Pliocene probably were restricted to dry valleys in the lee of low ranges, and in intra-range areas. Elsewhere, vegetation evidently was living under semiarid, not arid (=desert) climate. This is consistent with the

occurrence of rich floodplain vegetation in the western panhandle of Oklahoma in the early Pliocene (Chaney and Elias 1936) and also in the Clarendon beds of northern Texas (UC Mus. Pal.). Furthermore, during the late Pliocene precipitation increased sufficiently so that Rocky Mountain taxa—notably *Quercus gambelii*—penetrated eastward into northern Texas (Anderson and Kirkland 1969). Even in the late Pleistocene, rainfall increased sufficiently to enable juniper woodland to descend into the area of the present Sonoran Desert (van Devender and King 1971; van Devender 1976; Wells 1969, 1976b; Wells and Hunziker 1976).

The Neogene distribution of woodland vegetation thus provides a reliable basis for regarding the present day patches of woodland in the desert ranges as relicts of a formerly more widespread vegetation, as inferred by Clements (1936). As noted above, a particularly significant area is at San Júlio Canyon near San Ignacio, central Baja California, where taxa typical of oak woodland now in southern Arizona are associated with species that occur in coastal southern California (Fig. 5). This isolated community, which has persisted in a protected site above the desert, not only links the modern woodlands that are now on opposite sides of the desert, it simulates generally the composition of the Miocene and Pliocene floras of interior southern California and thus provides a significant link with the past.

This is consistent with the nature of the woodland that is scattered down the peninsula into the Cape Region. Represented in the southern peninsula region are species now confined to California (*Heteromeles arbutifolia, Malosma laurina*), others occur elsewhere only in southern Arizona and northern Mexico (*Pinus cembroides, Quercus oblongifolia, Q. reticulata*), and some are only in Sonora or nearby Sinaloa (*Populus monticola, Quercus albocincta, Q. tuberculata* [=*idonaea*], *Rhus brandegaena, Ilex discolor* var. *tolucana*). Some of these, together with certain restricted endemics in the Cape Region (*Arbutus peninsularis, Quercus brandegeii*), have very similar species in the Miocene floras of southern California (Axelrod 1939; 1958). A continuum is clearly implied for the middle Tertiary. At that time, the peninsula had not yet separated from the mainland of Mexico (Figs. 7, 8). Woodland presumably reached southward down a line of volcanos, linking the

flora of the Cape Region with that of Sonora-Sinaloa-Nayarit-Jalisco, which probably lived above scattered dry-tropic forest and thorn forest. Uplift of the central and southern peninsula following the Miocene continued to provide suitable moist upland environments for woodland as climate became progressively drier. Thus, the present links between the woodland vegetation of southern California and Arizona and border areas and between California and the Cape Region, and the uplands of western Mexico and southward (Fig. 2), are remnants of the Miocene vegetation which was much richer than that which has persisted in either area (Fig. 15). Taxa in the woodland and those that are vicarious between southern California and southern Arizona are listed in Tables 1 and 2 (above).

In addition, a number of woodland taxa that are now only in Arizona or in areas to the south or east are represented by close allies in the Miocene and Pliocene floras of southern California. Among these are: Arecaceae (*Sabal uresana*); Juglandaceae (*Juglans major* [*rupestris*]); Fagaceae (*Quercus arizonica, Quercus emoryii*); Ulmaceae (*Celtis pallida*); Lauraceae (*Persea podadenia*); Papilioniaceae (*Eysenhardtia polystachya, Robinia neomexicana*); Burseraceae (*Bursera microphylla*); Euphorbiaceae (*Sapium biloculare*); Aquifoliaceae (*Ilex brandegaena, Ilex rubra*); Anacardiaceae (*Rhus chondroloma, Rhus virens*); Sapindaceae (*Cardiospermum halicacabum, Sapindus drummondii, Thouinia pringleii*); Clethraceae (*Clethra lanata*); Sapotaceae (*Bumelia lanuginosa*). The occurrence in the Neogene of southern California of fossil plants that are very similar to these living taxa supports the notion that a more generalized, richer woodland covered southwestern North America well into the Pliocene, a woodland which then extended across much of the area of the present Sonoran Desert.

Local dry tracts increased in number and in area as precipitation was lowered during the middle Pliocene, the driest part of the Tertiary. To judge from the precipitation inferred for nearby areas to the north and east, a semidesert Sonoran flora probably then occupied scattered drier sites over the lowlands, interfingering with grassland and woodland in the bordering hills where rainfall exceeded 380–430 mm (15–17 inches), and with thorn forest now becoming rarer on its northern margin as temperatures decreased during the winter season.

A number of taxa have their northern outposts in southern Arizona. This evidently corresponds to their limit of tolerance for cold, as documented by Turnage and Hinckley (1938) on the basis of the severe frost damage inflicted by the cold wave of January 1937 to species of *Bursera, Celtis, Dodonaea, Eysenhardtia, Jatropha, Lysiloma, Mammillaria, Olneya, Simmondsia,* and *Sapindus.* In addition, several other taxa that have their northern limits in southernmost Arizona (e.g., *Atamisquaea emarginata, Bursera fagaroides, B. odorata, Cordia parvifolia, Sapindus saponaria*) probably are controlled also by frost. They are regular components of the Sonoran Desert flora in Mexico, and some contribute also to thorn forest which replaces desert vegetation farther south as rainfall increases and as winter temperatures rise.

Thorn Forest

This vegetation borders the southern margin of the Sonoran Desert and occurs also on the northeast coast of Mexico where it grades into mesquite grassland in Tamaulipas and Nuevo León and thence into the Chihuahuan Desert. Thorn forest, composed of species of *Acacia, Bursera, Cardiospermum,* arborescent Cactaceae, *Dodonaea, Eysenhardtia, Ficus, Jatropha, Karwinskia, Lysiloma, Pithecellobium, Randia,* and many others, requires essentially frostless winters. It occurs in areas of relatively low summer precipitation (380–510 mm; 15–20 inches) and is replaced by short-tree forest or oak woodland in areas of greater moisture or lower temperature. There are records of thorn forest taxa in the Pliocene (Mount Eden, Anaverde, Ricardo) and Miocene (Mill Creek, Mint Canyon, Tehachapi, Vasquez) floras of interior southern California. Species that may have contributed to this community are also in the Eocene Green River flora of Colorado, notably in the genera *Bursera, Caesalpinia, Celtis, Erythrina, Hibiscus, Mahonia, Mimosites,* and *Triumfetta.* Taxa in the Eo-Oligocene Florissant flora that probably contributed to thorn forest in the bordering region include *Bursera, Caesalpinia, Cardiospermum, Celtis, Colubrina, Conzattia, Dodonaea, Morus, Prosopis, Sapindus,* and *Zizyphus.* As depicted in Figure 16, the relations indicate a former continuum to the north, across the area of the present Sonoran (and Chihuahuan) Desert, at a time when rainfall was greater than in the desert at present, and when winter temperatures were much higher.

Hardy small trees and shrubs that may be regarded as relics of thorn forest vegetation persist in the Coloradan sector of the Sonoran Desert in southeastern California, notably species of *Acacia, Bursera, Cassia, Calliandra, Carnegiea, Cercidium, Fouquieria, Dalea, Olneya, Parkinsonia, Prosopis,* and *Washingtonia.* They increase in number and diversity in southern Arizona as summer rains become more frequent, though they do not form a thorn forest because winters are now too cold there for this vegetation zone. That they contribute to the Sonoran Desert flora, as well as to thorn forest, and occupied the present area of the Mohave-Sonoran Desert during the Miocene and Pliocene when live oak woodland also lived there, provides a significant clue to the role that spreading drought had in the origin of the present desert.

Semidesert

This term designates vegetation like that now at the upper, moister edge of the desert, where "desert taxa" mingle with those of woodland, thorn forest, or arid bushland ("mattoral") vegetation. It is distributed along the slopes of the Peninsular Ranges from southern California far into Baja California and occurs widely in southern Arizona, reaching southward into Sonora and Chihuahua. In addition, the Hidalgan desert areas of central Mexico are semidesert, occupying discontinuous areas in the valleys of Hidalgo, Puebla, Guerrero and southern San Luis Potosi, regions where it merges into thorn forest, or submontane mattoral, or woodland. In all these areas the vegetation is rich and diversified, with a large number of life forms and many plants of distinctive habit, structure, and behavior. The stature and density greatly exceed those of open deserts of low rainfall because precipitation is on the order of 380 mm (15 inches), and the moderate temperatures result in its greater effectiveness. Especially noteworthy is the fact that the great majority of the taxa contribute regularly to adjacent, more mesic vegetation zones, as well illustrated in the reports by Bravo (1936, 1937), MacDougall (1908), Quintero (1968), Rzedowski (1960), and Rzedowski and McVaugh (1966) on the vegetation of central Mexico.

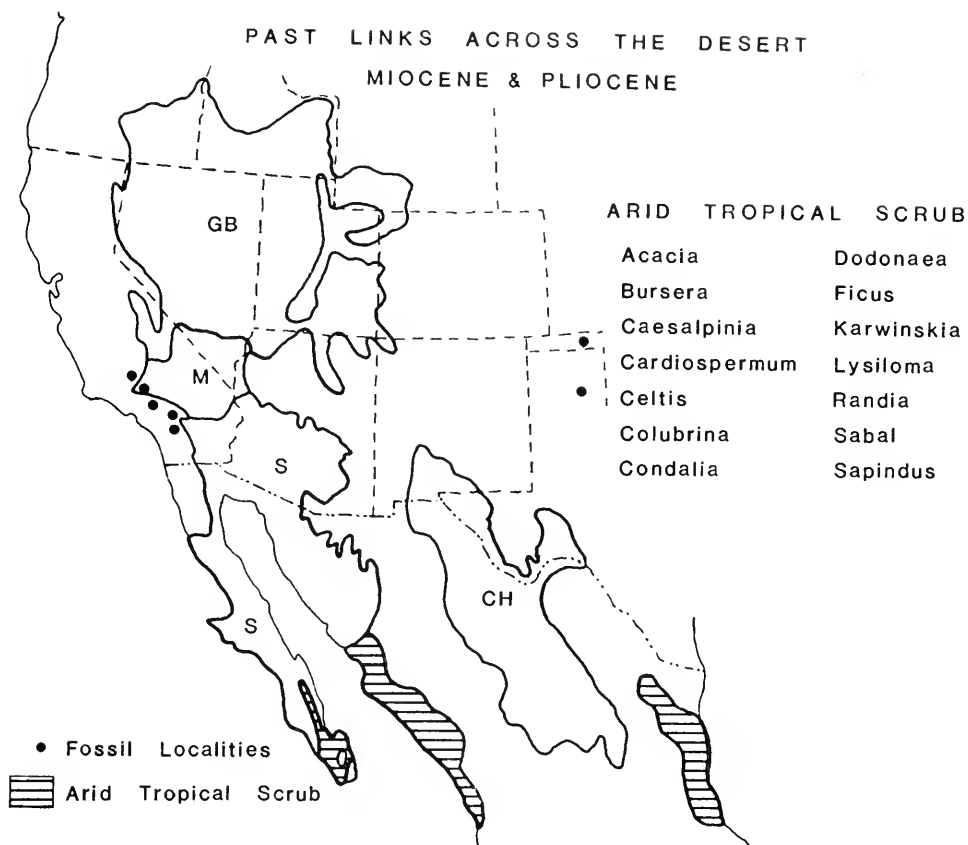The antiquity of semidesert vegetation is not

FIGURE 16.   Past links across the present desert area are implied by the Miocene occurrence of thorn forest taxa in areas north of their present distribution.

certainly known. However, the presence of taxa that are certainly referable to it in the Miocene indicates it has had a long history. There are indications of comparable alliances in the Florissant flora of Colorado, notably species referred to *Ephedra, Caesalpinites, Cardiospermum, Celtis, Colubrina, Conzattia, Dodonaea, Euphorbia, Mahonia, Morus, Philadelphus, Prosopis, Ptelea, Sapindus, Schmaltzia, Vauquelinia,* and *Zizyphus.* They seem ancestral to alliances that now occur in semidesert and desert areas, and they also contribute to shrubland and woodland vegetation. Furthermore, some of these taxa are represented in the middle Eocene Green River flora, notably *Cardiospermum, Celtis, Sapindus, Vauquelinia,* and numerous legumes. This is consistent with the occurrence of allied taxa in the Torrey Sandstone flora near Del Mar in coastal southern California as noted

above. That restricted, drier (often edaphic) sites over the interior region and in areas well to the south may have supported local semidesert communities in the later Paleogene seems highly probable.

Semidesert communities were certainly present in the Miocene of interior southern California. Among the taxa in the middle Miocene (17 m.y.) Tehachapi flora that appear to have formed local semidesert patches in the drier parts of that basin are: *Bursera* sp., *Bumelia* (*lanuginosa*), *Celtis* (*reticulata*), *Condalia* (*lycioides*), *Colubrina* (*arborea*), *Dodonaea* (*angustifolia*), *Ficus* (*palmerii*), *Euphorbia* (*hindsiana*), *Leucaena* (*microcarpa*), *Karwinskia* (*humboldtiana*), *Mahonia* (*fremontii*), *Pithecellobium* (*dulce*), *Pithecellobium* (*mexicanum*), *Prosopis* (*juliflora*), *Prunus* (*fasciculata*), *Rosa* (*mohavensis*). Streamways across the drier ba-

sins in this and the nearby area supported a riparian woodland composed of *Brahea* (=*Erythea*), *Populus*, *Quercus* (*brandegeii*), *Salix*, and *Sabal* that reached up into the woodland belt.

The late Miocene Mint Canyon flora, which was situated near the Mexican border (Fig. 9), has the largest representation of species that may be assigned to semidesert vegetation. Among the alliances presently recognized are: *Brahea*, *Quercus* (*turbinella*, *brandegeii*), *Celtis* (*reticulata*, *pallida*), *Fendlera* (*rupicola*), *Crossosoma* (*bigelovii*), *Cercocarpus* (*paucidentatus*), *Acacia* (*california*, *pringleii*), *Eysenhardtia* (*orthocarpa*), *Lysiloma* (*candida*), *Piscidia* (*mollis*), *Pithecellobium*, *Acalypha*, *Euphorbia* (*californica*), *Bursera* (*laxiflora*; *odoratum*), *Pachycormus* (*discolor*), *Rhus* (*microphylla*), *Tapirira*, *Condalia* (*lycioides*, *parryii*), *Colubrina* (*glabra*), *Rhamnus* (*pirifolia*), *Cardiospermum* (*halicacabum*), *Dodonaea* (*angustifolia*), *Fouquieria* (*splendens*), *Lippia* (*palmerii*), *Diospyros* (*palmerii*), *Forestiera* (*reticulata*), *Chiococca*, *Baccharis* (*sergiloides*). Lining the watercourses in the drier parts of the basin were species of *Populus* (*arizonica*), *Salix* (*lasiolepis*, *exigua*), *Juglans* (*rupestris*), *Platanus* (*racemosa*), and *Lyonothamnus* (*floribundus*). Semidesert vegetation was replaced by a rich oak woodland with numerous sclerophyllous shrubs on moister slopes and by thorn forest in warmer parts of the basin.

The Mount Eden flora (Axelrod 1937, 1950b) also has a number of taxa whose modern representatives occur along the upper margin of the Sonoran Desert. Eighty kilometers (50 miles) south of the Mount Eden area, on the desert slopes near Banner, are the following that have equivalents in the Mount Eden flora: *Agave* (new record), *Baccharis* (*sergiloides*), *Cercidium* (*floridum*), *Chilopsis* (*linearifolius*), *Condalia* (*parryii*), *Ephedra* (spp.), *Forestiera* (*neomexicana*), *Emplectocladus* (*fremontii*).

Associated with them are a number of woodland and chaparral taxa that have descended from the lower mountain slopes to below Banner at the upper edge of the desert, and which also have equivalent species in the Mount Eden flora, notably: *Arctostaphylos* (*glauca*), *Ceanothus* (*divaricatus*), *Ceanothus* (*cuneatus*), *Cercocarpus* (*betuloides*), *Quercus* (*agrifolia*), *Quercus* (*engelmannii*), *Rhamnus* (*ilicifolia*), *Rhus* (*ovata*). Additional taxa in the Mount

Eden flora that occupy similar sites in southern Arizona, where there is summer rainfall, include *Dodonaea* (*angustifolia*), *Eysenhardtia* (*orthocarpa*), *Juglans* (*rupestris*), and *Sapindus* (*drummondii*). That semidesert vegetation spread more widely as aridity increased during the later Tertiary can scarcely be doubted. But there is no reason to believe that a widespread desert like the present one was in existence at that time. The record as now known indicates that woodland (piñon-oak-juniper) reached well out into areas presently desert, much as it also did during the moister phases of the Quaternary.

Plio-Pleistocene Environments

Late Pliocene floras record a marked increase in precipitation and a decrease in temperature. This enabled yellow pine (*Pinus ponderosa*) forest to extend from the Sierra eastward into western Nevada where desert and sagebrush dominate today, and also into Coso and Panamint valleys in the Mohave Desert of eastern California (Axelrod and Ting 1960). This implies a considerable rise in precipitation, perhaps on the order of 380–510 mm (15–20 inches) at this time, before the major uplift of the Sierra. This is consistent with evidence of increased precipitation in the late Pliocene of central California as shown by the Sonoma floras from Napa (Axelrod 1950a) and Santa Rosa (Axelrod 1944), and by the record of mixed conifer forest (*Pinus lambertiana*, *Calocedrus decurrens*) in the Plio-Pleistocene Santa Clara Formation (Dorf 1930). Likewise, the Soboba flora from interior southern California (Axelrod 1966) records the lowering of mixed conifer forest fully 915 m (3,000 ft) into a region that is semidesert today. The early Pleistocene (?Nebraskan) pollen record in the desert area near Safford, eastern Arizona (Gray 1961), also provides evidence of a lowering of the pine-oak-juniper-sagebrush association down into the present desert area and indicates moister forest taxa (*Abies*, *Picea*, *Pseudotsuga*, *Betula*, *Ostrya*) in the higher mountains to the northwest.

A flora of similar age described from the Rita Blanca Formation near Channing northwest Texas, indicates a moister climate. This is contrary to the published opinion in which interpretations of the environment were based almost solely on the common taxa in the flora (Anderson and Kirtland 1969). No consideration was given to the absence from the present region of

Carya (in eastern or central Oklahoma and Texas), *Corylus* (now in east-central Oklahoma), *Juglans* (west-central Oklahoma, central Texas), *Ulmus* (eastern Texas and Oklahoma), or to the record of Sapotaceae (probably *Bumelia*, now in southern and western Texas). These taxa, when considered with the presence of eastern (*Quercus stellata*) and western (*Q. gambelii*) oaks as well as the more widely ranging taxa, clearly imply higher rainfall than that in the area today, as does the existence of the permanent lake in which the fossils accumulated.

When the evidence from all these floras is considered, they suggest that farther south the driest parts of the present desert region probably were semidesert, with local desert vegetation of highly restricted occurrence in arid pockets. Comparable evidence is provided also by the fossil record in the much larger desert region of northern Africa (see review in Axelrod 1973:265–267). Furthermore, a large pollen assemblage from the Plio-Pleistocene Koobi Fora Formation, East Rudolf, Kenya (Bonnefille 1976), shows that a prominent montane forest element, with numerous taxa like those now in the mountains of Abyssinia, lived much nearer the present site. The high representation of *Acacia, Commiphora,* and *Salvadora* also implies a shrub-tree cover denser than that now in the basin and reflects a cooler and wetter climate than that in this semidesert area today. Inasmuch as the pluvial stages affected the Sonoran region, the patches of Pliocene semidesert probably contracted, with the species retreating to favorable dry sites in intermontane valleys, lee slopes, and dry sites where they formed localized communities. It is recalled that many desert plants range out of the Sonoran Desert today, reaching into adjacent communities of moister requirements, where they occur on drier sites scattered in thorn forest, woodland, sage, and grassland vegetation.

The recent discovery of Pleistocene terrestrial mammals at several sites in southern Baja California is particularly significant in terms of environment during the pluvial phases of the Pleistocene. Among the taxa recorded by Miller (1977) from alluvial deposits 22 km (14 miles) southwest of San Miguel Commondú are *Nothrotherium, Canis, Urocyon, Termarctos, Felis, Mammuthus, Equus, Hemiauchenia, Camelops,* and *Bison.* Teeth of *Equus* and *Camelops* were recovered from a site near Santa Rita. In deposits about 19 km (12 miles) northeast of Santa Rita are a large and a small species of *Equus,* cf. *Hemiauchenia,* and a *Rhynchotherium,* previously unreported from the Pleistocene. As Miller properly notes, the taxa imply the presence of both wooded and grassland habitats, and hence a vegetative cover denser than that which now exists in these areas in southern Baja California. This is consistent with the late Pleistocene occurrence of *Juniperus* woodland in the Sonoran Desert northwest of Catavina, Baja California, in a region now dominated by forests of *Fouquieria* (*Idria*) *columnaris* (Wells 1969).

This evidence further supports the notion that during the moist pluvial ages desert environment largely disappeared from the area of the present Sonoran Desert. The data do not favor the idea that the Sonoran Desert was then restricted to the Lower Colorado River basin in California–adjacent Arizona (Martin and Mehringer 1965). Southern areas may well have served as refugia for thermophilous xerophytes because they are not associated with woodland conifers in the northern Sonoran Desert (Wells and Hunziker 1976). The data do suggest that the "desert taxa" simply survived in the driest sites in the bordering vegetation zones and contributed to them as well. In these sites climate was semiarid (semidesert), and woodland, grassland, and bordering shrubby communities regularly contained elements of the desert flora—as they still do today in Baja California, Sonora, and elsewhere in Mexico. This analysis is consistent with the preceding interpretation of the fossil evidence which suggests that the desert has been accumulating taxa from the diverse vegetation that occupied the present area of drought during the past.

