Late Pleistocene History of Coniferous Woodland in the Mohave Desert

New evidence records pluvial expansion of the pinyon-juniper zone at the close of the Wisconsin glacial.

Philip V. Wells and Rainer Berger

The Mohave Desert lies midway between the winter-cold Great Basin and the subtropical Sonoran deserts, in a sensitive zone where the expression of past climatic change happens to be well preserved in the paleobotanical record. The environmental history of now-arid regions of southwestern North America is of major interest to evolutionary biologists, and to anthropologists currently probing evidence of Early Man; it is also relevant to the regional problem of water resources. However, firm knowledge of the former distribution of vegetation in the arid Southwest has heretofore been limited by the paucity of macroscopic fossil material in Pleistocene and younger sediments.

Until the last few years the meager Quaternary data contrasted with the relative abundance of Tertiary leaf-impression floras (*1*). Pleistocene floras were virtually unknown in the Mohave Desert region, with the notable exception of coarsely comminuted plant remains present in unique coprolite deposits of the extinct ground sloth *Nothrotherium shastense*. Sloth dung has been found in Gypsum Cave, east of Las Vegas, Nevada, and in Rampart and Muav caves in the lower Grand Canyon, east of Lake Mead, Arizona. Much of the fecal plant material was difficult to identify, but a number of recognizable plant species from sloth dung, collected at the surface in Rampart and Muav caves (elevation, about 500 meters), were similar to desert species now growing in the vicinity of the caves, such as creosote bush (*Larrea*), saltbushes (*Atriplex*), cacti (*Opuntia*), and *Nolina* (*2*). The radiocarbon age of sloth dung from the surface of the Rampart Cave deposit has since been determined as 10,050 ± 350 years. Pollen analysis of the dung from the surface indicated a hot and dry climate like today's, but a sample from the 46-centimeter level (radiocarbon age, 12,050 ± 400 years) contained significantly more pine, juniper, and *Artemisia* pollens, suggesting cooler and somewhat moister conditions (*3*). Macrofossils preserved in sloth dung at Gypsum Cave (elevation, 610 meters) indicated that a decidedly different vegetation formerly grew there. The outstanding feature noted by Laudermilk and Munz (*4*) was the preeminent abundance of leaf fragments of the Joshua tree (*Yucca brevifolia*), which no longer grows in the vicinity of the cave but does occur at a somewhat higher elevation in Detrital Valley, some 70 kilometers to the southeast. Unfortunately, the material examined during this excellent early study has not yet been dated, but other dung samples collected in Gypsum Cave have yielded radiocarbon ages ranging from 8500 to 11,700 years (*5*). The sloth dung from Gypsum Cave dated by Libby (C-221; radiocarbon age, 10,455 ± 340 years) has been examined for fossil content by us. Macroscopic remains of woodland conifers are lacking, but leaf fibers and epidermis of the xerophytic family Agavaceae predominate, as in the undated samples of Laudermilk and Munz (*4*). A principal identifiable constituent in Libby's sample is *Agave utahensis* (mescal), a xerophyte with semisucculent fibrous leaves, which is now restricted to higher elevations of the desert.

Dr. Wells, associate professor of botany at the University of Kansas, Lawrence, is acting director, Botanical Garden, and visiting associate professor of botany, University of California, Berkeley. Dr. Berger heads the Isotope Laboratory, Institute of Geophysics and Planetary Physics, and is assistant professor of anthropology, University of California, Los Angeles.