It probably was only during the interglacials that a desert of regional extent came into existence. As judged from the record of wood-rat middens, there was sufficient precipitation during the last glacial to support oak-conifer woodland over much of the Sonoran Desert area in Arizona (King and van Devender 1977; van Devender 1976), in the Mohave region (Wells and Jorgensen 1964; Wells and Berger 1967; Leskinien 1975) and also in the Chihuahuan Desert (Wells 1966; 1976a). Scattered small patches of grassland may have been present, but there is no clear evidence for regional (zonal) grasslands in the desert area in the Wisconsin. Comparable changes are documented for the last glacial in
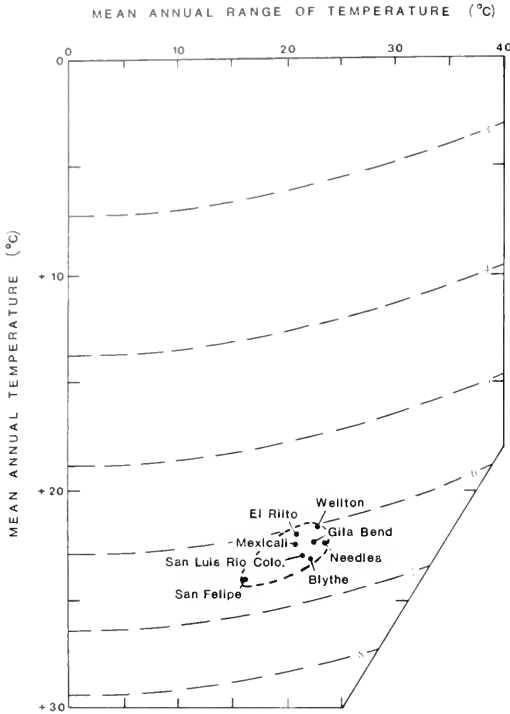
MEAN ANNUAL RANGE OF TEMPERATURE (°C)

FIGURE 17. Temperatures at representative stations in the northern Sonoran Desert indicate a water need (N) slightly in excess of N 6. Compare with Table 3.

the Saharan-Libyan and Kalahari Desert regions of Africa (Street and Grove 1976; Zinderen Bakker 1976) and Australia (Bowler et al. 1976; Butzer 1976), at which time those areas supported numerous lakes. It has been since the last glacial that deserts have been expanding, and they evidently are now wider in area and more extreme in climate than they have ever been— except perhaps for the Xerothermic period (ca. 8,000–4,000 B.P.). At that time the desert seems to have had a greater extent, as judged from relict, disjunct desert plants in cismontane and coastal southern California today (Axelrod 1966). In addition, under the influence of man (overgrazing, lowered water tables) the desert margin has been invading the adjacent grassland and also the margin of the woodland zone, a phenomenon that is well documented for the Mediterranean region and other areas (Naveh and Dan 1973; Aschmann 1973; de Vos 1975). The recency of extreme dry climate over the region is apparent also if we consider the water

need (N) of desert vegetation. As described by Bailey (1971), water need may be defined as

$$N = 0.5(1.025^{T+s} + 1.025^{T-s})$$

where T is mean annual temperature, and s is the standard deviation of the hourly temperatures around the annual mean (compiled from A [=mean annual range of temperature] if not available directly from summaries of hourly records). The equation expresses the principle that water need increases with temperature at the rate of 2.5% per F deg (4.54% per C deg). Such a rate agrees with certain aspects of evaporation theory (Bailey 1958) and with empirical evidence connecting the characteristics of plant communities with rainfall. In relation to mean annual temperature (T), N increases 8-fold over the span from -20 C to $+30$ C (Fig. 17). A smaller increase in N occurs with an increase in A, as seen in the upward curve of the lines of moisture need (N). Their pattern is a picture of the principle of precipitation effectiveness: to meet the water needs of plant life equally, more water is required in warm climates and warm seasons than in cool ones.

Table 3 lists the thermal and moisture conditions at several meteorological stations in the northern Sonoran Desert which are plotted in Figure 17. The stations have a similar mean temperature (T) and range of temperature (A), and a water need (N) slightly greater than 6. This implies that under these thermal conditions a precipitation near 300–380 mm (12–15 inches) is required to support semidesert vegetation. Since rainfall is scarcely one-third that amount at most of these stations, the region is clearly under the influence of an *extreme* desert climate. This is expressed by the nature of the vegetation in the drier part of the desert which is dominated by a *Larrea-Franseria* community that is markedly uniform over wide areas, very simple in composition, and has very few associates. *Larrea* and *Franseria* retain their dominance on soils which differ greatly in depth and texture, and they are also the chief constituents of the vegetation of deep alluvium as well as volcanic, or granitic, or metamorphic terranes. As Shreve notes (1951:49), these two plants are either dominant or abundant under differences of substratum which would support a very different vegetation under somewhat more favorable moisture conditions. Their dominance is due to the ".... remarkable physiological constitution of

TABLE 3. TEMPERATURE AND WATER NEED (N) FOR STATIONS IN THE NORTHERN SONORAN DESERT (see text).

Station	Mean annual temperature °C	Mean annual range*	Precipitation		** Water Need = N × V		
			mm	inches	index (N)	mm	inches
California							
Indio	22.8	21.7	79	3.1	6.3	401	15.8
†Blythe	23.1	22.2	81	3.2	6.4	406	16.0
†Needles	22.5	23.4	112	4.4	6.3	401	15.8
Arizona							
Yuma	22.1	20.9	61	2.4	6.1	386	15.2
†Gila Bend	22.3	22.3	142	5.5	6.2	394	15.5
†Wellton	21.6	22.8	107	4.2	6.0	381	15.0
Sonora							
Punta Peñasco	20.1	18.5	61	2.4	5.5	348	13.7
†San Luis Rio Colo.	23.1	21.7	52	2.0	6.4	406	16.0
†El Riito	22.1	20.9	47	1.8	6.1	386	15.2
Baja California							
†Mexicali	22.4	20.9	75	2.9	6.2	394	15.5
†San Felipe	24.2	16.3	58	2.3	6.6	419	16.5

* Mean annual range is defined by the difference in the mean temperature of the warmest and the coldest months.

** For the localities selected here, it is appropriate to think of the upper limit of precipitation of deserts in general, defined by a moisture index of V = 2.5 (Bailey 1958). Hence the precipitation in mm (or inches) is given by N × V, which for Indio is 6.3 × 2.5 = 401 mm (15.8 inches). Since the actual precipitation at Indio is only 79 mm (3.1 inches), it is apparent that this is an extreme desert locality.

† Stations plotted on Fig. 17.

these shrubs, and also to the simplicity of the flora, which has given them little competition." It is at higher, moister levels that *Larrea* gives way to a rich arboreal desert flora in which *Larrea* is a subordinant component of a many-dominant community composed of *Acacia, Carnegiea, Lemaireocereus, Lycium, Opuntia, Pithecellobium, Prosopis,* and many others, and with the wetter drainageways supporting *Juniperus, Pinus, Quercus, Platanus, Populus, Robinia, Sapindus,* and others from the nearby woodland. This is the sort of a semidesert flora that is inferred to have occupied the driest, local areas in the present Sonoran Desert region in the Pliocene, spreading gradually with increasing drought.

These observations are consistent with the notion that *Larrea* recently entered the region from South America (Axelrod 1950d:283), an inference consistent with its absence from the *Neotoma* midden records until about 10,580 ± 550 B.P. At that time it is recorded in the Wellton Hills (162-m elevation) in western Arizona, and then at more numerous sites in younger deposits, as reviewed by Wells and Hunziker

(1976). Granting that it may have been in only isolated dry areas early in the Quaternary, it nonetheless seems clear that it has become widespread only recently. Its evolution into diploid (n = 13), tetraploid (n = 26), and hexaploid (n = 39) chromosome races in the Chihuahuan, Sonoran, and Mohave Deserts, respectively, suggests progressive northward movement from an original (Chihuahuan?) area of immigration from South America (Wells and Hunziker 1976). Inasmuch as the present desert lowlands were occupied by conifer-oak woodland into the latest part of the Wisconsin, the present range of *Larrea* must be recent.

In each of these deserts the individuals of *Larrea* have multiplied many million-fold in the recent past, and chiefly since about 9,000 B.P. *Larrea* has seemingly spread into a new environment provided by the hotter and drier lowland basins that were *largely open* because conditions there were unsuited for taxa of the arboreal desert that now lives above it. The open lowland environment, in which competition was reduced, would have favored the easy establishment of *Larrea* following long-distance dispers-
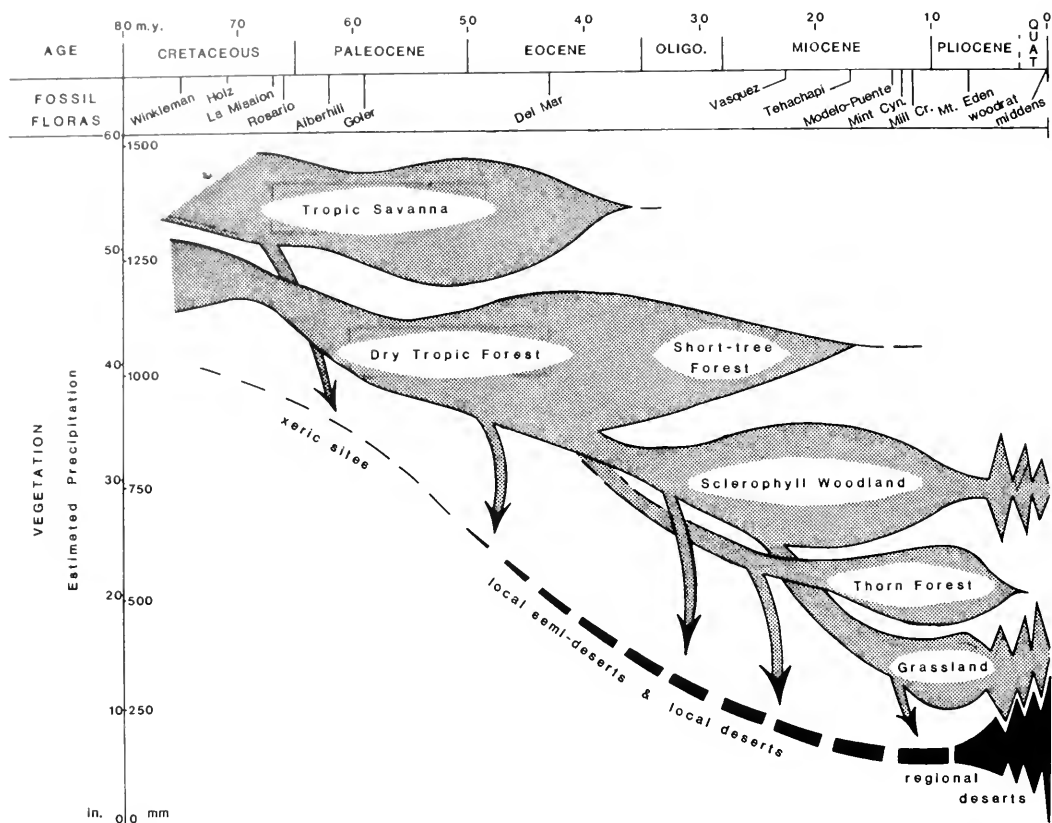
FIGURE 18. Vegetation sequence in the Sonoran Desert region from the Late Cretaceous into the Quaternary inferred from the fossil floras indicated. As discussed in the preceding pages, dry sites gradually increased in area and in the intensity of drought during the middle and later Cenozoic, and a full regional desert climate emerged only at the close of the period.

al, possibly by plover during the close of the Wisconsin (Wells and Hunziker 1976). On this basis, the lower and drier parts of the Sonoran Desert now dominated by *Larrea-Franseria* probably supported relatively few taxa when *Larrea* commenced to spread. These included occasional grasses, scattered *Franseria*, a few platyopuntias, occasional ocotillo, and with thickets of *Acacia* and *Prosopis* down the drainageways which were probably lined with a few shrubs, notably *Baccharis*, *Hymenoclea*, *Lycium*, and others. The nature of this conjectured, pre-*Larrea* environment finds a parallel today along Highway S-2 northwest of Ocotillo, California, where *Larrea* is quite rare locally in the desert. However, better examples occur widely in central and southern Baja California where invasion by *Larrea* is now in progress. It ..... ly along the shoulders of the ..... as in nearby stream wash-

es, yet is largely absent from the adjacent, very attractive desert.

Summary

Several different vegetation zones have occupied the area of the present Sonoran Desert since the Late Cretaceous (Fig. 18). They reveal a shift from tropical savanna and dry tropic forest that lived under relatively well-watered conditions and mild temperature, to woodland-savanna, to thorn scrub with scattered semidesert tracts living under lower moisture and moderate temperature, to a more recent regional desert of protracted drought and extreme heat. The shift to drier climate commenced in the early Eocene. The Eocene taxa that indicate dry climate probably originated earlier in local dry sites well removed from the lowlands where the sedimentary record accumulated. Drier tracts evidently were provided by south-facing slopes, by rainsha-

dows in the lee of low ranges, and by rocky outcrops composed of varied substrates. From such restricted areas, taxa already adapted to subhumid to semiarid conditions evidently shifted into the lowlands as those areas became progressively drier. That the taxa spread rather quickly over expanding dry areas in the present Sonoran region during the Oligocene and later is indicated by the fossil record now known from southern California and in the Rocky Mountains where dry climate was well established during mid-Eocene and later times.

By the late Eocene, semidesert vegetation may have occupied restricted dry slopes and lee valleys in the central Sonoran region wherever precipitation was near 380 mm (15 inches). Local semidesert tracts gradually increased in number and in size as the trend to aridity progressed during the Miocene and Pliocene. In the middle Pliocene, the driest part of the Tertiary, drier valleys and interfluves over most of the region probably were semidesert or desert-border, presumably with an aspect like that now at the upper edge of the Sonoran Desert where it is replaced by grassland, oak woodland, or thorn scrub.

Uplift of the Peninsular Ranges and the Mexican Plateau with its flanking Sierra Madre during the late Pliocene and later blocked the ingress of moisture to the Sonoran region from the Gulf of Mexico and also from the Pacific. In addition, the increasingly colder California Current now confined eastern Pacific hurricanes and accompanying summer rain to more southerly areas. These factors resulted in the appearance of more numerous and drier rainshadows, and in the spread of hotter and drier climate over the lowlands. As areas of semidesert contracted during the moist late Pliocene and in the pluvial stages of the Quaternary, relict stands persisted in local dry sites. At these times many desert and semidesert taxa were confined to the moister woodland, grassland, or thorn forest zones which dominated the present desert, environments where many of them still occur today. Post-glacial dry climates favored the rise to dominance of desert from semidesert vegetation which had earlier occupied most of the dry areas. Thus, the Sonoran Desert flora attained its greatest extent under the severe climates of the later interglacials, and especially during Xerothermic and Recent times. As aridity spread following the last pluvial, the rich Sonoran Desert flora that had dominated the lower desert flats retreated into the bordering hills and upper bajadas which earlier were covered with oak-piñon-juniper woodland or thorn forest. This left the lowlands essentially open, an environment which is now dominated by a *Larrea-Franseria* community. *Larrea* appears to represent a post-glacial immigrant into the region, (Wells and Hunziker 1976), possibly from a mid-Quaternary Chihuahuan center, and thence from South America.

EVOLUTION
GENERAL REMARKS

Evidence presented in the preceding section indicates that plants of generally subhumid requirements appeared initially along the west coast in the middle Eocene (Torrey Sandstone flora), that they were also well established over the interior at this time (Green River flora), and that taxa of more xeric requirements increased in diversity and in area during the rest of the Tertiary. It is inferred that taxa of semidesert requirements probably were present locally in dry valleys, on lee slopes, and on dry edaphic substrates in the central Sonoran region in the later Eocene, and spread gradually as aridity increased. The record as now known shows that when fossil plants allied to those that are now in desert and desert-border areas (i.e., *Acacia, Bursera, Cardiospermum, Celtis, Mahonia, Prosopis, Vauquelinia*) first appear in the record, their affinity with living species is quite apparent. Inasmuch as many of them are of Eocene age, they must have originated in earlier times. This raises the problem of the origin of the plants that now typify the Sonoran Desert.

The plants that now characterize the flora of the Sonoran Desert are not all of the same age. Some (e.g., *Fouquieria, Koeberlinia, Simmondsia*) have considerable antiquity because they are unique adaptive types and are also taxonomic novelties that represent ancient families which are well isolated from other alliances (Axelrod 1952:47; 1960:236). Other taxa represent genera (e.g., *Acacia, Cardiospermum, Ficus, Randia, Sabal*) that are recorded in early Tertiary floras, the species of which do not differ appreciably from those that range from dry tropic woodland or thorn forest into the Sonoran Desert today. In addition, some genera that are confined to the province are allied to those that are marginal to
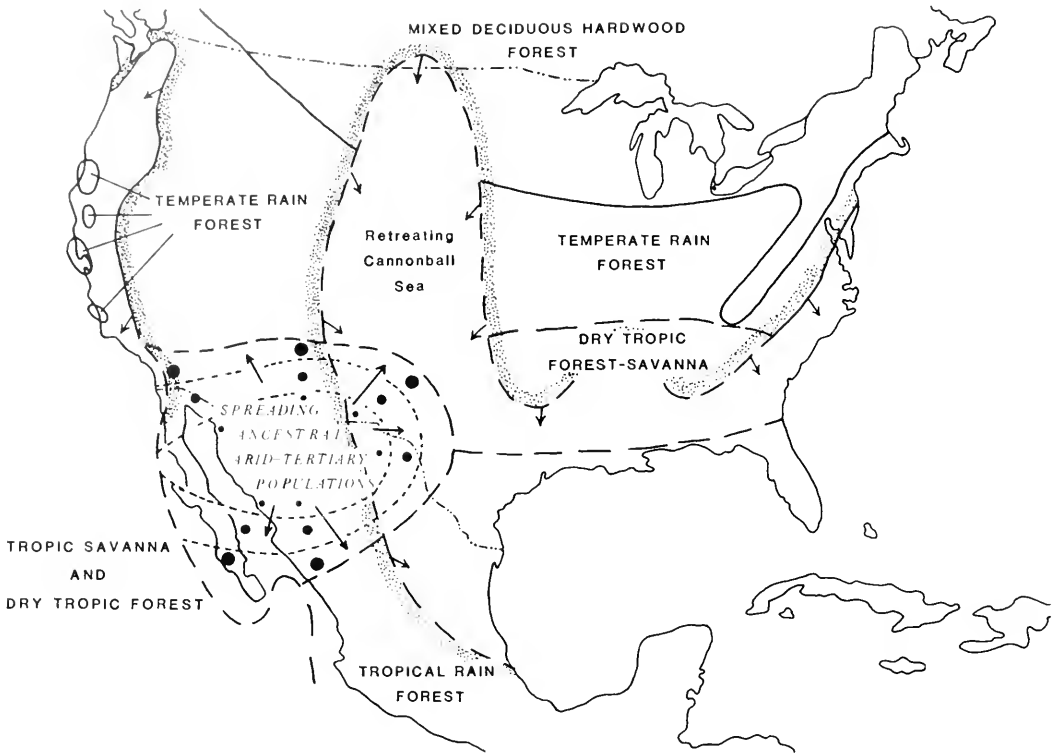
FIGURE 19.   General source of the arid to semiarid taxa of western North America as judged from the data in Fig. 18.

the desert (e.g., *Triteleopsis-Brodiaea, Harfordia-Pterostegia*) and evidently have been derived from them (Wiggins 1960). There are also many desert herbs and perennials (e.g., *Astragalus, Chaenactis, Eriogonum, Eschscholzia, Gilia, Mimulus, Penstemon*) that are related to species in the moister areas that now border the desert. Finally, some annual species of diverse genera (e.g., *Boutoleoua, Calandrinia, Layia, Lasthenia* (=*Baeria*), *Lepidium, Lomatium, Mimulus, Montia, Poa, Stellaria, Stipa, Trifolium*) that occur in the desert find optimum development in moister areas outside the desert. They appear to have entered the area during the pluvials and to have persisted there as desiccation progressed.

The origins of these different groups may be explained by the hypothesis that the forerunners of the plants now in the desert were adapted to, and were selected for, survival in a region where there was a general trend to the drier and hotter that spread over the area following the The data supporting this view are pro-

vided by (a) fossil plants that are similar to those that occur in the desert today, but lived earlier in more mesic communities, (b) fossil species closely allied to plants that range from moister regions into the desert at the present time, and (c) inferences that may be drawn from the past distribution, as well as the evolutionary and adaptive relations, displayed by taxa of the Sonoran Desert today. Viewed in the broadest possible manner, the taxa of the Sonoran Desert appear to represent the additions during time of alliances that were adapted both structurally and functionally to a climate that was becoming increasingly drier. Inasmuch as the oldest taxa evidently are Cretaceous, the history of the Sonoran Desert flora is bound up inseparably with that of Cretaceous angiosperms.

AREA

Taxa of many flowering plant families appear to have originated in seasonally dry, tropical regions by the middle of the Cretaceous (Axelrod 1952, 1960, 1970, 1972; Raven and Axelrod

1974). That the basic pattern of evolution in the regions of persistent high-pressure belts has been adaptation to drought is apparent: each landmass has developed a distinctive, autochthonous flora adapted to a dry season. Thus it is inferred that early angiosperms that lived in or marginal to dry climate soon became adapted to it. They radiated into its driest parts which in Cretaceous time were nowhere as extreme as those now in the dry tropics, apart from local edaphic sites which probably served as important evolutionary centers (Axelrod 1972) (Fig. 19).

As reviewed above, the fossil record demonstrates that the early evolution of taxa adapted to dry climate took place in response to the spread and increasing severity of seasonal drought and higher summer temperatures over southwestern North America. This is shown by the early appearance of taxa that represent dry tropical (short-tree forest, thorn forest) and warm temperate vegetation (woodland-chaparral) at low-middle latitudes on the west coast (Torrey Sandstone flora) and in the interior (Green River flora). Inasmuch as moister climates were present farther north, and presumably farther south, the presence of drier climate over the lower middle latitudes seems reasonably established. In addition, successively younger floras show that taxa of woodland, short-tree forest, and thorn forest vegetation radiated away from their inferred general area of origin. This also implies an evolution of dry-adapted taxa over the low-middle latitudes, a region where a high pressure system regularly develops and results in less frequent and seasonal rainfall. Finally, the adaptive relations of many taxa in desert and desert-border regions imply that they were derived from alliances that occur today in bordering, tropical and warm-temperate regions of moderate rainfall. This again suggests that the area of the present desert has been the center for the origin of taxa that are now typical of the region. However, this does not mean that deserts are of ancient origin: the fossil record demonstrates that forests, savannas, and woodlands covered the area of the present Sonoran Desert from the Late Cretaceous well into Neogene time (Fig. 18).