Plant Fossils Preserved in Pleistocene Wood-Rat Middens

Widespread occurrence in the Southwest of extremely old wood-rat midden deposits, containing abundant well-preserved plant macrofossils, has recently come to light (*6, 7*). Radiocarbon ages of middens from the Mohave Desert of California and southern Nevada and from the Chihuahuan Desert of western Texas range from about 4000 years to more than 40,000 years (the limit of the method), therefore encompassing some of the latest glacial maxima of the Pleistocene and extending into postglacial time. Cricetine rodents of the genus *Neotoma,* known as wood rats, pack rats, or trade rats, range widely through the arid and semi-arid lands of North America. The outstanding generic behavioral trait, from which the common names derive, is the gathering of a great diversity of plant materials within a limited foraging range and the accumulation of these, together with excreta, in often-large middens, dens, or stick-houses containing small fibrous nests in which the rats reside (*8*). *Neotoma* middens are compacted refuse heaps of plant-food debris, fecal pellets, and dried urine, usually merging with the loosely assembled principal abodes, which are designated dens when situated in caves or rock shelters, or houses when constructed in relatively open situations. The bulk constituents of these fortifications are woody, often-armed, branches, spiny cactus joints or areoles, leaves, leafy twigs, fibrous bark, grass, fruits, and seeds. The herbivorous wood rats utilize an astonishing variety of plant species, and, although the dominant plants of the surrounding vegetation usually make up the bulk of their deposits, a rather detailed inventory of the local flora often accumulates. Relative to the small size of the rats, *Neotoma* deposits may attain a very large volume, often more than 1000 liters, and sometimes contain surprisingly large objects such as woody branches nearly 1 meter in length and the long bones of much larger animals. The hoarding instinct is frequently diverted to objects having no apparent food or constructional value, including human artifacts, for which the rat "trades" whatever it happens to have in its mouth at the time.

Pleistocene *Neotoma* deposits, which are strictly confined to caves and rock shelters, are chiefly of the compacted midden type but often contain den and

nest material. Lustrous dark-brown or black masses of dried wood-rat urine are conspicuous veneers on many old (and some modern) deposits, or on the adjacent walls of the rock shelter. This conspicuous material has attracted some attention and been called "amberat" (*9*). The ancient deposits usually occupy a relatively dry and secluded space on a ledge or in a crevice or cavity, where the mummified plant materials have often remained excellently preserved for tens of thousands of years. Because of the rapid accumulation of plant debris by wood rats, the time span represented by any one period of constructional activity appears to be small relative to the total age of the deposit. The largest ancient deposit yet uncovered, which completely filled a small tunnel of a cave in the Chihuahuan Desert with several thousand liters of debris from a pluvial pinyon-juniper-oak woodland, contained about 75 centimeters of *Neotoma* deposition, with radiocarbon ages of 11,560 ± 140 and 12,550 ± 130 years near the top and bottom, respectively (*10*). However, different deposits provide samples of vegetation often widely different in age, extending over much of the range of the radiocarbon method (*6, 7*).

A total of 17 ancient wood-rat middens has been uncovered in the Mohave Desert in the northeastern (Frenchman Flat), north-central (Funeral Mountains), southwestern (Lucerne Valley), and southeastern (Turtle Mountains) sectors (Table 1; Fig. 1). All but one of the dated deposits (Newberry Cave, 7400 years old contain records of former juniper or pinyon-juniper woodland vegetation, evidenced by consistent abundance of leafy twigs and seeds of *Juniperus osteosperma* (Utah juniper) and, locally, of leaves, cone scales, and seeds of *Pinus monophylla* (pinyon pine; Fig. 2), together with many shrubby species characteristic of woodland, semidesert, or even desert vegetation. The late-Pleistocene macrofossil record clearly indicates that at least the higher areas of the Mohave Desert, now occupied by a scanty desert or semidesert shrub vegetation, supported xerophilous woodlands of pygmy conifers during pluvial times. One of the remarkable features of the history revealed to date is the hitherto-unsuspected late persistence of woodland trees at elevations that are now treeless desert. Prevalence of woodland vegetation at moderately low elevations throughout the Mohave Desert as recently as about 9000 years ago is apparent, and woodland persisted locally at elevations now desert in southern Nevada about 8400 and 7800 years ago (Table 1). Although radiocarbon dates associated with major fluctuations of the largest pluvial bodies of water in the Great Basin indicate an episode of aridity about 11,000 years ago (*11*), a precipitation-temperature regime inadequate to maintain vast lakes in a relatively arid region may have been sufficient then to maintain established xerophilous woodlands at moderately low elevations. However, a

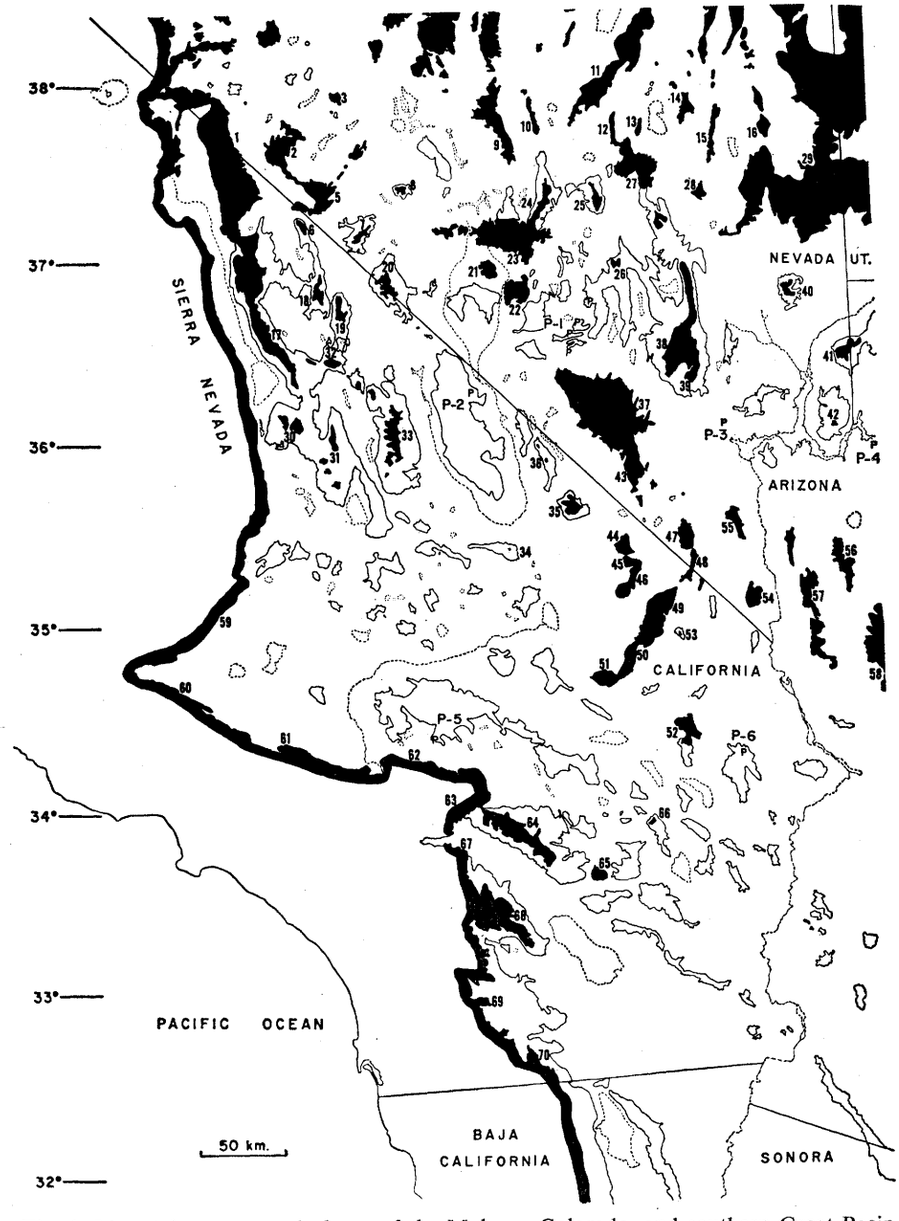

Fig. 1. Mountain ranges and playas of the Mohave, Colorado, and southern Great Basin deserts, showing in black the areas of higher elevation that now support woodland, forest, or other vegetation zones within the desert region to the east of the Sierra Nevada, Transverse, and Peninsular ranges. Mountain ranges are located by unbroken lines or by extent of existing woodland. Dashed lines show playas, which were often the sites of larger pluvial lakes, and principal streams. Symbols: *P*, Pleistocene wood-rat middens and coprolites of the ground sloth containing remains of former woodland or desert vegetation; *P-1*, Frenchman Flat series; *P-2*, Funeral Mountains; *P-3*, Gypsum Cave; *P-4*, Rampart and Muav caves; *P-5*, Negro Butte; *P-6*, Turtle Mountains. Other mountains cited are numbered as follows: *P-1* (northernmost of four), Aysees Peak; *P-1* (third from south), Ranger Mountains; *P-1* (second from south), Mercury Ridge; *P-1* (southernmost of four), Spotted Range; *P-5* (north side), Ord Mountains; *33*, Panamint Range; *34*, Avawatz Range; *35*, Kingston Range; *36*, Nopah Range; *37*, Spring Range; *44*, Clark Mountain; *52*, Old Woman Range; *61*, San Gabriel Range; *62*, San Bernadino Range; *66*, Coxcomb Mountains.

Table 1. Fossil plant debris in, radiocarbon ages of, and elevations of wood-rat middens in the Mohave Desert of Nevada and California. Abbreviations: S, Spotted Range; A, Aysees Peak; M, Mercury Ridge; F, Funeral Range; R, Ranger Mountains; N, Negro Butte; T, Turtle Mountains. Symbols (relative abundance): +, low; ++, intermediate; +++, high (principal constituent).

Species, structures	Midden site, elevation (meters), and radiocarbon age (years)											
	S-1, 1830, 8420 ±100	S-2, 1550, 9450 ±90	A, 1525, 9320 ±300	M-1, 1390, 9000 ±250	M-2, 1280, 7800 ±150	M-3, 1250, 12,700 ±200	F, 1280, 11,600 ±160	R-1, 1130, 16,800 ±300	R-2, 1100, 10,100 ±160	N, 1070, 9140 ±140	T-1, 850, 19,500 ±380	T-2, 730, 13,900 ±200
Trees and arborescent shrubs												
**Juniperus osteosperma*, leafy twigs, seeds, wood	+++	+++	+++	++	+++	+++	+++	+++	+++	+++	+++	+++
**Pinus monophylla*, leaves, cones, seeds		++									++	+++
**Acer glabrum*, twigs with buds, samaras		+										
**Cercocarpus ledifolius*, leaves			+				+					
Cowania mexicana, leaves		++	+	+++								