SOURCES

Two major floristic sources contributed taxa to the xerophyllous vegetation of western North America (Fig. 20). The chief source was basically tropical, derived from the sequence tropical savanna → dry tropic forest → thorn forest by gradual adaptation to decreased moisture. This is implied by the successive kinds of vegetation that have occupied the present area of the desert during the Tertiary. It may also be inferred from the similar pattern of adaptations shown by plants along the present gradient from savanna to dry tropic forest, thorn forest, and tropical (Sonoran) desert. Phylads of numerous genera, including species of *Acacia, Bauhinia, Caesalpinia,* Cactaceae, *Diospyros, Ficus, Gouania, Haematoxylon, Jatropha, Lysiloma, Randia, Trichilia, Zanthoxylon,* and many others, display a gradual reduction in stature, a decrease in leaf size, a more rapid response to a briefer period of growth and flowering, and a progressively shorter growing season as the desert is approached. In addition, many of the highly specialized adaptive types that occur in the savanna forest, dry tropical forest, and thorn forest range along a successively drier climatic gradient that extends into the desert. Not only is there a progression of related taxa from moister into drier vegetation zones, but also these zones replace one another as climate becomes drier, as can be seen today in Sonora and southern Baja California. In the latter area (Figs. 21–24), arborescent cacti become progressively more prominent in the landscape as the stature of the vegetation decreases and becomes more open as rainfall is lowered. It is this decrease in moisture that gives rise to the sequence arid tropic forest → arid tropic scrub → desert. The shift involves a decrease of from 760–635 mm (30–25 inches), to 635–380 mm (25–15 inches), to less than 380 mm (15 inches) in the desert. The giant columnar cacti attain maximum size in the dry tropic forest and scrub and in the upper (moister) part of the Sonoran Desert. They gradually decrease in numbers and disappear as the more arid microphyllous desert takes over in the driest areas. The shift corresponds to the several subprovinces of the Sonoran Desert described by Shreve (1951), notably the crassicaulescent, sarcocaulescent, and microphyllous deserts. Thus, the arborescent cacti become more prominent as members of the landscape, but probably not in numbers, as the trees and large shrubs are restricted to areas of somewhat higher precipitation. It probably was only along the northern part of the Sonoran Desert region
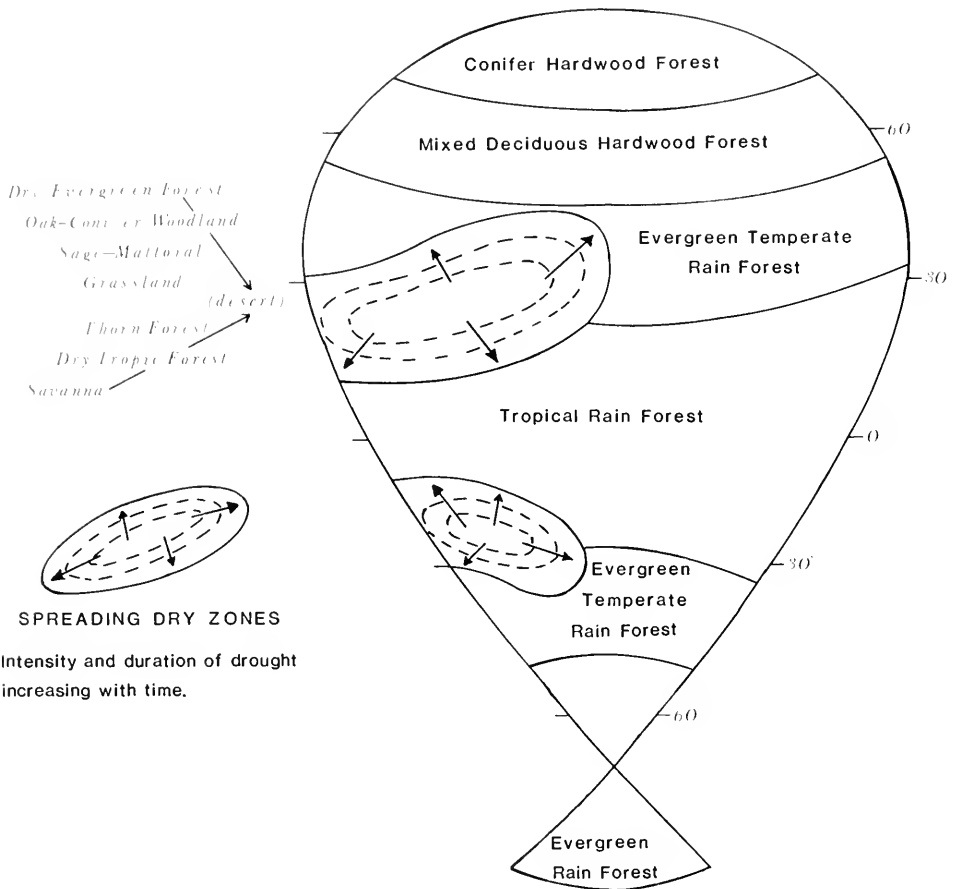
FIGURE 20. Inferred area of early ancestral populations of xeric-adapted taxa which spread with expanding dry climate.

that the arborescent cacti were eliminated temporarily during the glacial ages, for they are extremely frost sensitive (Shreve 1911; Turnage and Hinckley 1938). Thus, in southern Arizona and northern Baja California they appear to have reinvaded the present desert area as temperatures moderated in post-glacial time. Elsewhere they appear to be the hardy survivors, the relicts of more mesic arid tropic scrub and forest that earlier covered the area. Clearly, a trend to drought would further restrict the dry tropic forest and arid tropic scrub (or thorn forest) at the expense of desert. Such a trend characterized the middle and later Tertiary and best accounts for the present relations (Fig. 18).

That the chief source for the genera of the Sonoran Desert flora have been the dry tropics ·vident from the quantitative data presented ·zedowski (1973:table 3). Of the 272 genera

in the Sonoran Desert flora, 53% also occur in the dry tropical deciduous forests of southern Sonora and 28% are in the dry forests of Jalisco and Colima. Furthermore, 47% of the genera in the Chihuahuan Desert flora also occur in the tropic deciduous forests of southern Sonora, and 18% occur farther south in the dry tropic forests. Although quantitative data are not now available, it is critical to note that the semidesert of the Tehuacán-Cuicatlán valley rapidly gives way (near Coxcatlán) to a thorn forest. As noted by Smith (1965) and Rzedowski (1973), and observed by me as well (April 1977), there is a marked floristic affinity between the tropical elements of the Tehuacán-Cuicatlán valley with those of the dry tropic forest and scrub of the Pacific coast. Clearly, a detailed study of the floristic affinities of the flora of the Tehuacán-Cuicatlán valley can provide much needed crit-

FIGURES 21 and 22. (*Upper*) Fig. 21. Dry tropic forest (Cape Forest) in Cape Region, Baja California. Note columnar cacti are largely obscured by the tall trees. (*Lower*) Fig. 22. Dry tropic scrub, Cape Region of Baja California. Columnar cacti become more conspicuous as stature of taxa in vegetation decreases in response to lower rainfall.

FIGURES 23 and 24. (Upper) Fig. 23. Dry tropic scrub, Cape Region of Baja California. Vegetation is lower in stature and cacti are more conspicuous than in Fig. 22. (Lower) Fig. 24. Sonoran Desert vegetation, Cape Region of Baja California. Precipitation here is about 250–300 mm (approximately 10–12 inches) less than in the lower part of dry tropic forest

ical information. At present, the flora seems best regarded as a relict from the late Tertiary, surviving under an equable climate and recently isolated from the Chihuahuan region by volcanism (see below).

The evidence implies that it was chiefly from the more arid phases of dry tropic forest and savanna that derived taxa contributed not only to an impoverished and dwarfed dry tropic forest (=short-tree forest) but to thorn forest as well. These vegetation types were already differentiated by the middle Eocene, as shown by the composition of the Green River flora of the central Rocky Mountains and by the middle and late Eocene floras of the Atlantic and Gulf coastal plain (Berry 1916, 1924, 1930, 1934), where dry beach-jungle vegetation is well represented and where a dry tropic forest extended westward into south-central Texas (Ball 1931, 1939). Furthermore, evidence provided by the pollen record in the Torrey Sandstone implies that dry thorn forest was already present in that area in the middle Eocene, which is consistent with the nature of the Green River and Claiborne floras. The latter has a number of taxa that represent beach-jungle vegetation which represents an edaphically controlled thorn forest or dry short-tree forest that reached into moister forest belts in favorable dry areas—as it does today.

The second source for plants that contribute to the Sonoran Desert area is referable to vegetation that adapted to a progressively drier environment for evergreens. In this regard, first note that Rzedowski (1973:table 3), in his analysis of the relations of the arid floras of Mexico, estimates that 24% of 272 genera in the Sonoran Desert and 42% of the 258 genera in the Chihuahuan Desert occur also in the pine-oak forests of Durango. That adaptation was primarily to increasing drought may be inferred from the sequence of vegetation zones that lies along a gradient of increasing aridity from dry evergreen forest, into short-tree forest, sclerophyll woodland, dry evergreen thicket, and evergreen bushland (see Fig. 20), members of which also contribute to semidesert and desert habitats (e.g., *Cercocarpus, Forchammeria, Garrya, Mahonia, Quercus, Rhus, Simmondsia, Vauquelinia*). Phylads in these vegetation zones display a gradual decrease in stature, in leaf size, and in periodicity of response to growth and flowering in proceeding to drier areas. These different types of vegetation had also originated by the

middle Eocene, for taxa of short-tree forest, evergreen woodland, and thicket ("chaparral") are in the Torrey Sandstone, Green River, Clairborne, and Jackson floras, and some are also in the early Eocene to Late Cretaceous floras (Axelrod 1958). Included in this group are *Acacia, Bumelia, Cercocarpus, Clethra, Colubrina, Cordia, Dodonaea, Karwinskia, Lantana, Morus, Persea, Platanus, Quercus, Sabal, Thouinia, Vitex*, and others.

These general relations are well exemplified by the idealized sketches of seasonal vegetation types presented by Beard (1955). In a time sense (Fig. 25), regard the formation series on the left as Late Cretaceous–Paleocene in age, with the reduction in stature and composition and gradual change in vegetation taking place as progressively drier climate spread during Eocene and later times. Deciduous seasonal forest gave way to thorn forest in the Sonoran region in the Miocene and dry evergreen woodland to dry evergreen thicket in the Pliocene as semidesert scrub rose to dominance locally in the driest parts of the region.

MODE

The spread of progressively drier climate over southwestern North America provided the chief stimulus for the evolution of desert taxa. Stebbins (1952) showed that several factors tend to promote rapid evolution in dry areas. First, in seasonally dry areas local diversity of terrain, soil, and exposure have a greater control on plant distribution than in areas where precipitation is adequate. Second, since very different plant communities commonly occur in proximity in dry regions, local geographic isolation of taxa in them provides a basis for the origin of isolating mechanisms, and hence for speciation. Even with normal climatic fluctuation (moister and drier cycles), the migration of the resulting fragmented populations would enable new gene combinations to become established in the smaller units, and by merging of previously isolated populations, the opportunity for rapid evolution would be increased through hybridization, introgression, and mutation. And third, plants may become adapted to drier climate by developing varied specialized structures or responses, notably, reduced leaf size; deciduous habit; scales or hairy covering; diverse water-storage organs in trunks (cacti), underground bulbs, or corms; extensive root systems; small annual
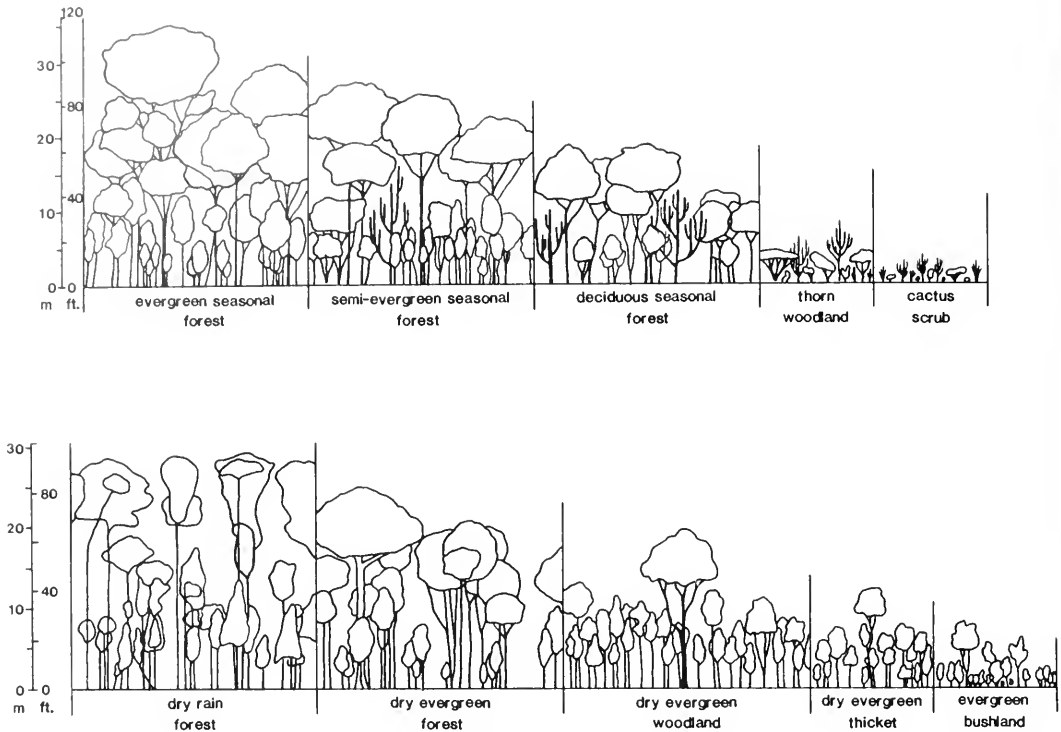
FIGURE 25.   Sequence of modern vegetation arranged according to increasing drought (Beard, 1955). The same general succession appears to account for the development of desert vegetation in southwestern North America (compare Fig. 14).

habit; aphylly with green stems; rapid flowering; and rapid seed production. Clearly, the great array of life forms possible in warm, dry regions would tend to favor divergent evolution in many ancient, ancestral alliances.

The role of aridity in southwestern North America was not due solely to its location in low-middle latitudes where climate was gradually becoming drier. The region has been active tectonically since the Late Cretaceous, producing a varied terrain with rainshadows and lee slopes that were drier than the regional climate. Furthermore, diverse rock types provided local sites drier than those normally in the region. Inasmuch as local rainshadows and xeric edaphic sites were drier than regional climate, selection for dry-adapted taxa would be strong, and evolution would be accelerated greatly (Axelrod 1967:fig. 1). As a result, new adaptive types appear in local dry areas at a very early date would persist inasmuch as dry sites and they would spread and evolve

further as the regional trend to aridity accelerated.

Late Cretaceous and Paleocene floras of southwestern North America show that lowland areas were well watered with high water table. Hence, the driest sites must have been confined to lee- and south-facing slopes and to intrarange valleys, as in savanna regions today. During the Late Cretaceous–Paleocene, a broad epeiric sea was withdrawing from southwestern North America. At the same time, orogenic movements were building up scattered low ranges over the region and there also were local areas of volcanism which continued into the Eocene and later. These topographic changes, occurring in a region of subtropical to warm temperate climate with a dry winter season, greatly increased environmental diversity over the area. Since taxa of tropical and warm temperate vegetation zones were already adapted to a period of slight to moderate drought in the savanna and border areas, the development of somewhat drier con-
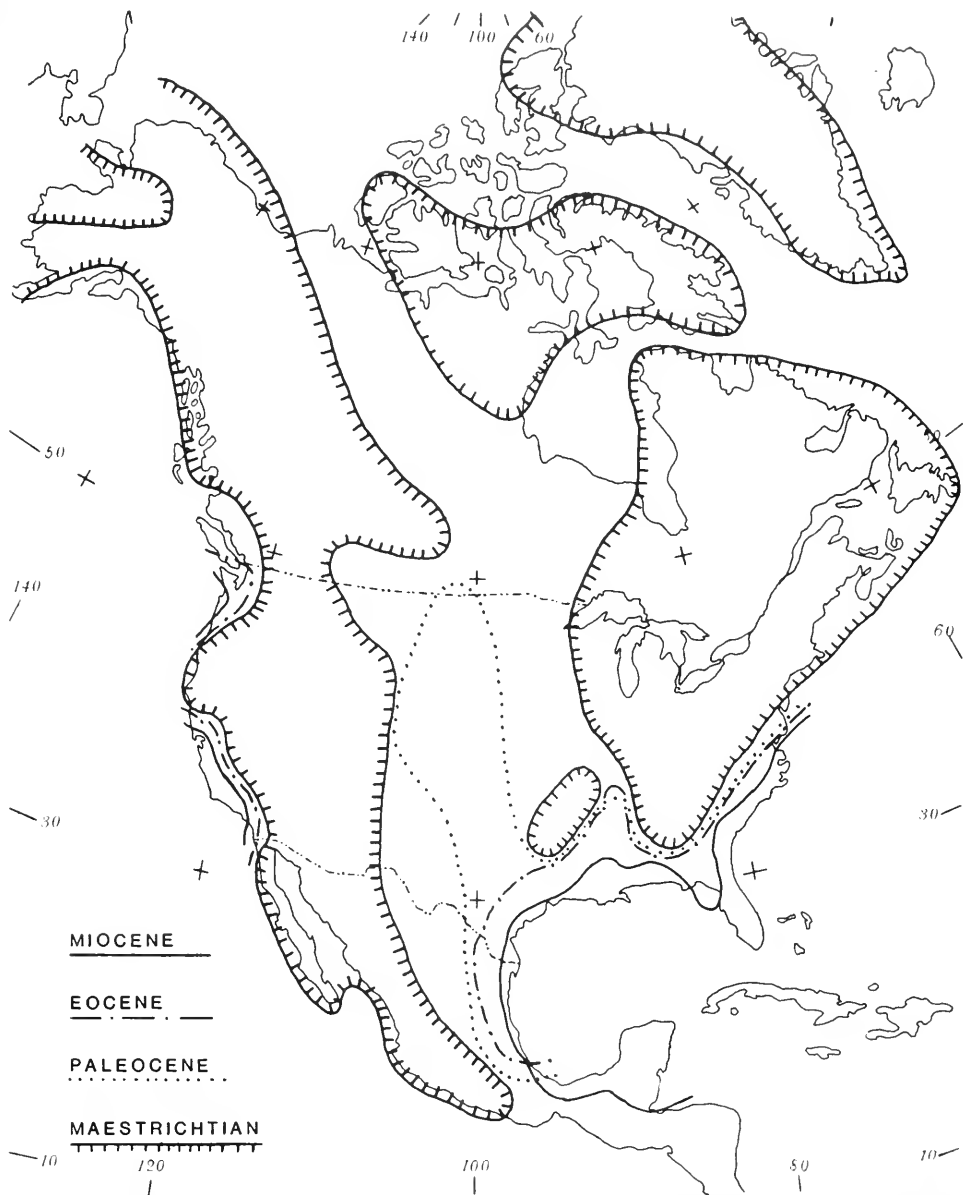
FIGURE 26. The general area of seaways on the continent has decreased progressively since the Late Cretaceous, bringing greater ranges of temperature and reduced precipitation.

ditions in the lee of low mountains and volcanic terrains would have stimulated the rapid evolution of any preadapted taxa. In brief, the appearance of drier tracts corresponded to the opening up of a major, new adaptive zone which expanded during the rest of the Tertiary (Figs. 18–20) and enabled taxa to spread into the ex-

panding zone which culminated in the present desert.

Attention must be directed to the evolutionary significance that major changes in land-sea relations had during the Late Cretaceous and Tertiary. The Cretaceous sea that bisected North America retreated rapidly at the close of the pe-

riod. By Paleocene time the Cannonball Sea was but a remnant of the former inundation, and by the Eocene the sea was confined to the Mississippi Embayment, extending from near Cairo, Illinois, southwesterly through eastern Arkansas–Texas, and thence south along the coastal strip of Mexico (Fig. 26). It is well established that seas are great conservers of heat and moderate climate, whereas land areas dissipate heat and bring greater seasonal contrasts. Retreat of the epeiric sea during the Tertiary thus brought increasing ranges of temperature, and hence an effectively cooler climate to the region. In addition, as the western interior was being elevated, temperature extremes increased and cooler climates spread.[1] Clearly, tropical and border-tropical (warm temperate) alliances in drier areas that had earlier adapted to gradually lowered temperature were now becoming adapted to penetrate into cooler areas of higher relief over the region. Thus, many taxa of subhumid to semiarid requirements that originated in warm climates at low elevations were able to persist over the Chihuahuan and Hidalgan areas where drier, cooler climates spread as the Mexican plateau and the bordering Sierra Madre were elevated in the late Cenozoic.

Regarding the origin of taxa in spreading dry regions, it is emphasized that while a "new" environment is necessary for the spread of product of rapid evolution, it is not necessary for its evolution *per se*. The chief factor in adaptation to dry areas is not the decrease in precipitation which makes the shift probable, but the length and severity of the dry period. We seem too preoccupied with measuring the rainfall, when in fact we should be measuring the duration, the severity, and the frequency of drought—which is of course more difficult. It is implicit that the shift from one adaptive zone to another is rapid and sharp (Simpson 1953), though it must be across an ecotone if equilibrium is to be maintained. Since local dry areas have steep rainfall gradients, it is the *duration* of the period of drought along this local gradient, not low rainfall *per se*, that is the crucial environmental factor in dry regions. A region with 380 mm (15 inches)

precipitation well spread through the year may support woodland-savanna or grassland, but if it is concentrated in 2 or 3 months and is followed by high temperature, desert or semidesert vegetation may result. Rapid evolution may therefore be particularly favored in the driest parts of a dry environment, in sites with a more prolonged and persistent drought owing to the reduced or less effective rain, as in edaphically dry sites especially (Axelrod 1972). These observations seem meaningful in an evolutionary sense because local dry areas may appear "instantaneously" in a geologic sense. Furthermore, in such areas competition is reduced and hence favors the establishment of a new, pre-adapted taxon. Since the origin of a new taxon involves adaptation to a new environmental relation, a spreading area of more extreme drought would enhance opportunities for the origin and continuing diversification of new taxa.

New taxa probably originated as rapidly as new dry sites appeared as a result of volcanism and mountain building. There would be strong selection for alliances preadapted to drier areas. Dry sites would appear much sooner (1 to 20 million years) on dry south or lee slopes, in local rainshadows, and in narrow, deep, intramontane valleys than on broad, well-watered, lowland floodplains with high water table where the plants of more mesic requirements were contributing to the bulk of the older geologic record (*see* Axelrod 1967). The small populations may therefore have evolved rapidly in local dry areas without leaving a fossil record. Such restricted dry areas probably were sites for rapid evolution because *1*) the taxa were already adapted to some seasonal drought, and *2*) there was strong selection, with a linear component imposed *a*) by a gradient to a greater duration of drought toward the center of each local dry area, and *b*) by a secular trend to an increasingly longer and more severe season of protracted and extreme drought. Under such dynamic conditions, the drier areas drew small populations into their centers, much as a whirlpool draws in debris from the surrounding area.

These local dry areas, which ranged from hot lowlands to dry montane sites of more equable climate, were, in essence, the areas where the emerging new dry vegetation zones (dry tropic forest, short-tree forest, thorn forest, pine-oak woodland, grassland) appeared that were later to spread out over the lowlands as the period of

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[1] Recall that the normal terrestrial lapse rate is 0.55 C/100 m (3 F 1,000 ft). With a regional uplift of 1,000 m, mean annual temperature would be reduced 5.5 C; or, 3,000 ft relift lowers mean annual temperature 9 F (see Axelrod 1976:238–241).

drought progressively lengthened and as increasing ranges of temperatures added to its severity. Furthermore, since local dry areas became even drier in time, small divergent populations that were adapted to somewhat longer periods of drought would continue to evolve in them, sending out new waves of taxa. In this manner, restricted dry sites probably would serve as *persistent* evolutionary pockets for new taxa that were more highly adapted to the climates of increasingly greater drought that spread over the region.

The scattered, spotwise distribution of these early populations in local dry sites was significant also in molding plant-animal ecosystems which developed in concert with the evolution of the taxa themselves. The role of scattered environments ("patchiness") in welding together unrelated taxa into a closely knit, functioning ecosystem has been reviewed in a notable paper by Wiens (1976). I can add to his cogent observations that the roots of all ecosystems extend in modified form far down into the past. The preceding discussion shows that the historical development of any ecosystem can best be understood by consulting the fossil record. Meager and incomplete though it is, it provides the only factual basis for interpreting the successive changes that gave rise to the modern ones. Many ecosystems directly ancestral to those of the present have been established for scores of millions of years, as shown by the history of sclerophyll vegetation, conifer forest, temperate (montane) rainforest, dry tropic forest, and others. By contrast, desert vegetation—like the tundra—emerged as a regional (zonal) ecosystem only recently, as has coastal sage scrub (Axelrod 1978).

The preceding discussion of the probable area, source, and mode of evolution of taxa that contributed to subtropical and tropical desert vegetation appears to account also for the different grades of evolution displayed by plants in the Sonoran and bordering tropical deserts today. Recalling that all taxa do not evolve at the same rate and that the rate may change in time (see Simpson 1953; Stebbins 1974), the different grades of morphologic diversity exhibited by modern desert taxa, for instance the coexistence of *Carnegiea* and *Fouquieria* with *Eschscholzia* and *Camissonia* probably are to be correlated largely with the times they originated, as judged from direct (fossil) and indirect evidence.

However, it must be emphasized that for the most part the time of origin of taxa did not correspond with the time that they entered into the matrix of desert vegetation. That event occurred much later. It was the result of the long period of adaptation by millions of generations to progressively increasing aridity. During this time their responses and structures were continually being perfected and modified to live in an emerging, spreading, dry zone that was becoming progressively more extreme both in the duration of the period of drought and in the severity of temperature extremes.

The different grades of morphologic diversity, as represented by widely divergent groups of taxa, thus appear to have originated at different times. They are the survivors of ancient, as well as more recent, taxa that have been able to adapt to the present extreme environment of the desert. Their times of origin can be considered conveniently in terms of their relative age. This does not mean that there were hiatuses in the tempo of evolution, but rather that evolution has been continuous and that there are both ancient as well as more recent taxa in the desert. Thus, the subtropical Sonoran Desert has numerous woody taxa—both ancient and more recent— and is also salted with diverse annuals and perennials from bordering regions in the mountains and on the upper slopes of the desert, as well as alliances from more distant areas. The times that these divergent groups appear to have originated can now be considered.

RESULTS

Late Cretaceous

Ancestors of plants assigned to this early phase are represented today by monotypic families and unique genera that appear to have been derived from alliances that adapted to dry tropical and warm temperate climates at an early date. They are believed to have considerable antiquity because they are well isolated taxonomically. Included here are the following 7 families: Cactaceae (many genera); Crossosomataceae (*Crossosoma* [2 spp.]); Fouquieriaceae (*Fouquieria* [8 spp., incl. *Idria*, Hendrickson 1972]); Garryaceae (*Garrya* [ca. 8 spp.]); Koeberliniaceae (*Koeberlinia* [1 sp.]); Krameriaceae (*Krameria* [8 spp.]); Simmondsiaceae (*Simmondsia* [1 sp.]). As for the uniqueness of some of these families, the Fouquieriaceae includes tree succulents (sect. *Idria*) as well as

highly branched shrubs with peculiar xero-
morphic features, notably the mode of spine de-
velopment, the formation of hard decurrent
ridges, and the anastomosing cortical water-
storage tissues, as outlined by Hendrickson
(1972). Its phyletic relations are not established;
it has been placed in Polemoniales, Tamaricales,
Ebenales, and Violales! (Why not in the Fou-
quieriales?) The Cactaceae are also unique and
have undergone considerable diversification in
body type. The family is often placed in its own
order (Cactales) or in Caryophyllales. Simmond-
siaceae includes one xeromorphic evergreen
sclerophyllous shrub of the upper desert slopes.

In addition, to these we can add a number of
very distinct genera (some monotypic) in their
respective families that contribute to the Sono-
ran Desert flora but which are centered chiefly
in warmer, moister regions to the south or on
the moister slopes above the desert, notably:
Agavaceae (*Beaucarnea, Dasylirion, Nolina,
Yucca*); Arecaceae (*Brahea, Sabal, Washing-
tonia*); Capparaceae (*Atamisquaea, Forcham-
meria*); Saxifragaceae (*Fendlera*); Rosaceae
(*Cercocarpus, Fallugia, Purshia, Vauquelinia*);
Mimosaceae (*Acacia, Prosopis*); Caesalpini-
aceae (*Bauhinia, Cercidium, Haematoxylon,
Parkinsonia*); Fabaceae (*Erythrina, Olneya, Pis-
cidia*); Zygophyllaceae (*Guaiacum, Viscainoa*);
Rutaceae (*Choisya* [*Astrophyllum*], *Zanthoxy-
lum*); Simaroubaceae (*Castela, Holocantha*);
Burseraceae (*Bursera*); Euphorbiaceae (*Phyl-
lanthus, Sapium, Tetracoccus*); Anacardiaceae
(*Pachycormus, Schmaltzia*); Celastraceae (*Can-
otia*); Rhamnaceae (*Adolphia, Ceanothus* [sect.
Cerastes], *Condalia, Colubrina, Microrham-
nus, Rhamnus* [sect. *Crocei*]; Bignoniaceae
(*Chilopsis*). They evidently have considerable
antiquity because the families to which they be-
long were already present in the Late Creta-
ceous–Paleocene, yet the desert novelties do not
have obvious affinities with living genera. For
example, the Anacardiaceae are known from the
Cretaceous and *Rhus* is in the Eocene, yet no
known genus provides a link to the isolated,
monotypic *Pachycormus* of the Sonoran Desert.
The Rosaceae are recorded in the Cretaceous
and the unique *Vauquelinia* is in the Eocene
(Green River, Wilcox floras). This implies a
——, unrecorded history and the extinction of
———ous taxa that must have linked them with
———ing *Vauquelinia*. Similarly, Rhamnaceae
—— the Cretaceous, yet *Ceanothus* subgenus

Cerastes (evergreen shrubs) is not clearly allied
to any other living taxon in the family.

Antiquity for palms is consistent with the oc-
currence of quite modern taxa in the Late Cre-
taceous. Drugg (1967) reports that grains "par-
ticularly close to the pollen of the extant genera
Sabal and *Washingtonia*" are in the Late Cre-
taceous of the central California Coast Ranges.
Sabal is widely recorded in the Eocene and Pa-
leocene floras, and various genera (*Brahea*
[=*Erythea*], *Sabal, Washingtonia*) contribute to
the Sonoran Desert flora today. The relations
suggest that other plants of generally similar
adaptive habit may have also considerable an-
tiquity, for instance, *Beaucarnea, Dasylirion,
Nolina,* and *Yucca* in the Agavaceae, which is
generally regarded as a relatively more primitive
group than the palms (Arecaceae). In addition,
the occurrence of taxa such as *Bauhinia, Cer-
cidium, Fouquieria, Forestiera,* and *Fremonto-
dendron* in the middle Eocene Torrey Sandstone
implies antiquity for these alliances; they are
here assigned provisionally to the Late Creta-
ceous as the most probable time of their origin.

The preceding taxa may be regarded as evo-
lutionary counterparts of *Cercidiphyllum, Lir-
iodendron, Platanus, Populus, Quercus, Sas-
safras,* and others that extend down into the
Cretaceous in essentially modern form: they are
bradyteles (Simpson 1953). Immediate forerun-
ners of the taxonomic novelties that now con-
tribute to the desert flora probably occupied
areas of seasonally dry climate in the Creta-
ceous-Paleocene and became adapted to cli-
mates characterized by increasingly longer,
more severe periods of drought during Eocene
and later times. This inference is supported by
the occurrence of a number of distinctive genera
that occur in the desert today in dry woodland
vegetation, including species of Cactaceae
(many genera), *Cercocarpus* (sect. *Intricatae*),
*Crossosoma, Choisya, Chilopsis, Dasylirion,
Fallugia, Fendlera, Garrya, Leucophyllum,
Lindleya, Mahonia, Nolina, Olneya, Sabal,
Vauquelinia, Yucca, Washingtonia,* and others.
Furthermore, some of them (e.g., *Cercocarpus,
Fouquieria, Mahonia, Sabal, Vauquelinia*) oc-
cur in the Eocene floras, implying their earlier
origin.

Paleogene

The taxa that are endemic to the Sonoran Des-
ert province in many cases represent unique

species in their respective genera. Many of the genera are represented in Eocene floras of the Atlantic and Gulf States, or the Rocky Mountain province. Species in the following genera in these floras seem allied to taxa that are found today in, or marginal to, the Sonoran Desert, or are members of the bordering vegetation, notably thorn forest, dry tropic forest, or woodland, and may be regarded as having some antiquity: Ulmaceae (*Celtis*); Moraceae (*Ficus, Morus*); Polygonaceae (*Coccoloba*); Nyctaginaceae (*Pisonia*); Berberidaceae (*Mahonia*); Platanaceae (*Platanus*); Rosaceae (*Amelanchier, Cercocarpus*); Mimosaceae (*Acacia, Pithecellobium, Prosopis*); Caesalpiniaceae (*Bauhinia, Caesalpinia, Cassia*); Fabaceae (*Erythrina*); Zygophyllaceae (*Guaiacum*); Burseraceae (*Bursera*); Euphorbiaceae (*Euphorbia*); Celastraceae (*Maytenus*); Sapindaceae (*Cardiospermum, Dodonaea, Sapindus, Serjania*); Rhamnaceae (*Colubrina, Zizyphus*); Vitaceae (*Cissus, Vitis*); Bombacaceae (*Bombax*); Sapotaceae (*Bumelia, Sideroxylon*); Boraginaceae (*Cordia*). The fossil species lived in areas that were considerably more moist than the Sonoran Desert region is at present: they were members of dry tropical forest, beach jungle, thorn scrub, and woodland vegetation, all of which now characterize the subhumid to semiarid parts of Mexico. Thus, it seems likely that the unique species of these genera in the present Sonoran Desert that range out of it into moister vegetation zones may well represent derivatives of Paleogene species that inhabited dry areas.

Species similar to those that now contribute to thorn forest and beach jungle occur in Eocene and early Oligocene floras. This suggests that a number of the more distinctive endemic species of tropical genera (listed above) in the Sonoran Desert area today may have attained essentially their modern form by mid-Eocene time. Some of them that occur in the Miocene (*Acacia, Ficus, Pithecellobium, Randia*) are scarcely separable from species in the Sonoran region today (Axelrod 1939). Furthermore, species in the Eocene Green River and Claiborne floras, and in the early Oligocene Florissant flora, resemble plants that now range into thorn forest and also occur on the moister margins of the desert, notably *Euphorbia* (*hindsiana*), *Cardiospermum* (*halicababum*), *Dodonaea* (*viscosa*), *Mahonia* (*trifoliata*), *Platanus* (*wrightii*), *Prosopis* (*chilensis*), *Sapindus* (*drummondii*), *Schmaltzia*

(*trifoliata*), *Zizyphus* (*obtusifolia*). The evidence implies that drier scrub probably was in existence by the close of the Eocene, and that semidesert plants evolving in *local* dry sites over the region have not changed significantly in adaptive type since then.

Under a climate with a lower range of temperature, areas of low rainfall may therefore have supported local, restricted semideserts during the later Eocene. These inferred local semidesert areas would have had only moderate extremes of temperature. They were desert chiefly because of lower rainfall (30–40 cm; 12–15 inches), not of extremely high temperature which would increase the drought stress. Such conditions may be seen today at moderate elevations at the upper edge of the desert in Baja California, in the foothills of Sonora-Sinaloa, and especially in the uplands of central Mexico, where there is mild temperature and semideserts occur in local dry basins. A good example is the valley of Tehuacán, south of Mexico City, where the range of mean temperature is only 4.4 C (10 F) between the coldest (15.8 C, 60.4F) and warmest (21.2 C, 70.2 F) months, respectively. Comparable conditions are implied for the early Tertiary local semideserts.

Neogene

There are about 12 endemic genera in the peninsula of Baja California (Wiggins 1960) that show relationship to taxa now in the moister bordering region (Table 4). Apart from these, there are many species in the area that are allied to taxa now on the mainland. The question arises as to whether they originated largely after the peninsula separated from the Sonora-Sinaloa-Nayarit coast. Although this problem cannot be solved until there is an adequate fossil record for some of these taxa, it is noteworthy that a number of these taxa do have a wide distribution on the peninsula (Wiggins 1960:figs. 9, 10).

This implies that they probably originated in the Sonoran region and have extended little beyond it, except possibly in the late Miocene to Pliocene when they may have reached into the southeastern California and adjacent Arizona-Sonora at a time when winters were milder than those at present. An example is *Triteleiopsis palmeri* which has now been discovered in the Gila Mountains of southern Arizona. This implies that some of the narrow endemic genera in the peninsula may have had a wider distribution

TABLE 4. GENERA LARGELY ENDEMIC TO BAJA CALIFORNIA AND THEIR GENERAL AFFINITIES (from Wiggins 1960).

Taxa	Affinities
Liliaceae	
Triteleiopsis (1 sp.)	A segregate of *Brodiaea* which is widespread to the north.
Behria (1 sp.)	Allied to *Brodiaea* and *Triteleiopsis*.
Polygonaceae	
Harfordia (1 sp.)	Related to *Pterostegia*, widely distributed in California-Utah above the desert.
Onagraceae	
Burragea (1 sp.)	Segregate of *Gongylocarpus*, which is also in Baja California and is the most generalized genus of the tribe Onagreae (Raven 1969).
Xylonagra (1 sp.)	Allied to *Camissonia* (Raven 1969), widespread in the Southwest and in California.
Cactaceae	
Bartschella (1 sp.)	
Cochemiea (6 sp.)	Allied to mainland genera of cacti.
Machaerocerus (2 sp.)	
Scrophulariaceae	
Clevelandia (1 sp.)	Both are related, and allied to *Gerardia* of the eastern U.S.
Ophiocephalus (sp.)	
Asteraceae (Heliantheae)	
Alvordia (3 sp.)	A reduced *Vigueria* (10 sp.) common outside of the desert region.
Coulterella (1 sp.)	Related to *Lagascea*.

in the past, and that their isolation has resulted from their restriction there as colder winters developed to the north. Note that *Harfordia* is discontinuous from the Rosario region to Cedros Island and to Bahía Magdalena. Four of the endemic genera (*Bartschella, Beheria, Clevelandia, Coulterella*) are confined to the La Paz–Cape Region, an area high in endemics which had a wider distribution in the past. This may be inferred from the relict occurrence of unique taxa such as the subgenus *Idria* (Fouquieriaceae) and *Viscainoa* (Zygophyllaceae), both of which extend out of the peninsula into local areas in coastal Sonora. Furthermore, there are other taxa in Baja California del Sur, notably *Pinus cembroides, Ilex brandegaena, Populus brandegeei, Quercus albocincta,* and *Q. tuberculata,* that occur also in the woodland of western Mexico. A Miocene to early Pliocene age seems likely for the endemic genera (Table 4) in Baja California because a large volcanic field (Commondú Volcanics) formed at that time, providing new, drier slopes which may have ⟨ser⟩ved as sites suited for them. Apart from the ⟨gen⟩era that are confined to the peninsula, a num⟨ber of⟩ unique peninsular species may also have

originated then, notably in the genera *Abutilon, Acacia, Agave, Atriplex, Bursera, Brickellia, Castilleja, Chenopodium, Chrysothamnus, Dalea, Dudleya, Encelia, Eriophyllum, Euphorbia, Fagonia, Franseria, Haplopappus, Houstonia, Ipomoea, Jatropha, Justicia, Krameria, Leptodactylon, Lycium, Malacothrix, Monardella, Opuntia, Pithecellobium, Salvia, Stephanomeria, Vigueria, Yucca,* and especially in the Cactaceae.

Quaternary

To this time probably is to be referred the origin of numerous species and subspecies that differ but little from their allies in the moister areas bordering the desert today. The alternating pluvial and dry cycles brought together divergent populations and greatly speeded up the evolution of new taxa. The only significant requirement for survival of a new population would be the ability to withstand a little less moisture and somewhat greater extremes of temperature. Inasmuch as they were already living in marginally arid environments and were well adapted to them by their habit (small size, rapid flowering and seed production, etc.), any

new populations might be expected to survive with no difficulty. Among the taxa that appear to have proliferated rapidly at this time are species of *Astragalus, Boerhavia, Calochortus, Camissonia, Chaenactis, Chorizanthe, Croton, Cryptantha, Delphinium, Descurainia, Ditaxis, Eriogonum, Euphorbia, Hofmeisteria, Hosackia, Lupinus, Lyrocarpa, Machaeranthera, Malacothrix, Nemacladus, Pectis, Penstemon, Perityle, Phacelia, Physalis, Senecio, Sphaeralcea, Stephanomeria, Streptanthus, Thysanocarpus*. A number of species that enter the Sonoran Desert or its margins have their chief centers of distribution well to the north in the semiarid parts of southern and central California, and some of them range farther north. They may well be relicts of the Wisconsin in the Sonoran region that had sufficient adaptability to survive there as desiccation increased. Representative members of this group are in the following genera (for species, see Shreve and Wiggins 1964): Poaceae (*Agrostis, Bouteloua, Bromus, Distichlis, Elymus, Eragrostis, Festuca, Leptoloma, Panicum, Poa, Sitanion, Stipa*); Cyperaceae (*Cladium, Cyperus, Eleocharis, Fimbrystylis, Scirpus*); Commelinaceae (*Commelina, Tradescantia*); Juncaceae (*Juncus*); Liliaceae (*Allium*); Urticaceae (*Parietaria*); Santalaceae (*Comandra*); Polygonaceae (*Chorizanthe, Eriogonum, Polygonum, Pterostegia, Rumex*); Chenopodiaceae (*Allenrolfea, Atriplex, Chenopodium, Eurotia, Monolepis, Nitrophila, Suaeda*); Amaranthaceae (*Amaranthus*); Portulacaceae (*Calandrinia, Calyptridium, Montia*); Caryophyllaceae (*Arenaria, Cardionema, Silene, Spergularia, Stellaria*); Ranunculaceae (*Clematis, Delphinium, Ranunculus*); Papaveraceae (*Eschscholzia, Platystemon*); Brassicaceae (*Arabis, Athysanus, Caulanthus, Descurainia, Erysimum, Lepidium, Stanleya, Streptanthus, Thysanocarpus*); Resedaceae (*Polanisia*); Fabaceae (*Astragalus, Hosackia, Lupinus, Trifolium, Vicia*); Polygalaceae (*Polygala*); Euphorbiaceae (*Croton, Euphorbia*); Anacardiaceae (*Rhus*); Malvaceae (*Sida*); Loasaceae (*Mentzelia*); Onagraceae (*Clarkia, Camissonia, Zauschneria*); Umbelliferae (*Apiastrum, Caucalis, Daucus, Lomatium*); Asclepiaceae (*Asclepias*); Polemoniaceae (*Gilia, Leptodactylon, Linanthus*); Hydrophyllaceae (*Emmenanthe, Eriodictyon, Phacelia, Pholistoma*); Boraginaceae (*Amsinckia, Cryptantha, Plagiobothrys*); Menthaceae (*Monardella, Salvia, Scutellaria*); Solanaceae (*Nicotiana*); Scrophulariaceae (*Castilleja, Mimulus, Orthocarpus, Penstemon*); Orobanchaceae (*Orobanche*); Plantaginaceae (*Plantago*); Rubiaceae (*Galium*); Campanulaceae (*Nemacladus*); Asteraceae (*Artemisia, Aster, Lasthenia* [=*Baeria*], *Chrysothamnus, Erigeron, Eriophyllum, Filago, Franseria, Helianthus, Layia, Lessingia, Malacothrix, Microseris, Senecio, Stephanomeria*).

With the drying-up of the lakes and the streams brought on by the reduction in precipitation and increasing ranges of temperature during the past 12,500 years, important changes have occurred over the area of the Sonoran Desert. Some of the distinctive floristic regions probably came into existence at this time. They represent subdivisions that correspond to a desert climate with different degrees of moisture, warmth, and temperateness. The minor differences between them probably would tend to disappear under a more genial climate. With an increase of 125–180 mm (about 5–7 inches) in rainfall the "moist" Arizona upland succulent desert would move down into the driest parts of the *Larrea-Franseria* zone. A rise of 250–300 mm (about 10–12 inches) in rainfall would essentially eliminate most of the Sonoran Desert as a regional lowland vegetation—as was the case during the late Pleistocene as well as in Neogene and earlier times (see Fig. 15).

Finally, there are fully 100 introduced and escaped weeds, mostly from Europe, that are found largely in disturbed areas, as along roadsides, in overgrazed patches, etc., in the Sonoran Desert (in Shreve and Wiggins 1964). Here they are removed from competition, much as in disturbed areas outside the desert where they also enter grassland and oak woodland. It is emphasized that they do not invade desert communities. The only "weed" that has done so, and is now doing so, is *Larrea* in the peninsula of Baja California where it has a patchy distribution and is slowly invading the desert flora marginal to the new highway.

PROBLEMS OF THE SONORAN DESERT FLORA

The preceding analysis of the age and origin of Sonoran Desert vegetation indicates that local semideserts probably were present by the later Eocene, that they spread gradually with ex-

panding dry climate during the rest of the Tertiary, and that a *regional* desert climate appeared only recently. The evidence also suggests that taxa now in the desert have been derived from alliances that occupied the area before it was a desert, having adapted gradually to the increasing drought and heat that spread over the region. This general thesis provides new insight into several major problems concerning the Sonoran Desert flora that have been considered earlier by others, notably the sources of its taxa, the relative impoverishment of the flora, and diversity of life forms in the vegetation. Consideration of the relict nature of the related Hidalgan Desert of central Mexico further illuminates the history of the Sonoran Desert flora and its vegetation.

SOURCES

The taxa that contribute to the Sonoran region have come from divergent sources and at different times during the Tertiary and Late Cretaceous. It is not necessary to consider these in detail because they have been discussed earlier, and they need only be recalled here. The sources can be separated into two broad categories, autochthonous and allochthonous. Discrimination between them is not always easy, but the general groups have been reasonably well defined.

Autochthons

Autochthons are the taxa that appear to have originated in the region of the Sonoran Desert and its environs which, from an historical standpoint, includes the dry parts of southwestern North America from the Late Cretaceous on down to the present. Those that are centered in the region are outlined in a significant paper by Rzedowski (1962). He notes that in Mexico a total of 217 genera are confined to arid regions, of which 93 (43%) are endemic, and of the 410 genera in the semiarid regions of Mexico 113 (28%) are endemic. By contrast, out of a total of 1,163 genera in both humid and subhumid regions, only 93 (15%) are endemic to those areas. The abundance of endemic genera in the flora of Mexico is clearly related to dry climate, and their scarcity correlates with a more humid climate. Rzedowski attributes the abundance of this autochthonous element in the Mexican xerophyllous flora to an origin and diversification in ancient times, and agrees that they represent members of the Madro-Tertiary Geoflora which

originated over southwestern North America, as outlined provisionally by Axelrod (1958:fig. 2). However, Rzedowski goes on to conclude that the data do not support the postulate of Axelrod (1950c) that desert climate and desert plants are of recent (Pliocene-Pleistocene) age in North America. Inasmuch as his view rests on a misinterpretation of my earlier work, clarification seems desirable.

The point was made earlier (Axelrod 1950c, 1958), and has been a recurrent theme in the preceding pages, that *regional* deserts like those of the present are phenomena of relatively recent times (Fig. 16). Local areas probably did support semideserts by the late Eocene, and they certainly were present in the middle Miocene, as discussed for the Tehachapi flora (Axelrod 1939) and implied also by the Mint Canyon flora (Axelrod 1940; Mss.). Those floras were situated in local basins in the lee of hills which placed them in rainshadows, in drier climates than those indicated by vegetation of nearby areas to the west or north. Since the lowlands of the present desert region were covered with woodland, thorn forest, and grassland into the Pliocene, the deserts of southwestern North America could not have been extensive, as inferred by Rzedowski (1962), Johnson (1968), Blair (1976), and Otte (1976) for North America, by Zinderen Bakker (1975) for the Namib of Africa, by Solbrig (1976) for Argentina, by Sarmiento (1976) for the Caribbean, and by Beard (1976) for Australia.

Reference should also be made here to the Sonoran entomofauna which comprises a group of taxa, chiefly at the generic level, which are endemic to the southwestern United States and adjacent Mexico and whose center of evolution seems to have been in that area. Evans (1966) notes that this fauna, whose genera have no close relatives in either the Old World or in South America, "have either evolved in or been long isolated in the deserts of northern Mexico." A similar view is presented by Halffter (1976) who states that the Sonoran Ceonocron[2] had a two-fold phyletic-biogeographic origin (ancient

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[2] A term coined by Reig (1962, 1968) and used by Halffter (1976), and equivalent to the term horofauna which refers to a group of organisms that originated in, or became associated in a given area, and which have coexisted for a prolonged period and have a common biogeographic history. This is essentially the equivalent of the Geoflora concept of major vegetation zones.