**Fraxinus anomala*, twigs with buds, samaras							+					
Shrubs												
Artemisia nova, leaves	+	+	+		+		+		+	+		+
Atriplex canescens, fruits	+		+									
A. confertifolia, leaves, twigs, fruits	++	++						+	+++			
**Ceanothus greggii*, leaves		+										
Cercocarpus intricatus, leaves, calyces, achenes	++	++	+				+					+
**Chamaebatiaria millefolia*, twigs with buds, follicles		+										
Chrysothamnus sp., involucres		+							+			
Coleogyne ramosissima, achenes		+	+		+							
Encelia virginensis, achenes							+					
Ephedra viridis, twigs, seeds	++	++	++	+	+		+	+		++		+
Eriogonum microthecum, leaves			+						+	+		
Fallugia paradoxa, leaves, achenes		+	+	+	+		+					
Fendlerella utahensis, capsule		+										
Haplopappus cuneatus, leaves										+		
Hecastocleis shockleyi, leaves		+										
**Lepidospartum latisquamum*, involucres			+						+			
Petrophytum caespitosum, leaves, inflorescences, follicles		++							+			
Prunus fasciculata, leaves, drupes	++	++	++		+		+++					
**Purshia glandulosa*, leaves, fruits										+++		
**Ribes montigenum*, twigs with trifid spines or prickles		++					+		+	+		
**Ribes* cf. *velutinum*, twigs with spines											+	+
Senecio douglasii, involucres	+	+	+	+		+			+			
Sphaeralcea ambigua, leaves, fruits		+	+									
Symphoricarpos longiflorus, leaves, twigs, flowers, seeds	+	++	+	+	+		++	+	+			
Tetradymia canescens, involucres		+										
Agavaceae, Cactaceae (*succulents*)												
Agave utahensis, leaves, seeds	+		+									
**Nolina parryi*, leaves							+					
Yucca brevifolia, leaves, seeds	+	+	+							+		
Opuntia erinacea areoles, fruits, seeds	++	+	+	+	+	+	+	+	++	+	++	+++
Grasses and forbs												
Oryzopsis hymenoides, fruits	+	++	+	+	+		+	+	+			+
Stipa arida, fruits		+										
S. speciosa, fruits	+	+	+	+					+			
Artemisia ludoviciana, leaves, twigs, flowers			++						+			
Amsinckia tessellata, nutlets		+										
Cryptantha confertiflora, nutlets	+											
C. flavoculata, nutlets		+										
Crypthantha sp., nutlets									+			
Penstemon palmeri, leaves, capsules		+	+	+		+						
Viguiera multiflora, achenes		++			+				+			