TABLE 5. GENERA LARGELY OR WHOLLY ENDEMIC TO THE DESERT REGION OF THE SOUTHWESTERN UNITED STATES AND MEXICO (data chiefly from Rzedowski 1962).

Taxa	Approximate No. of species	Area of Occurrence (and remarks)
Arecaceae		
Brahea (=*Erythea*)	10	SW U.S. to Central Amer.
Washingtonia	2	SE Calif., W Ariz., N Baja Calif.
Agavaceae		
Dasylirion	18	SW U.S., Mexico
Hesperaloe	2	So. U.S., Mexico
Nolina	30	SW U.S., Mexico
Samuela	2	So. U.S., Mexico
Poaceae		
Pringleochloa	1	Mexico
Amaranthaceae		
Dicrairus	1	So. U.S., Mexico
Achatocarpaceae		
Phaulothamnus	1	N Mexico
Portulacaceae		
Talinopsis	1	So. U.S., Mexico
Nyctaginaceae		
Selinocarpus	8	SW U.S., Mexico
Capparaceae		
Atamisquea	1	NW Mexico, Argentina
Setchellanthus	1	Tehuacán
Cleomaceae		
Cleome (=*Isomeris*)	1	Centr. Calif. to Mexico
Philadelphaceae		
Fendlera	4	SW U.S., Mexico
Fendlerella	3	SW U.S.
Pterostemonaceae		
Pterostemon	1	Hidalgo-Puebla
Crossosomataceae		
Crossosoma	3–4	So. Calif., SW U.S., Mexico
Rosaceae		
Cowania	5	SW U.S., Mexico
Fallugia	1	SW U.S., Mexico
Lindleyella	1	Mexico
Vauquelinia	8	SW U.S., Mexico
Fabaceae		
Eysenhardtia	14	So. U.S. to Guatemala
Hesperothamnus	6	Baja Calif., Mexico
Olneya	1	Calif., Mexico
Zygophyllaceae		
Sericodes	1	N Mexico
Viscainoa	1–2	So. Calif.–Baja Calif.
Rutaceae		
Choisya	6	So. U.S., Mexico
Cneoridium	1	So. Calif., N Baja Calif.
Taravalia	1	N Baja Calif. (segreg. of *Ptelea*)
Simaroubaceae		
Holocantha	1	SE Calif.–Ariz.–N Mexico

<div align="center">TABLE 5. CONTINUED.</div>

Taxa	Approximate No. of species	Area of Occurrence (and remarks)
Simmondsiaceae		
Simmondsia	1	So. Calif.–Baja Calif.–Ariz.–N Sonora
Anacardiaceae		
Pachycormus	1	Baja Calif.
Celastraceae		
Acanthothamnus	1	Puebla (habit of *Koeberlinia*)
Mortonia	8	So. U.S., Mexico
Orthosphenia	1	Tamaulipas, Nuevo León
Malpighiaceae		
Echinopterys	3	Mexico
Euphorbiaceae		
Halliophytum	4–5	No. Mexico (segreg. of *Tetracoccus*)
Malvaceae		
Horsfordia	4	SW U.S., Mexico
Rhamnaceae		
Adolphia	2	SW U.S., Mexico
Microrhamnus	1	SW U.S., N Mexico
Fouquieriaceae		
Fouquieria (incl. *Idria*)	11	Calif.–Texas–Mexico
Koeberliniaceae		
Koeberlinia	1	SW U.S., Mexico
Onagraceae		
Burragea	1	Baja Calif.
Xylonagra	1	Baja Calif.
Buddlejaceae		
Emorya	1	So. U.S.
Asclepiadaceae		
Basistelma	2	Mexico–Central America
Himantostemma	1	Baja Calif. (a segregate of *Matelea*, with 130 spp. in American tropics)
Loasaceae		
Eucnide	10	SW U.S., Mexico
Petalonyx	4	SE Calif.–Arizona–N Mexico
Cactaceae		
Ariocarpus	5	Mexico
Astrophytum	6	So. U.S., Mexico
Carnegiea	1	SE Calif.–Arizona–N Sonora
Cochemiea	6	Baja California
Coryphantha	64	SW U.S., Mexico, Cuba
Echinocactus	10	So. U.S., Mexico
Echinocereus	75	So. U.S., Mexico
Echinofossulocactus	32	Mexico
Echinomastus	10	So. U.S., Mexico
Epithelantha	3	So. U.S., Mexico
Escobaria	20	SW U.S., Mexico
Ferocactus	35	SW U.S., Mexico
Grussonia	1	Baja Calif. (=*Opuntia*)
Homalocephala	1	Mexico (=*Echinocactus*)
Leuchtenbergia	1	Mexico
Lophocereus	4	SW U.S., Mexico

TABLE 5. CONTINUED.

Taxa	Approximate No. of species	Area of Occurrence (and remarks)
Lophophora	1–3	So. U.S., Mexico
Machaerocereus	2	Baja California–Sonora
Myrtillocactus	4	Mexico–Guatemala
Neolloydia	8	So. U.S., Mexico, Cuba
Pelecyphora	2	Mexico
Rathburnia	4	Mexico
Roseocactus	1	Mexico (=*Ariocarpus*)
Solisia	1	Mexico (segregate of Mammalaria, with 200–300 sp. ranging into N South America.
Strombocactus	1	Mexico
Thelocactus	17	S U.S., Mexico
Wilcoxia	7–8	SW U.S., Mexico
Menthaceae (Labiatae)		
Salazaria	1	So. Calif.; SW U.S., Mexico
Scrophulariaceae		
Leucophyllum	14	So. U.S., Mexico
Bignoniaceae		
Chilopsis	1	So. Calif.; SW U.S., Mexico
Acanthaceae		
Berginia	3	NW Mexico
Carlowrightia	20	SW U.S., Mexico
Holographis	4	Mexico
Asteraceae		
Alvordia	3	Central–So. Baja Calif.
Bebbia	2	So. Calif.–SW U.S.
Chrysactinia	4	SW U.S., Mexico
Clappia	2	So. U.S., Mexico
Coreocarpus	8	Calif.-Mexico
Hofmeisteria	10	SW U.S., Mexico
Hymenoclea	4	Calif.–SW U.S., Mexico
Oaxacania	1	Mexico–Tehuacán Valley
Pelucha	1	Baja Calif.
Perityle	25	Calif.–SW U.S., Mexico
Psilotrophe	6	So. U.S., Mexico
Selloa	1	Mexico
Varilla	2	So. U.S., Mexico
Venegasia	1	So. Calif., NW Mexico
Zaluzania	12–15	Mexico

South American and Paleoamerican) resulting in "adaptation to aridity and marked endemism, both of which indicate a strong degree of *in situ* evolution." As an alternative, it seems more probable that the insects, as with the plants, also originated in local dry sites, notably in dry topographic and edaphic areas which would also favor the origin of unique taxa, and with later environmental change resulting in their narrow restriction as relict forms in the young regional desert.

The evidence overwhelmingly supports the in-ference that *local* dry sites were the areas where taxa now in desert regions most probably originated (cf. Stebbins 1952, 1974; Stebbins and Major 1965). They were preadapted to spread into the expanding dry regions which finally merged (anastomosed) to form the regional deserts of the present day during the late Quaternary. This now seems well established not only for the American deserts, but also for the South African (see Axelrod and Raven 1977; Tankard and Rogers 1978) and Australian deserts (see Bowler 1976).

Rzedowski's list of the endemics, reassembled here with additional information (Table 5), points up certain facts which further support the notion of their origin in local dry areas and their later spread as regional climate became drier. Table 5 shows that of the 93 genera endemic to dry regions, members of 2 families account for over a third of them. Cactaceae have 27 genera, the Asteraceae 14. Apart from these large families, most of the genera are small, with from 1 to 4 species, though some have more and these are chiefly wider-ranging taxa. The small size of the alliances, some of which are segregates of other genera, is consistent with an origin in local dry sites during the Late Cretaceous or Tertiary, depending on the alliance under consideration. Note that the taxa can be arranged according to grades of morphologic difference, from unique isolates (*Simmondsia, Fouquieria, Koeberlinia, Olneya*), to those that are progressively more nearly "normal." Such relations indicate that the taxa are of several ages, and they conform in a general way to the "stages" outlined above. The data are agreeable to the hypothesis of the origin and *gradual accumulation*, through time, of taxa that were adapted to gradually spreading dry climate, and not to an origin in an ancient regional desert that reaches back into the Cretaceous.

Apart from these taxa that evidently originated in the drier parts of southwestern North America, there are others that are also autochthonous but have a wider distribution in the region. These include warm temperate or desert taxa that range northward into the California floristic province and have been listed elsewhere (Raven and Axelrod 1978:table 8). Among these are species of *Abronia, Abutilon, Acacia, Acalypha, Adolphia, Agave, Amaranthus, Atriplex, Baccharis, Bebbia, Bergocactus, Bernardia, Bidens, Boerhavia, Brahea, Brickellia, Buddleja, Chamaesyce, Chrysothamnus, Condalia, Croton, Dalea, Echinocereus, Ephedra, Eucnide, Euphorbia* subg. *Agaloma, Forestiera, Fouquieria, Grindelia, Haplopappus, Harfordia, Hibiscus, Hoffmanseggia, Hymenopappus, Hyptis, Ipomoea, Lepidospartum, Lobelia, Lophocereus, Lycium, Machaerocereus, Menodora, Mentzelia, Nolina, Oligomeris, Opuntia, Pachycereus, Pectis, Perityle, Pentalonyx, Physalis, Pluchea, Proboscidea, Prosopis, Rhus* subg. *Schmaltzia, Salicornia, Simmondsia, Solanum, Sphaeralcea, Tetracoccus, Vauqueli-*

nia, *Washingtonia, Yucca*, and others. In the same way, there are many more additional taxa that range from the Sonoran region into warmer parts of western Mexico where they contribute to thorn forest and dry tropic forest. These are well noted in the admirable flora of the Sonoran Desert (Shreve and Wiggins 1964), where ranges are given for diverse species of *Acacia, Bumelia, Bursera, Caesalpinia, Cebia, Cercidium, Cordia, Coursetia, Croton, Erythrina, Ficus, Guaiacum, Guazuma, Haematoxylon, Ipomoea, Jatropha, Karwinskia, Lantana, Malpighia, Mascagnia, Mimosa, Randia, Sapium, Sapindus, Vallesia, Vitex, Zizyphus* and many others. The preceding groups, both the endemic genera with few species, as well as the taxa that range out of the province, either to the north or south, account for the bulk of the flora of the Sonoran Desert region. Emphasis is again placed on the notion that these taxa are of diverse ages, ranging from ancient relicts (*Fouquieria, Simmondsia*), to early Tertiary taxa (*Acacia, Bursera, Ficus, Pithecellobium*), to those that are progressively younger and have adapted to the area, probably as recently as the last glacial (e.g., diverse annuals). These alliances, which have been *accumulating* in the area since the Late Cretaceous, are most abundant on the slopes. On the low desert flats, where the climate is more extreme, there is nearly a "vacuum" so far as taxa are concerned (see below).

Allochthons

Some of the taxa in the Sonoran Desert recur in more distant regions. They suggest that ancient as well as more recent dispersals have contributed to the flora of the Sonoran and bordering region. Taxa that may represent "pan-xeric" ancient dispersals (probably Cretaceous) include *Atriplex* and other chenopods, *Ephedra, Frankenia*, and *Menodora*, and similar taxa that occur in other dry regions on other continents. The inference of antiquity is based on the records of palynomorphs of *Ephedra* well back into the Cretaceous, and the presence of megafossil remains of Chenopodiaceae (*Atriplex?*) in the Late Cretaceous of Baja California (Gastil, Phillips, and Allison 1975:50). These records support the possibility that such distributions may have been attained during the Cretaceous separation of the land areas across the lower, warmer latitudes of the Atlantic into the later part of the period (85

m.y.). The taxa may then have attained a pan-tropic to subtropic distribution along sandy shores over the lower latitudes where dry climates were present and have persisted there through time with but minor change.

Another allochthonous group that is important in the desert flora includes a number of xerophytes that may have originated in South America. These include the families Cactaceae and Bromeliaceae which moved into the drier parts of North America, probably by overseas dispersal in the early Tertiary, to judge from the nature of the genera involved (Raven and Axelrod 1974:fig.4). In addition, there are numerous genera in the drier parts of northern South America (some extend well to the south) that also have allied species in North American tropic and subtropic desert regions, notably in *Acacia, Bursera, Capparis, Cercidium, Croton, Lemaireocereus, Opuntia, Pithecellobium*, and *Prosopis*, that may well have differentiated from more widely ranging ancestors (Axelrod 1948). Some of these, notably *Acacia* and *Prosopis*, were already present in the drier parts of North America by the later Eocene, suggesting that interchange has been continuing through time. Some interchange has occurred more recently, with dispersal from South to North America, as in *Larrea* (Axelrod 1950d; Wells and Hunziker 1976), and with later differentiation into polyploid races as noted above. A large number reflect recent transtropic migration and establishment of northern taxa in the temperate parts of South America (Axelrod 1948, 1950). These were monographed by Raven (1963), who demonstrated that they are successful chiefly because they are self-compatible and occur chiefly in open habitats. Among the approximately 200 taxa involved are species in the following genera (see Raven 1963): *Agrostis, Triglochin, Bromus, Deschampsia, Festuca, Poa, Stipa, Eleocharis, Chorizanthe, Eriogonum, Calandrina, Anemone, Ranunculus, Lepidium, Crassula, Lupinus, Lotus, Trifolium, Gayophytum, Jussiaea, Oenothera, Bowlesia, Osmorhiza, Sanicula, Ginia, Linanthus, Polemonium, Cryptantha, Lappula, Pectocarya, Plagiobothrys, Orthocarpus, Downingia, Plantago, Antennaria, Lasthenia, Madia, Malacothrix, Perityle*, and *Solvia*. The migration of numerous herbaceous taxa southward was not paralleled by a comparable northward movement from South America. The chief reason for this seems to be that the taxa in Chile-

Argentina that may have dispersed northward were not able to become established here. The more extreme climate in the north probably militated against establishment, and competition no doubt was also a factor.

IMBALANCE

The flora of the Sonoran Desert displays imbalance in two different ways. First, there are about 32 families in the province that range widely but are represented in the Sonoran region by a single genus (Table 6). Of the latter, 24 are represented by a single species. Several of the genera range into tropical regions far to the south, notably *Erythroxylon, Trichilia*, and *Passiflora*. They appear to be Tertiary relicts of the drier phases of thorn forest, short-tree forest, and savanna forest which were able to survive in the area of desiccation. Most of the taxa (*Sparganium, Naias, Phyllospadix, Echinodorus, Pistia, Aristolochia, Ceratophyllum, Oxalis, Bergia, Myriophyllum*) are basically hydrophytes and survive in the desert region around seepages and water holes. Of the others, *Cocculus, Juglans*, and *Platanus* are also regularly confined to moist sites and drainageways in the desert region and have Eocene records at middle latitudes in North America. The near-modern species may have originated in warm temperate areas by Eocene time, if not earlier. The presence of these groups in the Sonoran region not only indicates that they are relicts from times when moister climates and other vegetation zones occupied the area, but that they have two principal sources, from more tropical and temperate regions.

The second kind of imbalance in the Sonoran flora was discussed by Wiggins (1960). He noted that many of the genera that contribute importantly to tropical savanna, dry tropic forest, and thorn forest, and are represented by numerous species in those vegetation zones, have only a few species in the Sonoran Desert. For example, there are 17 species of *Acacia* in the Sonoran region of which 7 are endemic, yet the flora of Mexico to the south and east includes fully 70 species. There are 5 species of *Pithecellobium* in the Sonoran province, 2 of them endemic, but 25 species are known from other parts of Mexico. *Ficus* has 4 species in the Sonoran Desert of which 2 are endemic, yet no less than 25 species occur elsewhere in the moister parts of Mexico. Similar relations are exhibited by gen-

TABLE 6. FAMILIES IN THE SONORAN DESERT REGION REP-
RESENTED MOSTLY BY A SINGLE SPECIES (data from Shreve
and Wiggins 1964).

Taxa	Remarks
Sparganiaceae *Sparganium* (1)	Mainly temperate, perennial aquatic herb.
Naiadaceae *Naias* (2)	Cosmopolitan, fresh-water annuals.
Zosteraceae *Phyllospadix* (1)	Marine aquatic, Japan and Pacific Coast, North America.
Juncaginaceae *Triglochin* (1)	Cosmopolitan, fresh- and salt-water marshes.
Alismataceae *Echinodorus* (1)	Warm temperate to tropical, aquatic to marshy perennial herbs.
Araceae *Pistia* (1)	Tropical and subtropical, floating aquatic.
Saururaceae *Anemopsis* (1)	Temperate perennial herbs, common in wet alkaline sites.
Juglans *Juglans* (1)	Temperate and warm temperate trees.
Santalaceae *Comandra* (1)	Temperate genus, tropical family; perennial herb, at margin of desert.
Aristolochiaceae *Aristolochia* (2)	Perennial climbing shrubs or vines, reaching into tropical zone.
Rafflesiaceae *Pilostyles* (1)	Fleshy parasite, the species is parasitic on *Dalea*.
Batidaceae *Batis* (1)	Warm temperate to tropical; only genus in family. Prostrate or low subshrubs on tidal flats and beaches.
Ceratophyllaceae *Ceratophyllum* (1)	Cosmopolitan, submerged aquatics.
Menispermaceae *Cocculus* (1)	Scandent shrubs, vines, ranges into tropical regions.
Resedaceae *Oligomeris* (1)	Only New World genus of very small Old World family. Small annual on desert flats along margins of saline washes.

TABLE 6. CONTINUED.

Taxa	Remarks
Platanaceae *Platanus* (1)	Temperate to warm temperate, trees.
Geraniaceae *Erodium* (3)	Temperate, few sp. in New World, annuals.
Oxalidaceae *Oxalis* (3)	Cosmopolitan, temperate regions. Herbaceous perennial of moist or shady sites.
Erythroxylaceae *Erythroxylon* (1)	Only genus in this tropical-subtropical family, trees or large shrubs.
Meliaceae *Trichilia* (2)	Warm temperate to subtropical, tropical trees.
Elatinaceae *Bergia* (1)	Cosmopolitan family and genus, slightly woody herbs about seepages and moist places.
Frankeniaceae *Frankenia* (2)	Only genus in family, perennial herbs or shrubs common in saline marshes or along the seashore above high-tide level.
Violaceae *Hybanthus* (1)	Perennial herb chiefly in moist places or shady.
Turneraceae *Turnera* (1)	Shrub of drier ridges, ranges into tropics.
Passifloraceae *Passiflora* (6)	Herbaceous or woody vines, tropical to subtropical.
Rhizophoraceae *Rhizophora* (1)	Marine aquatic, tree.
Haloragaceae *Myriophyllum* (1)	Cosmopolitan, aquatic.
Araliaceae *Aralia* (1)	Tropical chiefly, shrub to small tree of deep shaded canyons.
Theophrastaceae *Jacquinia* (1)	Shrub to small tree, ranges into tropical regions.
Martyniaceae *Proboscidea* (4)	Desert warm temperate to tropical family and genus, annual or perennial herbs of sandy places.
Orobranchaceae *Orobranchae* (4)	Temperate and subtropic, mainly desert and dry regions, root parasites.
Goodeniaceae *Scaevola* (1)	Ranges into tropics, shrub of sandy places and upper beaches.

era of other families, some of which are listed in Table 7. These examples also point up the relatively low number of species in the flora of the Sonoran Desert as compared with that of the California floristic province that adjoins it to the north (Raven and Axelrod 1978:table 1).

Wiggins (1960) suggested that these relations indicate that the adaptability of flowering plants to conditions of extreme aridity is much less than their ability to withstand conditions of extreme high or low temperature. An alternate explanation is suggested by the evidence reviewed above which indicates that (1) although many genera are represented by very few species in the desert, these genera do have numerous species in regions of moister climate; (2) many Eocene to Miocene woody plants are similar to those in the desert today, and they lived earlier in more mesic regions; (3) the degree of aridity and the ranges of temperature have increased gradually over the present desert regions and reached their zenith following the last glacial.

These data indicate that the imbalance of the desert flora probably is not due to low adaptability to limited moisture or to the slow intrusion of plants into an ancient desert region. On the contrary, the data support the suggestion that relatively few plants have had a genetic reservoir capable of adapting them to the very rapid appearance, following the last pluvial stage, of a widespread regional climate characterized by exceedingly low and uncertain precipitation and excessively high temperature.

This ability, possessed by a few, has enabled them to persist in a region that has become progressively drier since the past pluvial and has in some measure involved preadaptation. All of the taxa that are in the desert have special adaptations, features that were gained in the Tertiary under seasonally dry, moister climates that were far less rigorous than those that reached the acme of aridity and subcontinental extent only recently. It must be emphasized again that these specialized adaptive types, whether they involve reduced body size, aphylly, green stems, deciduous habit, rapid production of flowers and seeds, underground storage organs, very small annual habit, shadowless plants, etc., are not confined to the desert. They occur in numerous families that range along a climatic gradient that extends far out of the desert, into thorn forest, cactus savanna, short-tree forest, dry tropical forest, and savanna to the south, or into woodland-chaparral, sage, and grassland to the north. The fact that many species of the desert commonly occur in adjoining, moister vegetation zones, all of which have a dry season of less intensity than that of the desert and temperatures that are not so extreme, suggests that survival in the desert has been possible for those that have the appropriate vegetative and functional adaptations, plus the ability to withstand extreme heat and drought. Thus it seems probable that relatively few taxa of numerous families have the proper combinations of genes required to survive in extreme desert climate simply because the invasion of desert areas by plants already well adapted to somewhat moister bordering regions began so recently that few have had the time to adapt physiologically to this novel environment—one in which in some areas may receive no rain for several consecutive years, or occasionally for a decade. In other words, it seems probable that if the desert environment persists, more numerous plants from the bordering communities may be expected to invade this "vacuum" as they gradually acquire the proper gene combinations to cope with a precipitation-temperature regime that is only slightly more extreme than that now at the edge

TABLE 7. REPRESENTATION OF SPECIES OF DIFFERENT GENERA IN MEXICO AND IN THE SONORAN DESERT WHICH INDICATE THE GENERAL IMBALANCE IN THE PRESENT DESERT FLORA.

	Number of species in		
		Sonoran Desert	
Taxa	Mexico (Approx.)	*Wide	Endemic
Burseraceae			
Bursera	45	4	6
Euphorbiaceae			
Jatropha	35	2	5
Rubiaceae			
Randia	26	7	3
Polygonaceae			
Coccoloba	13	0	1
Rutaceae			
Zanthoxylon	20	0	2
Malpighiaceae			
Malpighia	11	1	1
Sapindaceae			
Serjania	40	0	3

* Also in Mexico column.

of the desert. Further, many of the species in the desert might be expected to produce additional new taxa that are better adapted to it. A hint of this is seen in the many subspecies (or varieties) of annuals that have been described from the Sonoran Desert which are segregates of taxa that range far to the north (see above, under Pleistocene) into areas of moister climate.

Annuals are rarer in the Sonoran Desert than in the California floristic province (27% vs. 21%) (Raven and Axelrod 1978:table 3). As noted earlier by Went (1948, 1949), the annuals have different adaptations in each region. The winter annuals of the dry summer climate of California germinate and complete their life cycles in the winter and spring. The summer annuals of the summer-wet Sonoran region germinate and complete their cycles during summer and fall. As reviewed by Mulroy and Rundel (1977), the groups have other divergent morphological, phenological, and physiological adaptations. For instance, C_3 metabolism predominates in the winter group whereas C_4 metabolism increases in annuals to the south and southeast where summer rainfall becomes more frequent and predictable. The C_3 annuals of the California floristic province range also in the dry Mohave Desert and have radiated in response to the spread of Mediterranean climate. C_4 annuals range well south of the Sonoran Desert, entering into the matrix of thorn scrub and arid tropic scrub as well, and probably originated in the subtropics. On the basis of the fossil records of a number of their woody associates, we may infer that during the Pliocene, summer annuals also formed an important part of the California flora, but were eliminated here as summer rains decreased.

Life-Form Spectra

Shreve pointed out that the flora of the Sonoran Desert has a remarkable diversity of codominant life forms. In areas of slightly higher rainfall and more moderate temperature away from the lower bolsons, as many as 20 different adaptive types can be found in a very limited area. This provides a marked contrast with plant formations outside the desert which usually are dominated by plants of similar life form. In regions of mediterranean climate with winter rain, the vegetation bordering the desert is composed of coastal sage of semi-woody half shrubs, or an savanna-woodland, or a dense chaparral

composed chiefly of evergreen shrubs of nearly even height. Desert grassland borders the Sonoran region in the summer-rain area of southern Arizona and Sonora. To the south, desert vegetation is replaced by a tall canopy of moderate-sized trees that are chiefly drought-deciduous and make up a rich thorn forest. In these semiarid regions marginal to the desert where climate is more favorable for plant growth, intense competition between individuals, species, and life form has resulted in the development of a high degree of uniformity among the dominants as compared with the Sonoran Desert (Shreve 1951:19).

To explain these fundamental differences between the variety of codominants of the vegetation of the Sonoran Desert, and the similar life forms of the vegetation zones that border it, Shreve (1951:32) pointed out that in desert regions the "struggle" has not been between the plants, but with the environment. He notes that the successful establishment of a perennial depends on whether its first few seasons are wetter or drier than normal; whether the specific spot where it germinates is sheltered or exposed; whether it has a shallow or deep soil; and whether it is protected or unprotected by notable changes in the surface level on which it germinates. He adds that the presence of closely adjacent, mature perennials seems to be advantageous to a new plant, for the number that appear and survive close to mature ones greatly exceeds those of open or bare spaces because there are very few spots where the conditions for germination and growth are favorable.

These observations have an important bearing on the mode of origin of the admixture of diverse life forms in the Sonoran Desert. Shreve has emphasized that there is no evidence to indicate that any one life form has a more "successful" mode of behavior than the others. The different life forms live under more nearly similar conditions during germination and early growth than at any later time. The development of their individual features of structure and behavior soon brings each one into a slightly different set of relations with the environment, as expressed by differences in the height and spread of branches, depth and distribution of the root system, and the season of foliation and defoliation. These are the features that serve to separate the activities of the varied life forms in time and space, and hence reduces or eliminates severe competition

between them (Shreve 1951:32). In view of these relations, Shreve (1951:19) concluded that the conditions tending toward the elimination of certain life forms, and the survival and dominance of a relatively uniform one, as in grassland or oak woodland, have not been operative in subtropical deserts. It is this, he believes, that has produced the diversity of plant forms which characterized the warm desert regions. "The opportunity which the desert has offered for the persistence of unstandardized plant types has undoubtedly resulted in the survival in it of species, and even of genera, for very long periods of time" (ibid:19).

This also implies that deserts have considerable antiquity and that plants have been adapted to desert climates for a long period of time. However, the geologic and paleobotanic evidence reviewed above supports the conclusion that the diverse plant forms that typify the Sonoran, as well as other subtropical deserts, are the survivors of taxa which were derived from alliances in vegetation zones that occupied the area now desert when it was non-desert (Fig. 18). The record implies that they persisted over the region of desiccation because they were preadapted to a progressively drier climate. This interpretation is based in part on the occurrence of essentially all of the adaptive types that distinguish the Sonoran Desert in vegetation zones that are marginal to it today. Emphasis has already been placed on the notion that *Fouquieria* is not confined to a desert environment, but extends into arid tropical scrub, thorn forest, and dry (deciduous) tropical forest. Also *Beaucarnea* has a similar distribution, from the Tehuacán Desert into dry (deciduous) tropical forest. Apart from these unique adaptive types, there are palms, yuccas, agaves, grasses, leafless shrubs, deciduous shrubs and trees, thorny woody plants, evergreen shrubs, and many others that now occur in savanna, dry evergreen forest, short-tree forest, thorn forest, evergreen and deciduous woodland, and sage vegetation. Furthermore, the fossil record shows that as drought increased during the Tertiary these vegetation zones successively replaced one another over the area of the present desert (Fig. 18). Clearly, the great diversity of life forms in the Sonoran Desert, and no doubt in other tropical deserts as well, results chiefly from the persistence there of the hardy, drought-adapted, residual taxa from the diverse vegetation zones

that were able to survive over the area as drought increased, and not from their origin in ancient, regional deserts.

FLORISTIC DIVERSITY

It is in the deserts with the most favorable conditions and the largest flora, that distinctive desert genera are found, and also a very small number of families which are wholly or almost wholly confined to the desert. (Shreve 1951:20)

The richest desert floras are those at the margins of the tropics. They are richer than those of the cool (Mohave) or cold (Great Basin, Central Asian) deserts because their areas have had a dry climate for a much longer period of time, and they have therefore accumulated more taxa. The Great Basin desert and its counterparts in central and middle Asia are relatively recent, their areas having supported temperate mixed deciduous hardwood forests into the close of the Miocene. Since dry-climate areas have been in existence much longer in the southern, warmer, horse latitudes, first in local areas and then more widely, it is expectable that they have families that are unique to them (e.g., Fouquieriaceae, Koeberliniaceae, Krameriaceae, Simmondsiaceae), though none is known from the cold deserts. There is also a much higher concentration of unique adaptive types in the subtropical deserts (*Acacia, Beaucarnea, Canotia, Chilopsis, Choisya, Fouquieria, Lindleya, Nolina, Olynea, Opuntia, Pachycormus, Pachycereus, Viscainoa*). This attests to the continued addition of taxa to the region as very different kinds of vegetation successively dominated the area, taxa which were preadapted in form and function to the increasing drought. By contrast, the present desert areas of cooler temperate regions were occupied by rather similar forests of the Arcto-Tertiary Geoflora during most of the Tertiary and have therefore had a much smaller reservoir of adaptive types to draw from.

The arid region of southwestern North America, though relatively small, has more genera (about 200) and families (7) restricted to it than the entire region of the United States and Canada east of the Rocky Mountains. This can now be attributed in part to a favorable setting for evolution in dry climate (Stebbins 1952, 1974), and especially in a regionally expanding one (Axelrod 1967); to a longer period (+80 m.y.) of selection for survival in an emerging, new adaptive zone in which numerous taxa accumulated; and in part to the colder post-Miocene climates

which eliminated many taxa from eastern North America that required equable climates, like those now in the uplands of western Hupeh and adjacent Szechuan, and in the Sierra Madre Oriental of eastern Mexico, areas where they now persist as relicts.

THE HIDALGAN DESERT: A RELICT LATE TERTIARY SEMIDESERT?

Shreve (1940, 1942) noted that there are discontinuous areas in central to southern Mexico that support vegetation which displays the essential features of the less extreme type of deserts (also see Rzedowski 1968; Smith 1965; Bravo 1936, 1937; Quintero 1968). These areas have a rich and diversified flora, a large number of life forms, and many plants of distinctive habit, structure, and behavior. The stature and density of the plants greatly exceed those of the desert. These southern desert areas (see Fig. 1), chiefly in Hidalgo-Guerrero-Puebla, were captioned the Hidalgan Desert by Shreve (1940), a term that is used here.

The flora of the southern deserts is much richer than that of the deserts to the north, whether the Chihuahuan or Sonoran. They are closely related to the arid bushland (arid tropical scrub) and cactus savanna, and gradually merge into them, a relation also discussed by Smith (1965). Although desert plants and the ecological features of the desert recur frequently in the diverse, rugged terrain of southern Mexico, these areas cannot be regarded strictly as desert owing to the closer spacing of the plants and to the much less bare ground. In the Hidalgan Desert areas the valley floors are the most arid habitat, and it is the vegetation there that most nearly resembles that to the north. Throughout these desert areas only a *slight* improvement in soil and moisture conditions is sufficient to support more mesic vegetation, including arid bushland, oak woodland, and other types of xeric vegetation which cover the nearby hills, canyons, and floodplains. The proximity of the Hidalgan Desert vegetation of the valley floors to other vegetation types, notably oak woodland, matorral, and thorn forest, recalls the setting of the Miocene Mint Canyon and Tehachapi floras in their local basins. This again points up the critical significance of local dry areas to the evolution of taxa adapted to more arid regions (see Stebbins 1952, 1974; Axelrod 1967, 1972).

Almost all of the features of form, habit, structure, and behavior that distinguish desert plants are found in the Hidalgan Desert. The lists of typical genera in the Sonoran, Chihuahuan, and Hidalgan deserts assembled by Rzedowski (1962, 1973) show that a number of them occur in all three deserts (Table 5), a relation also noted by Smith (1965) and Morafka (1977). Shreve pointed out that many of the genera which have contributed to one or two highly specialized forms to the northern Chihuahuan and Sonoran deserts are represented in the Hidalgan region by a larger number of species. All of the life forms in the Sonoran and Chihuahuan deserts are present in the southern desert areas. The features of form, habit, structure, and behavior that are distinctive characteristics of desert plants are also found in the Hidalgan Desert. The members of these genera show structural features which have undergone further development in certain species that make life possible for them in very arid regions. The small size of the leaves and leaflets is a very common feature of the plants in the Hidalgan Desert of arid southern Mexico. The assumption of photosynthetic work by the stem is common, though not often accompanied by the entire loss of leaves. Plants with succulent leaves are more abundant in the southern than in the northern deserts. Semi-succulent plants are as abundant in species in the south, but not so numerous in the matrix of the vegetation.

However, the stem-succulent cacti are more abundantly represented both in species and individuals in the Hidalgan Desert areas than in the Sonoran or Chihuahuan, and many unique forms are endemic to the area especially in the Tehuacán basin (MacDougal 1908; Smith 1965). Many other taxa in the area exhibit unique storage functions, including the large stems of yuccas and the fleshy leaves of *Agave* and *Hectia*. *Euphorbia* and *Pedilanthus* have thick stems in which storage function is also effective (MacDougal 1908). A tree-*Ipomoea* has a soft, thick trunk for storage, and the unique *Beaucarnea* also has a parenchymatous trunk for water storage. *Cissus* species have enlarged bases to the stems and also thick globular tubers. Apart from storage specializations, the flora has numerous epiphytes as well as spinose plants, notably *Fouquieria* (one species with a small trunk simulates *Idria*), the cacti, *Cnidoscolus,* diverse leguminous shrubs, and *Acanthothamnus,* a leafless shrub simulating *Koeberlinia.*
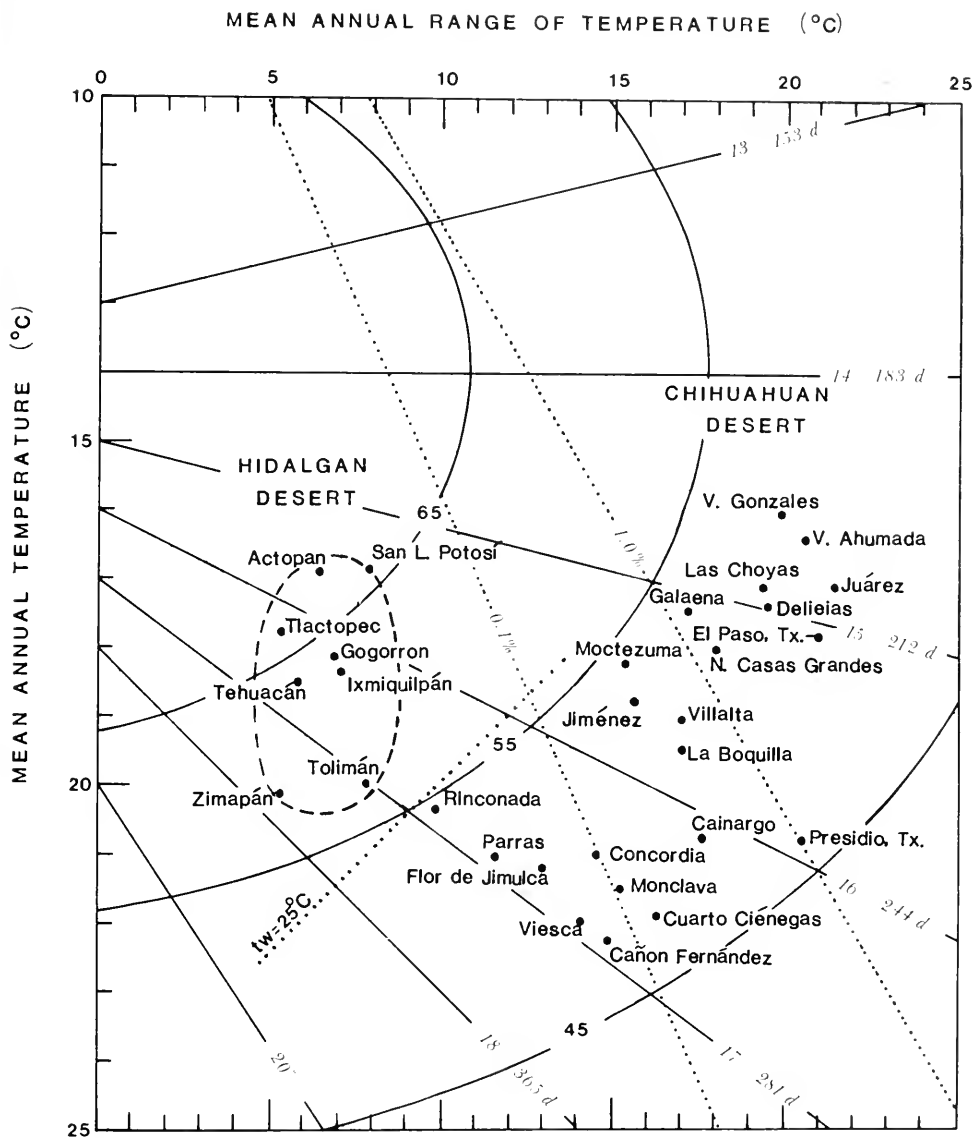
MEAN ANNUAL RANGE OF TEMPERATURE (°C)

FIGURE 27. Comparison of the warmth and temperateness of climate at stations in the central and southern Chihuahuan Desert with those in the Hidalgan Desert region. Note that the warmth of climate (radians) in the Hidalgan Desert is similar to that in the central and southern Chihuahuan, but the latter has greater ranges of temperature and is therefore less equable (i.e., M 45–54 vs. M 57–68). Dotted line = percent hours of year subject to freezing.

The nature of the arid tropical scrub of the Río Balsas, Guerrero, provides an example of how desert and semidesert taxa may have been derived gradually from alliances in local dry basins. The valley of the Río Balsas trends westerly and is shut off from the sea by the highlands of the Sierra Madre del Sur to the south, and is therefore quite dry receiving 650–750 mm in the warm season; at Mescala, 84 per cent of the yearly total of 730 mm falls during the period from May through September. The xeric vegetation resembles that of a cactus desert in many ways. The region has patches of thorn forest, and deciduous tropical forest occurs locally. Organ cactus (*Cephalocereus*) is frequent in the arid tropical scrub of *Acacia, Bursera, Cordia,*

Haematoxylon, Hibiscus, Mimosa, Caesalpinia, and others, and the more humid slopes support species of *Bauhinia,* numerous leguminous trees (*Acacia, Mimosa, Caesalpinia*), *Zizyphus,* and other thorny plants. This environment is only a step removed from the Tehuacán semidesert (Smith 1965; MacDougal 1908), characterized by species of *Cereus, Opuntia,* and numerous other cacti, *Beaucarnea, Fouquieria, Pithecel-lobium, Prosopis,* and many others. These morphologic, vegetative, and community relations point to the probable evolutionary significance of the vegetation and flora of the Hidalgan arid region. They seem to represent more nearly the ancestral type from which the Sonoran and Chihuahuan deserts have been derived. The "more primitive" features have been preserved in the Hidalgan Desert, a region characterized by greater rainfall and by more equable temperature.

This is evident from a comparison of the climates of the Hidalgan and the central to southern Chihuahuan Desert region. The chief climatic differences are in the ranges of mean monthly temperature, and hence in the difference in equability (Fig. 27). The range of temperature (A) in the Hidalgan semidesert is generally less than 8 C (14 F), whereas it is more than 14 C (24–25 F) in the central Chihuahuan. As a result, stations in the Chihuahuan Desert are subject to greater frost frequency (which increases northward) than any of the Hidalgan semidesert areas, all of which are well removed from its effects (Fig. 27).

The high degree of endemism in the Hidalgan Desert (see Bravo 1936, 1937; Quintero 1968), and especially in the Tehuacán sector, raises the problem of age and origin. There is no evidence to support Smith's (1965:140) contention that:

A long-term stability in climatic regimen might have been responsible for an increased rate of endemism in the flora of the Tehuacán valley. Since the biggest influence on the climate of the valley seems to be the Gulf of Mexico to the north and east, the elevation of the masses of the Sierra de Zongolica has played a major role in the control of rainfall. Probably there has been no major change in rainfall pattern or distribution since the mountain mass became elevated during the Laramide Revolution at the close of the Cretaceous (Dunbar, 1949).

Actually, the Laramide movements extended from the Upper Cretaceous into the Oligocene, and they did not produce major mountains, but only folded rocks that formed low ridges for the most part (Schuchert 1935:133; R. E. King 1939; P. B. King 1977; Eardley 1962:chap. 43; Clark and Stearn 1968; Tweto 1975; Mejorada and Ramos 1968). Furthermore, using a conservative estimate of rates of erosion (e.g., Gilluly, Waters, and Woodford 1974:78), the Sierra de Zongolica could not have persisted since the Cretaceous: it would have been reduced to sea level within 14 million years (or less) if there were no compensating uplifts. Examination of Tehuacán valley (April 1977) shows that it is a fault trough, and that the episode of faulting that elevated the Sierra de Zongolica is quite recent. This is shown not only by the nature of the fault block (very steep V-valleys, some nearly hanging; truncated spurs, linear mountain front), but also by the faulting that has greatly disturbed the younger Neogene rocks in the basin. These well-bedded sedimentary rocks are fine grained throughout and thus provide no evidence of high relief nearby. Only the overlying alluvial fans and terraces of younger age are composed of fanglomerate, conglomerate, and other coarse detritus derived from the bordering, newly uplifted mountains. Since the evidence indicates that the towering Sierra de Zongolica is a recently elevated fault-block range, it cannot account for low rainfall in Tehuacán valley from Late Cretaceous into the later Tertiary, and for the origin of that desert in ancient times.

The unique taxa and the adaptive types that they represent clearly have had a long history. Inasmuch as a number of these taxa extend into the bordering vegetation zones, notably tropic savanna, oak woodland, as well as thorn scrub and arid bushland, they no doubt had their origin in the dry subtropics at an early date—certainly by the Eocene to judge from the fossil record reviewed above. In this connection, it is recalled that *Fouquieria* is recorded in the middle Eocene La Jolla Sandstone, associated there with taxa that represent a dry tropic forest. While *Fouquieria* is commonly thought of as a typical member of the desert flora today, several species range into moister areas as members of thorn forest and dry tropic scrub. As recorded by Hendrickson (1972), in Guerrero *F. formosana* inhabits tropical deciduous forest in areas where precipitation totals 1,000 mm (40 inches), and also occurs in Oaxaca where precipitation is only 300 mm (about 12 inches). Furthermore, the unique *Beaucarnea* which is a co-dominant in parts of the Tehuacán Desert also contributes

TABLE 8. COEFFICIENTS OF SIMILARITY BETWEEN THE FLORAS OF DIFFERENT DRY AREAS IN MEXICO (from Rzedowski 1973:table 1).

Regions	Sonora and Baja California %	Chihuahua %	San Luis Potosi %	Hidalgo %
Baja California and Sonora (272 genera)	—	51.9	45.4	41.0
Chihuahua (258)	51.9	—	71.8	67.8
San Luis Potosi (177)	45.4	71.8	—	87.0
Hidalgo (189)	41.0	67.8	87.0	—

importantly to the dry tropical forest of southern Tamaulipas and San Luis Potosi (Rzedowski 1966:124). On the slopes where the Sierra Madre meets the coastal plain, in an area where precipitation is fully 900 to 1,000+ mm (35–40 inches), it is an important associate of the dry (deciduous) tropical forest. Among the associated trees are species of *Acacia, Bursera, Cedrela, Guazuma, Lysiloma, Piscidia, Phoebe,* and *Sabal,* and large shrubs in the understory are represented by species of *Acalypha, Bombax, Chiococea, Colubrina, Eugenia, Karwinskia, Pithecellobium, Trichilia,* and many others as well as arborescent species of cacti and yucca. During the early Tertiary, dry sites were available for comparable communities and even drier ones were on limestone slopes where Mesozoic rocks that make up the bulk of the Sierra Madre Oriental and the bordering ranges were exposed. Limestones made up much of the area on the plateau prior to their burial under the younger later Cenozoic volcanics.

During the Miocene and into the early Pliocene, the Mexican plateau had only a low to moderate altitude, and the Sierra Madre Oriental and Occidental had not yet been elevated appreciably (Schuchert 1935; Eardley 1962; R. E. King 1939; de Cserna 1960; Guzman and de Cserna 1963). As a result the plateau region must have received higher rainfall than at present and was also warmer owing to its lower elevation. The vegetation that now covers the east and west coasts, notably dry tropic forest, woodland, and thorn scrub, must have been more widely spread over the plateau prior to its uplift. Hence it is understandable that modern taxa in these vegetation zones link the eastern and western Sierra Madre and the bordering coastal strips. Drier areas which supported semiarid taxa were more restricted than at present and

probably included drier lee slopes and basins and dry edaphic sites. In view of the more widespread environments and the absence of marked differentiation between the east and west coast floras, semiarid taxa were more widespread then than at present. This agrees with the interrelations of the taxa that now contribute to the Sonoran, Chihuahuan, and Hidalgan desert floras (see Shreve 1942; Rzedowski 1962; Smith 1965; Quintero 1968; Wiggins 1960), which indicate that there are numerous links between them (Table 8). Hence, they must have been more frequent in the past. This is consistent with the general similarity of the herpetofauna across the continental divide in the region of southern Arizona–New Mexico, as documented by Morafka (1977:181–182) for diverse anurans and snakes. He also provides a useful diagram (Morafka 1977:map 9) that illustrates the reversely symmetrical vegetation of the North American deserts and their border areas, from the Mohave region of California southeastward for 1,000 km to Doctor Arroyo, Nuevo León.

During the later Pliocene and Quaternary, the Sierra Madre of eastern and western Mexico were rapidly elevated (King 1939; Schuchert 1935; Eardley 1962; Baker 1971; de Cserna 1960, 1961; Guzman and de Cserna 1963). As a result, dry climate in the lee of the ranges now spread and provided a corridor for the movement of the semidesert and thorn scrub vegetation down the plateau into the lower latitudes (the Pueblan desert of Tehuacán is at lat. 18°21'N). At the same time, the elevation of the plateau was increasing, probably as much as 1,000 m in the Hidalgan semidesert areas, but less to the north for the plateau decreases in elevation there. Thus, semiarid to arid taxa now spread into the expanding dry zone as the more mesic woodland, forest, and thorn scrub communities retreated

into moister sites in the bordering hills. Inasmuch as the taxa were already adapted to withstand drought, they rapidly assumed dominance as a new regional plant formation. As the plateau was elevated in the later Pliocene, climate became more equable (see Fig. 27) and a rich semidesert flora characterized by numerous arboreal cacti and an associated rich shrub and small-tree flora now covered the drier areas wherever rainfall was as low as 380 mm (15 inches). We may infer that it had a composition and structure much like that now seen in the Hidalgan semidesert today and was widely spread to the north into the Chihuahuan and Sonoran regions. At that time the floras of the semidesert regions were more nearly alike than their derivatives are at present.

During the late Cenozoic uplift of the Mexican region, an extensive volcanic field was being built up on the central plateau. This isolated the present Hidalgan and Pueblan semidesert areas from each other and from the Chihuahuan Desert region to the north (Fig. 1). The volcanic fields buried (and exterminated) wide areas where semidesert vegetation was present earlier, and the new, higher terrain provided environments suited for the more mesic woodlands and forests that still occupy them. These relationships provide a basis for understanding the high degree of endemism which characterizes the Hidalgan semidesert, and especially the Tehuacán sector (see Smith 1965). Apart from the high diversity of cacti, which include a number of endemics, there also are endemic genera, notably *Oaxacana* (Asteraceae, 1 sp.), *Acanthothamnus* (Celastraceae, 1 sp.), and *Setchellanthus* (Capparaceae, 1 sp.) [see below]. The semidesert areas of Hidalgo-Querétaro-Puebla are rich in unique endemics, and many of them have considerable antiquity because they are not closely allied to any living taxa. The intermediate links have been exterminated, and the surviving taxa are phylogenetic isolates. However, their present restricted occurrences in these isolated semideserts need not be explained by an ancient origin in their present local areas, as suggested by Smith (1965). It seems more probable that they have been confined to them by climatic and topographic changes. It is recalled that the climate of the Hidalgan Desert areas is very equable (M 60–64) and well removed from the likelihood of frost (Fig. 27). This mild climate only reflects the moderate altitude, but also

the sheltering effect of the young volcanic mountains which shield them from the colder climate to the north, both now and in the recent past. At times of major glacial advance, outbreaks of polar air certainly must have penetrated far southward. These incursions endangered frost-sensitive taxa, notably the arboreal cacti in the genera *Cephalocereus*, *Pachycereus*, *Lemaireocereus* (see Shreve 1911), as well as other thermophytes. Their survival probably is due in large measure to the protected environments in which they occur.

This inference is consistent with the disjunct occurrence of a number of Chihuahuan Desert taxa in the Hidalgan semidesert. As recorded by Quintero (1968) and discussed by Wells and Hunziker (1976), 47 species in 34 genera that are important members of the Chihuahuan Desert vegetation occur in the Valle del Mesquitál of Hidalgo, including *Agave lecheguilla*, *Celtis pallida*, *Euphorbia antisyphilitica*, *Flourensia cernua*, *Jatropha dioca*, *Koeberlinia spinosa*, *Larrea divaricata*, *Rhus microphylla*, and *Yucca filifera*. This is expectable, for temperatures in the southern Chihuahuan region are transitional in nature (see Fig. 27). The occurrence of a number of taxa in the Tehuacán sector that range well to the north into the Chihuahuan region (Smith 1965) is understandable on the same basis. It seems unlikely that all of these disjunct taxa arrived in these basins by long-distance dispersal. However, it is probable that they represent an element of a formerly more widespread, richer flora that was impoverished at the north by the increasingly colder climate over that area. It was the building up of the young volcanic field on the plateau of central Mexico that provided protection for the relict taxa (endemics) of the Hidalgan semidesert flora during the cold periods of the Quaternary. At such times, however, as judged from the limited record provided by two small late Pleistocene leaf floras from the region (Arsène and Marty 1923; Rul and Rzedowski 1968), the spread of forest and woodland under the moister, cooler climates must also have greatly reduced the area of dry climate and that of the semideserts as well.

On the Mexican plateau, the effects of cold increase northward and certainly did so during the glacial ages. This probably accounts for the elimination of many Hidalgan taxa from the Chihuahuan region. These would have been chiefly alliances that were adapted to the more equable

climates which were present there earlier, but occur now only at the south in the Hidalgan semidesert regions. Especially noteworthy in this regard is the recent discovery of *Setchellanthus* (Capparaceae, 1 sp.) in Tamaulipas (Rzedowski, letter of June 1977), a genus previously considered restricted to the Tehuacán Desert. It lends credence to the thesis that the Tehuacán flora is filled with many other taxa that had a wider distribution to the north prior to the development of colder climates there. The impact of cold may also account for the lower diversity of the Chihuahuan as compared with the richer Sonoran Desert flora which lives under a warmer climate.

The importance of the trans-volcanic terrain of late Cenozoic age as an important climatic barrier is evident from the general distribution maps of plant families that reach northward from tropical regions into central Mexico (see Vester 1940). The following families for the most part range northward on the plateau into the volcanic chain, but rarely beyond it. The taxa are tropical to warm temperate in their requirements and do not withstand frost of any intensity or duration. Annonaceae, Balanophoraceae, Begoniaceae, Cannaceae, Caricaceae, Clethraceae, Cochlospermaceae, Combretaceae, Connaraceae, Corariaceae, Cunoniaceae, Cyclanthaceae, Dilleniaceae, Elaeocarpaceae, Erythroxylaceae, Flacourtiaceae, Gesneriaceae, Hippocrateaceae, Lacistemonaceae, Meliaceae, Monimiaceae, Musaceae, Myristicaceae, Myrsinaceae, Myrtaceae, Olacaceae, Opiliaceae, Sabiaceae, Theaceae, Zingiberaceae. In addition, there are about 10 other families that do not range much farther north except for a few genera represented chiefly by reduced numbers of species. Among these are Arecaceae, Basellaceae, Gibnoniaceae, Bombacaceae, Lauraceae, Malpighiaceae, Marcgraviaceae, Melastomataceae, Sapindaceae, Sapotaceae, Simaroubaceae, Sterculiaceae. With respect to all these families, it is noteworthy that butterflies (whose larvae feed on plants) show a distribution in Mexico that generally parallels them. Hoffman (1940), who gives a good account for the zoogeography of Mexican butterflies, notes that the trans-Mexican volcanic chain provides a nearly impenetrable barrier for most of the Lepidoptera of tropical Central America, which range northward only to its southern slopes. Similarly, the taxa of the southern United States range more or less extensively southward to central Mexico, to the northern slopes of the great transverse volcanic belt, but rarely beyond it.

The fossil record shows that many of the plant families listed above ranged far north of the trans-volcanic belt during the early and middle Tertiary. They lend further credence to the notion that the endemics of the Hidalgan semideserts are relict. The evidence thus suggests that they probably did not originate in situ in arid basins which have been in existence since the Cretaceous, but rather that they were confined to them by geologic and climatic events of late Cenozoic time. The numerous taxa in the Hidalgan semideserts of Puebla, Hidalgo, Guerrero, and border areas that occur also in the Chihuahuan and Sonoran are thus the residual members of more widespread late Cenozoic thorn forest, woodland, and semidesert vegetation that have been segregated into more local, new dry climates.

SUMMARY AND CONCLUSIONS

The vegetation of the Sonoran Desert has derived its taxa from those in the diverse plant formations that successively occupied the region during Late Cretaceous and Tertiary times—tropic savanna, dry tropic forest, thorn forest, piñon-oak woodland, grassland. The taxa probably originated in local dry sites provided by diverse terrain and edaphic situations. They lived initially under a subtropical high pressure system much weaker than that of today because the thermal gradient was lower, about 20 C as compared with over 30 C. As the thermal gradient increased following the middle Eocene, the high pressure system strengthened, the period of drought increased in duration and intensity, and new taxa originated in response to spreading aridity. Local semiarid areas probably supported semidesert vegetation by the late Eocene, and many near-modern semidesert species were already in existence by the Miocene. Semideserts probably attained maximum area under the mild, dry climate of the middle Pliocene (5–7 m.y.), being interrupted by oak-conifer woodland, grassland, thorn forest, and possibly by local desert patches. Reduced in area during the moist late Pliocene and the Pleistocene pluvials, a full regional desert environment first appeared only during the interglacials and now has its greatest extent under a dry climate whose severity has not previously been equalled.

The diverse plant forms in the Sonoran Desert were derived from hardy taxa which contributed to the varied vegetation zones that occupied the region before it was a desert. They persisted over the area because they were preadapted both in form and function to the trend to increased drought. These diverse taxa, each of which was preadapted to greater drought and higher ranges of temperature, and which have persisted over the region with relatively little basic change, are referred provisionally to several ages:

1. Monotypes (*Fouquieria, Koeberlinia, Pachycereus, Simmondsia*) of unique adaptive type and isolated taxonomic position probably are relicts of the Late Cretaceous.
2. Distinctive genera of large tropical families that are recorded in the Late Cretaceous may also have appeared at that early date, notably *Brahea, Washingtonia* (Arecaceae); *Beaucarnea, Nolina, Yucca* (Liliaceae); *Forchammeria* (Capparaceae).
3. Distinct genera of warm temperate alliance (*Morus, Mahonia, Vauquelinia*) were present in the Late Cretaceous–Paleocene, as judged from fossil evidence, and their species were adapted to semiarid climate by the middle Eocene.
4. Many distinctive desert species which belong to genera that are highly diversified in tropical regions (e.g., *Acacia, Bursera, Ficus, Pithecellobium, Randia*) had assumed near-modern form by the middle Eocene, with species of these and other genera that are less distinctive having originated later.
5. Endemic genera of the Sonoran region that differ only slightly from those in bordering areas (e.g., *Triteleiopsis-Brodiaea*) may be as young as Miocene or Pliocene.
6. Herbaceous and perennial plants that are scarcely distinguishable from allies in the adjacent region probably are Pliocene and Pleistocene.
7. Taxa that range from moister regions into the desert evidently were able to persist there as desiccation increased following the last glacial-pluvial because they were preadapted to greater drought. In addition, the Sonoran Desert flora contains riparian and aquatic habitats where non-xerophytic species, some ancient, can and do exist.
8. Over 100 species, chiefly weeds from the European region, have become established in open, disturbed areas in the driest parts of the Sonoran Desert in the last 300 years.

The vegetation zones that surround the Sonoran Desert usually are dominated by a single life form, but the vegetation of the Sonoran Desert has many. This reflects the persistence there of varied life forms from the vegetation zones that earlier occupied the region, not their origin in an ancient desert climate. The marked imbalance of the Sonoran Desert flora owes its existence to the recency of extreme desert climate, not to the inability of plants in semiarid regions to withstand increased drought or heat. Numerous species now common to the Sonoran, Chihuahuan, and Hidalgan deserts imply an earlier, greater unity of semidesert vegetation, followed by segregation into new, drier subclimates. The Hidalgan Desert has many more "primitive" taxa, chiefly because they were preserved as the Mexican plateau was uplifted into a more equable dry climate than that of the colder Chihuahuan or the hotter Sonoran. The Hidalgan environment more nearly approximates that which is inferred for the Tertiary semideserts.

Most of the 200-odd genera and 7 families confined to the dry climate of Mexico and bordering areas have only one or a few species. Ranging from ancient monotypes to more recently derived genera, these autochthons of the Madrean floristic province support paleobotanical evidence which indicates that local sites in the present area of the Sonoran and Chihuahuan deserts served as the prime centers for the evolution and accumulation of taxa adapted to the progressively spreading, and increasingly more severe, dry climate of the Cenozoic.

As different subclimates developed during the later Cenozoic, many desert taxa were eliminated from the areas of more extreme climate and have survived in those with more equable conditions. These are precisely the areas where the most numerous relicts occur. The resultant segregation of taxa into regional subclimates in the later Pliocene and Pleistocene fashioned the composition of the major warm deserts (Sonoran, Chihuahuan, Hidalgan) and also their subprovinces.

ACKNOWLEDGMENTS

The manuscript has been reviewed by A. W. Johnson, J. Major, H. A. Mooney, P. H. Raven, J. Rzedowski, and P. W. Wells, all of whom have added to its substance. Thanks are also extended to Sandra Chase for her expertise, and also her patience, in drafting the figures.

LITERATURE CITED

ABBOTT, P. L. AND T. E. SMITH. 1978. Trace-element comparison of clasts in Eocene conglomerates, southwestern California and northwestern Mexico. J. Geol. 86:753–762.

ALLEN, V. T. 1929. The Ione Formation of California. Univ. Calif. Publ. Bull. Dep. Geol. Sci. 18:347–448.

ANDERSON, R. Y., AND D. W. KIRKLAND. 1969. Paleoecology of an early Pleistocene Lake on the High Plains of Texas. Geol. Soc. Am. Mem. 113. 215 p.

ARSÈNE, F. G., AND P. MARTY. 1923. Sur quelques emprintes de feuilles fossiles de la loma del Zapote à Morelia, Michoacán, Mexique. Covington, Louisiana. 16 pp., mimeogr. (Private report.)

ASCHMANN, H. 1973. Man's impact on the several regions with Mediterranean climates. Pages 363–371 in F. di Castri and H. A. Mooney, eds., Ecological Studies 7, Mediterranean type ecosystems, origin and structure. Springer-Verlag, New York, Heidelberg & London.

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

———. 1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash. Publ. 516:1–128.

———. 1940. The Mint Canyon flora of southern California: a preliminary statement. Am. J. Sci. 238:545–551.

———. 1944. The Sonoma flora. Carnegie Inst. Wash. Publ. 553:167–206.

———. 1948. Climate and evolution in western North America during middle Pliocene time. Evolution 2:127–144.

———. 1950a. A Sonoma florule from Napa, California. Carnegie Inst. Wash. Publ. 590:23–71.

———. 1950b. Further studies of the Mount Eden flora, southern California. Carnegie Inst. Wash. Publ. 590:73–117.

———. 1950c. The Anaverde flora of southern California. Carnegie Inst. Wash. Publ. 590:119–158.

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

———. 1952. A theory of angiosperm evolution. Evolution 6:29–60.

———. 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Publ. Geol. Sci. 33. 316 p.

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

———. 1960. The evolution of flowering plants. In S. Tax (ed.), Evolution after Darwin, 1:227–305.

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

———. 1966. The early Pleistocene Soboba flora of southern California. Univ. Calif. Publ. Geol. Sci. 60:1–109.

———. 1967. Drought, diastrophism and quantum evolution. Evolution 21:201–209.

———. 1968. Tertiary floras and topographic history of the Snake River Basin, Idaho. Geol. Soc. Am. Bull. 79:713–734.

———. 1970. Mesozoic paleogeography and early angiosperm history. Bot. Rev. 36:277–319.

———. 1972. Edaphic aridity as a factor in angiosperm evolution. Am. Nat. 106:311–320.

———. 1973. History of the Mediterranean ecosystem in California. Pages 225–277 in F. di Castri and H. A. Mooney, Mediterranean type ecosystems: origin and structure. Springer-Verlag, New York, Heidelberg, & Berlin.

———. 1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. Ann. Missouri Bot. Gard. 62(2):280–334.

———. 1978. Origin of coastal sage vegetation, Alta and Baja California. Am. J. Bot. 65:1117–1131.

———, AND H. P. BAILEY. 1976. Tertiary vegetation, climate and altitude of the Rio Grande depression, New Mexico-Colorado. Paleobiology 2:235–254.

———, AND P. H. RAVEN. 1977. Late Cretaceous and Tertiary vegetation history of Africa. Monographiae Biologicae 31:79–130.

———, AND W. S. TING. 1960. Late Pliocene floras east of the Sierra Nevada. Univ. Calif. Publ. Geol. Sci. 39:1–118.

BAILEY, H. P. 1958. A simple moisture index based upon a primary law of evaporation. Geogr. Ann. 40:196–215.

———. 1960. A method of determining the warmth and temperateness of climate. Geogr. Ann. 42:1–16.

———. 1971. On recognition of climatic similarities in global perspective, Origin and structure of ecosystems. Internat. Biol. Program, Tech. Rep. 71–4:1–12.

BAKER, C. L. 1971. Geologic reconnaissance in the eastern Cordillera of Mexico. Geol. Soc. Am. Spec. Pap. 131. 83 p.

BALL, O. M. 1931. A contribution to the paleobotany of the Eocene of Texas I. Agric. Mech. Coll. Texas Bull., Ser. 4, 2:1–172.

———. 1939. A contribution to the paleobotany of the Eocene of Texas II. Agric. Mech. Coll. Texas Bull., Ser. 4. 10:1–54.

BEARD, J. S. 1955. The classification of tropical American vegetation types. Ecology 36:89–100.

———. 1976. The evolution of Australian desert plants. Pages 51–64 in D. W. Goodall, ed., Evolution of desert biota. Univ. Texas Press, Austin and London. 250 p.

———. 1977. Tertiary evolution of the Australian flora in the light of latitudinal movements of the continent. J. Biogeogr. 4:111–118.

BERRY, E. W. 1916. The lower Eocene floras of southeastern North America. U.S. Geol. Surv. Prof. Pap. 91. 466 p.

———. 1919. An Eocene flora from Trans-Pecos Texas. U.S. Geol. Surv. Prof. Pap. 125A:1–9.

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

———. 1930. Revision of the Lower Eocene Wilcox flora of the southeastern States. U.S. Geol. Surv. Prof. Pap. 156. 196 p.

———. 1934. The middle and upper Eocene floras of southeastern North America. U.S. Geol. Surv. Prof. Pap. 92. 206 p.

BLAIR, W. F. 1976. Adaptation of anurans to equivalent desert scrub of North and South America. Pages 197–222 in D. W. Goodall, ed., Evolution of desert biota. Univ. Texas Press, Austin and London. 250 p.

———, A. C. HULSE, AND M. A. MARES. 1976. Origin and affinities of the vertebrates of the North American Sonoran Desert and the Monte Desert of northwestern Argentina. J. Biogeogr. 3:1–18.

BLAKE, M. C., JR., R. H. CAMPBELL, T. W. DIBBLEE, JR., D. C. HOWELL, T. H. NILSEN, W. R. NORMARK, J. C. VEDDER, AND E. A. SILVER. 1978. Neogene basin formation

in relation to plate-tectonic evolution of San Andreas fault system, California. Am. Assoc. Pet. Geol. 62:344–372.

BOHANNON, R. G. 1975. Mid-Tertiary conglomerates and their bearing on Transverse Range tectonics, southern California. Calif. Div. Mines Geol. Spec. Rep. 118:75–82.

BONNEFILLE, R. 1976. Implications of pollen assemblage from the Koobi Fora Formation, East Rudolf, Kenya. Nature 264:403–407.

BORNMAN, C. H. 1972. *Welwitschia mirabilis*: paradox of the Namib Desert. Endeavour 31:95–99.

———. 1974. *Welwitschia mirabilis*: observations on cuticular efficiency. A comparative study. Madoqua, Ser. 2, 3:17–25.

———. 1977. *Welwitschia mirabilis*: structural and functional anomalies. Madoqua 10:21–31.

———, J. A. ELSWORTHY, V. BUTLER, AND C. E. J. BOTHA. 1972. *Welwitschia mirabilis*: observations on general habit, seed, seedling, and leaf characteristics. Madoqua, Ser. 2, 1:53–66.

BOWLER, J. M. 1976. Aridity in Australia: age, origins and expression in aeolian land forms and sediments. Earth-Sci. Rev. 12:279–310.

———, G. S. HOPE, J. N. JENNINGS, G. SINGH, AND D. WALKER. 1976. Late Quaternary climates of Australia and New Guinea. Quat. Res. (N.Y.) 6:359–394.

BRAVO, H. 1936. Observaciones floristicas y geobotanicas en el Valle de Actopan. An. Inst. Biol. Univ. Nac. Auton. Mex. 7:169–233.

———. 1937. Observaciones floristicas y geobotanicas en el valle de Mezquital. An. Inst. Biol. Univ. Nac. Auton. Mex. 8:3–82.

BROWN, R. W. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U.S. Geol. Surv. Prof. Pap. 375. 119 p.

BUTZER, K. W. 1976. Pleistocene climates. Geoscience and Man 13:27–43.

CAMPBELL, M. R. 1904. The Deer Creek coal field, Arizona. U.S. Geol. Surv. Bull. 225:240–258.

CHANEY, R. W., AND M. K. ELIAS. 1936. Late Tertiary floras from the High Plains. Carnegie Inst. Wash. Publ. 476:1–72.

———, AND E. I. SANBORN. 1933. The Goshen flora of west central Oregon. Carnegie Inst. Wash. Publ. 439:1–103.

CHIGURYAEV, A. A. 1951. [About the find of the microspores of *Welwich* in the Eocene deposits of W. Kazakhstan.] Botanicheskii Zhurnal (Leningrad) 36(5):315–316. [in Russian]

CHRISTIANSEN, R. L., AND P. W. LIPMAN. 1972. Cenozoic volcanism and plate-tectonic evolution of the western United States. II. Late Cenozoic. Philos. Trans. R. Soc. Lond. A Math Phys. Sci. 271:249–284.

CLARK, T. H., AND C. W. STEARN. 1968. Geologic evolution of North America, 2nd ed. Ronald Press, New York. 570 p.

CLARKE, S. J., JR., AND T. H. NIELSEN. 1973. Displacement of Eocene strata and implications for the history of offset along the San Andreas fault, central and northern California. Stanford Univ. Publ. Geol. Sci. 13:358–367.

CLEMENTS, F. E. 1936. The origin of the desert climax and climate. Pages 87–140 *in* T. H. Goodspeed, ed., Essays in geobotany in honor of William Albert Setchell. Univ. Calif. Press, Berkeley. 319 p.

CROWELL, J. C. 1952. Probable large lateral displacement of the San Gabriel fault, southern California. Am. Assoc. Pet. Geol. Bull. 36:2026–2035.

———. 1962. Displacement along the San Andreas fault, California. Geol. Soc. Am. Spec. Pap. 71:1–61.

———. 1973. Problems concerning the San Andreas fault system in southern California. Stanford Univ. Publ. Geol. Sci. 13:125–135.

———. 1975. The San Andreas fault in southern California. Calif. Div. Mines Geol. Spec. Rep. 118:7–27.

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

———. 1961. Tectonic map of Mexico (scale 1:2,500,000). Geol. Soc. Am.

DE VOS, ANTOON. 1975. Africa, the devastated continent? Monogr. Biol. 26:1–235.

DIBBLEE, T. W., JR. 1954. Geology of the Imperial Valley region, California. Chap. 2, pp. 29–52 *in* Geology of southern California. Calif. Div. Mines Geol. Bull. 170.

———. 1968. Displacements of the San Andreas fault system in the San Gabriel, San Bernardino and San Jacinto mountains, southern California. Stanford Univ. Publ. Geol. Sci. 13:260–278.

———. 1975. Late Quaternary uplift of the San Bernardino Mountains on the San Andreas and related faults. Calif. Div. Mines Geol. Spec. Rep. 118:127–135.

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

DOYLE, L. J., AND D. J. GORSLINE. 1977. Poway conglomerate in northwest Baja California derived from Sonora. Am. Assoc. Pet. Geol. Bull. 61:903–917.

DRUGG, W. S. 1967. Palynology of the upper Moreno Formation (Late Cretaceous–Paleocene), Escarpado Canyon, California. Paleontogr. Abt. B Paleophytol. 120:1–71.

DUNBAR, C. O. 1949. Historical geology. John Wiley and Sons, New York. 567 p.

EARDLEY, A. J. 1962. Structural geology of North America, 2nd ed. Harper and Row, New York & Evanston. 743 p.

EHLERT, K. W., AND P. L. EHLIG. 1977. The "polka-dot" granite and the rate of displacement of the San Andreas fault in the southern California. Geol. Soc. Am., Abstract with Programs 9(4):415–416.

EHLIG, P.L., K. W. EHLERT, AND B. M. CROWE. 1975. Offset of the upper Miocene Caliente and Mint Canyon formations along the San Gabriel and San Andreas faults. Calif. Div. Mines Geol. Spec. Rep. 118:83–92.

EVANS, H. E. 1966. A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Mem. Am. Entomol. Soc. 20:1–442.

FAIRBANKS, H. W. 1896. Notes on the geology of eastern California. Am. Geol. 17:63–74.

FARLEY, T., AND P. L. EHLIG. 1977. Displacement on the punchbowl fault based on occurrence of "polka-dot" granite clasts. Geol. Soc. Am., Abstracts with Programs 9(4):419.

FIFE, D. L. 1968. Geology of the Bahia Santa Rosalia quadrangle, Baja California, Mexico. M.A. Thesis, San Diego State Univ., Calif. 100 p.

FRAKES, L. A., AND E. M. KEMP. 1973. Palaeogene continental positions and evolution of climate. Pages 539–558 *in* D. H. Tarling and S. K. Runcorn, Implications of continental drift to the earth sciences, vol. 1. Academic Press, London & New York. 622 p.

GARCIA, ENRIQUETA. 1973. Modificaciones al sistema de clasificación climatica de Köppen. Univ. Nac. Autó. México, Instituto de Geografia. Mexico, D.F. 246 p.

GASTIL, R. G., AND W. JENSKY. 1973. Evidence for strike-slip displacement beneath the Trans-Mexican volcanic belt. Stanford Univ. Publ. Geol. Sci. 13:181–190.

————, AND D. KRUMMENACHER. 1977. Reconnaissance geology of coastal Sonora between Puerto Lobos and Bahia Kino. Geol. Soc. Am. Bull. 88:189–198.

————, R. P. PHILLIPS, AND E. C. ALLISON. 1975. Reconnaissance geology of the State of Baja California. Geol. Soc. Am. Mem. 140. 170 p.

————, R. P. PHILLIPS, AND R. RODRIQUEZ-TORRES. 1972. The reconstruction of Mesozoic California. 24th Int. Geol. Congr., Montreal. Sect. 3:217–229.

GENTRY, H. S. 1942. Rio Mayo Plants. Carnegie Inst. Wash. Publ. 527:1–328.

————. 1946a. Sierra Tacuichamona—a Sinaloa plant locale. Torrey Bot. Club Bull. 73:356–362.

————. 1946b. Notes on the vegetation of Sierra Surotato in northern Sinaloa. Torrey Bot. Club Bull. 73:451–462.

GILLULY, J., A. C. WATERS, AND A. O. WOODFORD. 1974. Principles of geology, 3rd ed. W. H. Freeman and Co., San Francisco & London. 687 p.

GOLZ, D. J. 1976. Eocene Artiodactyla of southern California. Nat. Hist. Mus. Los Angeles Cty Sci. Bull. 26:1–85.

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

————. 1961. Early Pleistocene paleoclimatic record from Sonoran Desert, Arizona. Science 133:38–39.

GUZMAN, E., AND Z. DE CSERNA. 1963. Tectonic history of Mexico. Am. Assoc. Pet. Geol. Mem. 2:113–129.

HALFFTER, G. 1976. Distribución de los insectos en la zona de transición Mexicana. Relaciones con la entomofauna de Norteamerica. Folia Entomol. Mex. 35. 64 p.

HAMILTON, W. 1961. Origin of the Gulf of California. Geol. Soc. Am. Bull. 72:1307–1318.

HANNA, M. A. 1926. Geology of the La Jolla Quadrangle, California. Univ. Calif. Dep. Geol. Sci. Bull. 16:187–246.

HENDRICKSON, J. 1972. A taxonomic revision of the Fouquieriaceae. Aliso 7:439–537.

HILL, M., AND T. W. DIBBLEE, JR. 1953. San Andreas, Garlock, and Big Pine faults, California. Geol. Soc. Am. Bull. 64:443–458.

HOFFMAN, C. C. 1940. Catalogo systematico y zoogeografico de los Lepidopteros Mexicanos. Primera parte. Papilionoidea. An. Inst. Biol. Univ. Nac. Auton. Mex. 11:639–739.

HOWELL, D. G. 1975. Early and middle Eocene shoreline offset by the San Andreas fault, southern California. Calif. Div. Mines Geol. Spec. Rep. 118 :69–74.

————, C. J. STUART, J. P. PLATT, AND D. J. HILL. 1974. Possible strike-slip faulting in the southern California borderland. Geology (Boulder) 2:93–98.

HUFFMAN, O. F., D. L. TURNER, AND R. N. JACK. 1973. Offset of late Oligocene–early Miocene volcanic rocks along the San Andreas fault in central California. Stanford Univ. Publ. Geol. Sci. 13:368–373.

JAHNS, R. H. 1954. Geology of the Peninsular Range province, southern California and Baja California. Chap. 2, pp. 29–52 in Geology of southern California. Calif. Div. Mines Geol. Bull 170.

————. 1973. Tectonic evolution of the Transverse Ranges province as related to the San Andreas fault system. Stanford Univ. Publ. Geol. Sci. 13:149–170.

JOHNSON, A. W. 1968. The evolution of desert vegetation in western North America. Pages 101–140 in G. W. Brown, Jr., ed., Desert biology, vol. 1. Academic Press, New York & London. 635 p.

JOSEPH, S. E., AND DAVIS, T. E. 1977. 87Sr/86Sr correlation of rapakivi-textured porphyry to measure offset on the San

Andreas fault. Geol. Soc. Am., Abstract with Programs 9(4):443.

KARIG, D. E., AND W. JENSKY. 1972. The proto-Gulf of California. Earth and Planet. Sci. Lett. 17:169–174.

KEMP, E. M. 1978. Tertiary climatic evolution and vegetation history in the southeast Indian Ocean region. Palaeogeogr. Palaeoclimatol. Palaeoecol. 24:169–208.

KENNEDY, M. P., AND G. W. MOORE. 1971. Stratigraphic relations of Upper Cretaceous and Eocene formations, San Diego coastal area, California. Am. Assoc. Pet. Geol. Bull. 55:709–722.

KENNETT, J. P., R. E. HOUTZ, P. B. ANDREWS, A. R. EDWARDS, V. A. GOSTIN, M. HAJOS, M. HAMPTON, D. G. JENKINS, S. V. MARGOLIS, A. T. OVENSHINE, AND K. PERCH-NIELSEN. 1975. Cenozoic paleooceanography in the southwest Pacific Ocean, Antarctic glaciation, and the development of the circum-Antarctic Current. Initial Reports of the Deep Sea Drilling Project 29:1155–1169. U.S. Government Printing Office, Washington, D.C.

KILMER, F. H. 1963. Cretaceous and Cenozoic stratigraphy and paleontology, El Rosario area, Baja California. Univ. Calif., Berkeley. Ph.D. Thesis. 227 p.

KING, J. E., AND T. R. VAN DEVENDER. 1977. Pollen analysis of fossil packrat middens from the Sonoran Desert. Quat. Res. 8:191–204.

KING, P. B. 1977. The evolution of North America. Rev. ed. Princeton Univ. Press, Princeton. 197 p.

KING, R. E. 1939. Geological reconnaissance in northern Sierra Madre Occidental of Mexico. Geol. Soc. Am. Bull. 50:1625–1722.

KING, T. J., JR. 1976. Late Pleistocene–early Holocene history of coniferous woodlands in the Lucerne Valley region. Mohave Desert, California. Great Basin Nat. 36:227–238.

KNOWLTON, F. H. 1917. Fossil floras of the Vermejo and Raton formations of Colorado and New Mexico. U.S. Geol. Surv. Prof. Pap. 101:223–435.

————. 1924. Flora of the Animas Formation. U. S. Geol. Surv. Prof. Pap. 134:71–117.

KRYSTOFOVICH, A. N. 1954. The origin of xerophyte plant formations in the light of paleobotany. Pages 583–596 in Deserts of the USSR and their utilization. [Transl. from Russian.] Komarov Institute, Academy of Sci. USSR.

LANNER, R. M., AND T. R. VAN DEVENDER. 1974. Morphology of pinyon pine needles from fossil packrat middens in Arizona. For. Sci. 19:207–211.

LEOPOLD, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507–518.

LEOPOLD, E. B., AND H. D. MACGINITIE. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. Pages 147–200 in A. Graham, ed., Floristics and paleofloristics of Asia Eastern North America. Elsevier Publ. Co., Amsterdam.

LESKINEN, P. H. 1975. Occurrence of oaks in late Pleistocene vegetation in the Mohave Desert of Nevada. Madroño 23:234–235.

LOWENSTAM, H. A. 1963. Paleotemperatures of the Permian and Cretaceous periods. Pages 227–252 in A. E. M. Nairn, ed., Problems in palaeo-climatology. Interscience Publ., London, New York, & Sydney.

MACDOUGAL, D. T. 1908. Botanical features of North American deserts. Carnegie Inst. Wash. Publ. 99. 111 p.

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

————. 1953. Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash. Publ. 599. 188 p.

————. 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. Univ. Calif. Publ. Geol. Sci. 83. 140 p.

————. 1974. An early middle Eocene flora from the Yellowstone-Absaroka volcanic province, northwestern Wind River basin, Wyoming. Univ. Calif. Publ. Geol. Sci. 108:1–103.

McGinnies, W. G., B. J. Goldman, and P. Laylore. 1968. Deserts of the world: an appraisal of research into their physical and biological properties. Univ. Ariz. Press, Phoenix. 788 p.

Martin, P. J., and P. J. Mehringer. 1965. Pleistocene pollen analysis and biogeography of the Southwest. Pages 433–451 in H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States. Princeton Univ. Press, Princeton.

Matthews, III, V. 1976. Correlation of Pinnacles and Neenach volcanic formations and their bearing on the San Andreas fault problem. Am. Assoc. Pet. Geol. Bull. 60:2128–2141.

Mejorada, S. H. S., and E. L. Ramos. 1968. Carta geológica de la Republica México (scale 1:2,000,000).

Merriam, R. H. 1968. Geologic reconnaissance of northwest Sonora. Stanford Univ. Publ. Geol. Sci. 11:287 (abstr.).

Miller, W. E. 1977. Pleistocene terrestrial vertebrates from southern Baja California. Geol. Soc. Am., Abstract with Programs 9(4):468.

Mina, V. F. 1956. Bosqueto geológico de la parte sur de la península de Baja California. 20th Inter. Geol. Congr., Mexico, D. F. Excurs. A-7:1–79.

Minch, J. A. 1971. Early Tertiary paleogeography of the northern Penninsular Ranges, Baja California, Mexico. Geol. Soc. Am., Cordilleran Section, Abstract with Programs 3(2):164.

Moore, D. G. 1973. Plate-edge deformation and crustal growth, Gulf of California structural province. Geol. Soc. Am. Bull. 84:1883–1906.

Morafka, D. J. 1977. A biogeographical analysis of the Chihuahuan Desert through its herpetofauna. Biogeographica 9:1–313.

Morris, W. J. 1967. Baja California: Late Cretaceous dinosaurs. Science 155:1539–1541.

Mulroy, T. W., and P. W. Rundel. 1977. Annual plants: adaptation to desert environments. Bioscience 27:109–115.

Naveh, Z., and J. Dan. 1973. The human degradation of Mediterranean landscapes in Israel. Pages 373–390 in F. di Castri and H. A. Mooney, eds., Ecological Studies 7. Mediterranean type ecosystems. Springer-Verlag, New York, Heidelberg & Berlin.

Nicol, A. A. 1937. The natural vegetation of Arizona. Univ. Ariz. Coll. Agric. Agric. Exp. Stn. Tech. Bull. 68:181–222.

Otte, D. 1976. Species richness patterns of New World desert grasshoppers in relation to plant diversity. J. Biogeogr. 3:197–209.

Potbury, S. S. 1935. The La Porte flora of Plumas County, California. Carnegie Inst. Wash. Publ. 465:29–81.

Quintero, L. G. 1968. Tipos de vegetacion del Valle de Mezquital, Mexico. Ser. Paleoecologia, Dep. Prehist., Inst. Nac. Antropol. Hist. Mex. 2:1–53.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38:151–177.

————. 1969. A revision of the genus Camissona (Onagraceae). U.S. Natl. Herb. Contrib. 37(5):161–396.

————, and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61:539–673.

————, and ————. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72.

Read, C. B., and R. W. Brown. 1937. American Cretaceous ferns of the genus Tempskya. U.S. Geol. Surv. Prof. Pap. 186-F.

Reed, R. D., and J. S. Hollister. 1936. Structural evolution of southern California. Am. Assoc. Pet. Geol., Tulsa, Oklahoma. 175 p.

Reig, O. 1962. Las intergraciones cenogeneticas en el desarrolo de la fauna de vertebrados tetrapodos de America del Sur. Ameghiniana 2:131–140.

————. 1968. Pueplement en vertebres tetrapodes de l'Amerique du Sud. Pages 215–260 in Biologie de l'Amerique Australe 4.

Rul, J. Espinosa de G., and J. Rzedowski. 1968. Florula del Pleistoceno superior del Cerro de La Estralla próximo a Ixtapalapa, D. F., México. An Esc. Nac. Cienc. Biol. Mex. 16:9–39.

Rusnak, G. A., R. L. Fisher, and F. P. Shepard. 1953. Bathymetry and faults of Gulf of California. Am. Assoc. Pet. Geol. Mem. 3:59–75.

Rzedowski, J. 1960. Notas sobre la flora y la vegetación del Estado San Luis Potosi. VII. Vegetación en el Valle de San Luis Potosi. Acta Cient. Potosina 4:5–112.

————. 1962. Contribuciones a la fitogeografia floristica e histórica de México. I. Algunas consideraciones acerca del elemento endémico en la flora Mexicana. Bol. Soc. Bot. Mex. 27:52–65.

————. 1966. Vegetación del Estado de San Luis Potosi. Sobretrio de Acta Cient. Potosi 5:1–291. (Also listed as Contrib. del Instit. de Investig. de Zonas Desérticas. Univ. Autonoma de San Luis Potosi, No. 20.)

————. 1968. Las principales zonas aridas de México y su vegetación. Bios, Revista del Seminario de Estudios Biol. 1:4–24.

————. 1973. Geographical relationships of the flora of the Mexican dry regions. Pages 61–72 in A. Graham, ed., Vegetation and vegetational history of northern Latin America. Elsevier Sci. Publ. Co., Amsterdam, London, & New York.

————, and R. McVaugh. 1966. La vegetación de Nueva Galicia. Univ. Michigan Herb. Contrib. 9:1–123.

Sage, O., Jr. 1973. Paleocene geography of the Los Angeles region. Stanford Univ. Publ. Geol. Sci. 13:348–357.

Sanborn, E. I. 1935. The Comstock flora of west central Oregon. Carnegie Inst. Wash. Publ. 465:1–28.

Sarmiento, G. 1976. Evolution of arid vegetation in tropical America. Pages 65–100 in D. W. Goodall, ed., Evolution of desert biota. Univ. Texas Press, Austin & London. 250 p.

Schile, C. A. 1974. Sedimentology of the "El Gallo Formation" (Upper Cretaceous), El Rosario, Baja California, Mexico. San Diego State Univ., M.S. Thesis. 85 p.

Schuchert, C. 1935. Historical geology of the Antillean-Caribbean region. Wiley and Sons, Inc., New York. 811 p.

Shackelton, N. J., and J. P. Kennett. 1975. Late Cenozoic oxygen and carbon isotopic changes in D.S.D.P. sites 279, 277 and 281. Initial Reports of the Deep Sea Drilling Project 29:743–755. U.S. Government Printing Office, Washington, D.C.

SHREVE, F. 1911. The influence of low temperature on the distribution of giant cactus. Plant World 14:136–146.

———. 1936. The transition from desert to chaparral in Baja California. Madroño 3:257–264.

———. 1937. The vegetation of the Cape Region of Baja California. Madroño 4:105–113.

———. 1940. The edge of the desert. Assoc. Pacific Coast Geographers Yearbook 6:6–11.

———. 1942. The desert vegetation of North America. Bot. Rev. 8:195–246.

———. 1951. Vegetation of the Sonoran Desert. Carnegie Inst. Wash. Publ. 591:1–192.

———, AND I. L. WIGGINS. 1964. Flora and vegetation of the Sonoran Desert. 2 vols. Stanford Univ. Press, Stanford, California.

SIMPSON, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York. 434 p.

SMITH, A. G. 1976. Plate tectonics and orogeny: a review. Tectonophysics 33:215–285.

SMITH, G. E., JR. 1965. Flora, Tehuacan Valley. Fieldiana Bot. 31:105–143.

SOLBRIG, O. T. 1976. The origin and floristic affinities of the South American temperate desert and semidesert regions. Pages 7–50 in D. W. Goodall, ed., Evolution of desert biota. Univ. Texas Press, Austin & London. 250 p.

SPALDING, V. M. 1909. Distribution and movements of desert plants. Carnegie Inst. Wash. Publ. 113. 144 p.

STEBBINS, G. L. 1952. Aridity as a stimulus to plant evolution. Am. Nat. 86:33–44.

———. 1974. Flowering plants: evolution above the species level. Belknap Press of Harvard Univ. Press, Cambridge. 399 p.

———, AND J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35:1–35.

STOYANOW, A. 1949. Lower Cretaceous stratigraphy in southeastern Arizona. Geol. Soc. Am. Mem. 38:1–169.

STREET, F. A., AND A. T. GROVE. 1976. Environmental and climatic implications of Late Quaternary lake-level fluctuations in Africa. Nature 261:385–389.

SUTHERLAND, J. C. 1935. Geological investigation of the clays of Riverside and Orange counties, southern California. Calif. J. Mines Geol., State Mineralogists Rep. 31:51–87.

SYLVESTER, A. G., AND R. R. SMITH. 1976. Tectonic transgression and basement-controlled deformation in San Andreas fault zone, Salton Trough, California. Am. Assoc. Pet. Geol. Bull. 60:2081–2102.

TALIAFERRO, N. L. 1933. An occurrence of Upper Cretaceous sediments in northern Sonora, Mexico. J. Geol. 41:12–37.

TANKARD, A. J., AND J. ROGERS. 1978. Late cenozoic paleoenvironments on the west coast of Southern Africa. J. Biogeogr. 5:319–337.

TURNAGE, W. V., AND A. L. HINCKLEY. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. 8:529–550.

TWETO, O. 1975. Laramide (Late Cretaceous–early Tertiary) orogeny in the southern Rocky Mountains. Geol. Soc. Am. Mem. 144:1–44.

VAN DEVENDER, T. R. 1976. The biota of the hot deserts of North America during the last glaciation: the packrat midden record. Am. Quat. Assoc. Abstr. 4th Biennial Mtg., p. 62–67.

———, AND J. E. KING. 1971. Late Pleistocene vegetational records in western Arizona. Ariz. Acad. Sci. J. 6:240–244.

———, P. S. MARTIN, A. M. PHILLIPS, AND W. G. SPAULDING. 1976. Late Pleistocene biotic communities from the Guadalupe Mountains, Culberson County, Texas. Pages 107–113 in R. H. Wauer and D. H. Riskind, eds., Transactions of the symposium on the biological resources of the Chihuahuan Desert, United States and Mexico. Natl. Park Serv. Trans. Proc. 3.

VAN STEENIS, C. G. G. J. 1936. Cycles of drought and reafforestation in the U.S.A. seen in the light of a new botanical hypothesis on the origin of deserts in general. Jard. Bot. Buitenzorg Bull., Ser. 3, 14:50–55.

VESTER, H. 1940. Die Areale and Arealtypen der Angiospermen-Familien. Bot. Archiv. 41:203–275; 295–356; 520–577.

U.S. DEPT. COMMERCE. 1960. Climatography of the United States. California, Nevada, Utah, Arizona, New Mexico, Texas. U.S. Government Printing Office, Washington, D.C.

WEBBER, I. E. 1933. Woods from the Ricardo Pliocene of Last Chance Gulch, California. Carnegie Inst. Wash. Publ. 412:113–134.

WELLS, P. V. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153:960–975.

———. 1969. Prevues paléontologuques d'une vegetation tardi-Pleistocène (datée par le ¹⁴C) dans les regions aujohord'hui désertiques d'Amérique du Nord. Rev. Geogr. Phys. Géol. Dynam. 11:335–340.

———. 1976a. Post-Glacial origin of the Chihuahuan Desert less than 11,500 years ago. Pages 66–83 in R. H. Wauer and D. H. Riskind, eds., Transactions of the symposium on the biological resources of the Chihuahuan Desert, United States and Mexico. Natl. Park Serv. Trans. Proc. 3.

———. 1976b. Macrofossil analysis of wood rat (Neotoma) middens as a key to Quaternary vegetational history of arid America. J. Quat. Res. (NY) 6:223–248.

———. 1976c. A climax index for broadleaf forest: an n dimensional, ecomorphological model of succession. Proc. Central Hardwood Forest Conference. Southern Illinois Univ., Carbondale. Pp. 131–176.

———, AND R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science 155:1640–1647.

———, AND J. H. HUNZIKER. 1976. Origin of the Creosote bush (Larrea) deserts of southwestern North America. Ann. Missouri Bot. Gard. 63:843–861.

———, AND C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in Mohave Desert: a record of Juniper woodlands. Science 143:1171–1174.

WINT, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. Ecology 29:242–253.

———. 1949. Ecology of desert plants. II. Effect of rain and temperature on germination and growth. Ecology 30:1–13.

WIENS, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7:81–120.

WIGGINS, I. L. 1960. The origin and relationships of the land flora. Pages 148–165 in The biogeography of Baja California and adjacent seas. Syst. Zool. 9(3):148–165.

WOODBURNE, M. O. 1975. Cenozoic stratigraphy of the Transverse Ranges and adjacent areas, southern California. Geol. Soc. Am. Spec. Pap. 162:1–91.

WOODFORD, A. O., E. E. WELDAY, AND R. MERRIAM.

1968. Siliceous tuff clasts in the upper Paleogene of south-
ern California. Geol. Soc. Am. Bull. 79:1461–1468.

YANG, T. W., AND C. H. LOWE, JR. 1956. Correlation of
major vegetation climaxes with soil characteristics in the
Sonoran Desert. Science 123:542.

ZINDEREN BAKKER, SR., E. M. VAN. 1975. The origin and
paleoenvironment of the Namib desert biome. J. Biogeogr.
2:65–74.

———. 1976. The evolution of late Cenozoic paleoclimates
of southern Africa. Palaeoecol. Africa 9:160–202.