* Species no longer present in mountain range of midden site.

wood-rat midden having a radiocarbon age of 7400 ± 100 years, from Newberry Cave in the *Larrea* zone of the south-central Mohave Desert, shows an absence of woodland species and records the presence of creosote bush (*Larrea*), a warm-desert shrub, at about the onset of the period of maximum postglacial warmth (Hypsithermal time).

A Paleozonation of Vegetation

Evidence of an approximately synchronous zonal differentiation of vegetation in response to a gradient of elevation, on limestone in the northeastern Mohave Desert, has now become available. Briefly, the evidence consists of wood-rat middens at 1550, 1525, 1390, and 1100 meters with radiocarbon ages of about 9450, 9320, 9000, and 10,100 years, respectively, and ground-sloth coprolites at 610 and 530 meters with radiocarbon ages of 10,455 (also 8500 to 11,700) and 10,020 years, respectively. The deposit at 1550 meters in Spotted Range, near Frenchman Flat, Nevada, is the only midden in the sequence that contains remains of the more mesophytic pinyon-juniper woodland species; these include mountain maple (*Acer glabrum*), fernbush (*Chamaebatiaria millefolium*), and *Ceanothus greggii*, as well as *P. monophylla* and *J. osteosperma*. Closely associated with them in the midden are many relatively xerophytic, semidesert species (Table 1).

Similar combinations of species occur today at elevations of about 2200 meters in the highest mountains of the region. Despite the dramatic postglacial disappearance of the woodland conifers, the maple, and the more mesophytic shrubs, many of the species closely associated with them in the midden are now growing in the canyon at the midden site at this relatively high elevation (1550 meters), including small populations of characteristic woodland species such as a mountain mahogany (*Cercocarpus intricatus*), cliff rose (*Cowania mexicana*), Apache plume (*Fallugia paradoxa*), snowberry (*Symphoricarpos longiflorus*), and rock-spiraea (*Petrophytum caespitosum*). Also still present on open slopes, but in greater numbers, are the desert shrubs blackbrush (*Coleogyne*) and shadscale (*Atriplex confertifolia*).

The plant contents of the Aysees Peak deposit at 1525 meters also show a limited overlap of species with the existing canyon vegetation near the midden site, again including *Cercocarpus intricatus*. No trace of pinyon pine was detected in this midden, although leaves of the more mesophytic mountain mahogany, *C. ledifolius*, were present, and *J. osteosperma* was the principal constituent. On the other hand, the deposits at 1100 meters in Ranger Mountains contain a much more xerophytic assemblage paralleling the more arid aspect of existing vegetation: present in the middens are remains of juniper, the only characteristic woodland species, accompanied by great abundance of fruits, leaves, and spinose twigs of shadscale, a dominant shrub of existing cold-desert vegetation in the Great Basin. Absence of big sagebrush (*Artemisia tridentata*) and abundance of shadscale signify distinctly dry, though cool, conditions near the lower limit of woodland (*12*).

This roughly synchronous, late-Wisconsin zonation from relatively mesophytic pinyon-juniper-maple woodland to xerophytic juniper-shadscale semidesert occurred on limestone within an elevational span of 450 meters near Frenchman Flat basin, southern Nevada. A lower limit of elevation in this

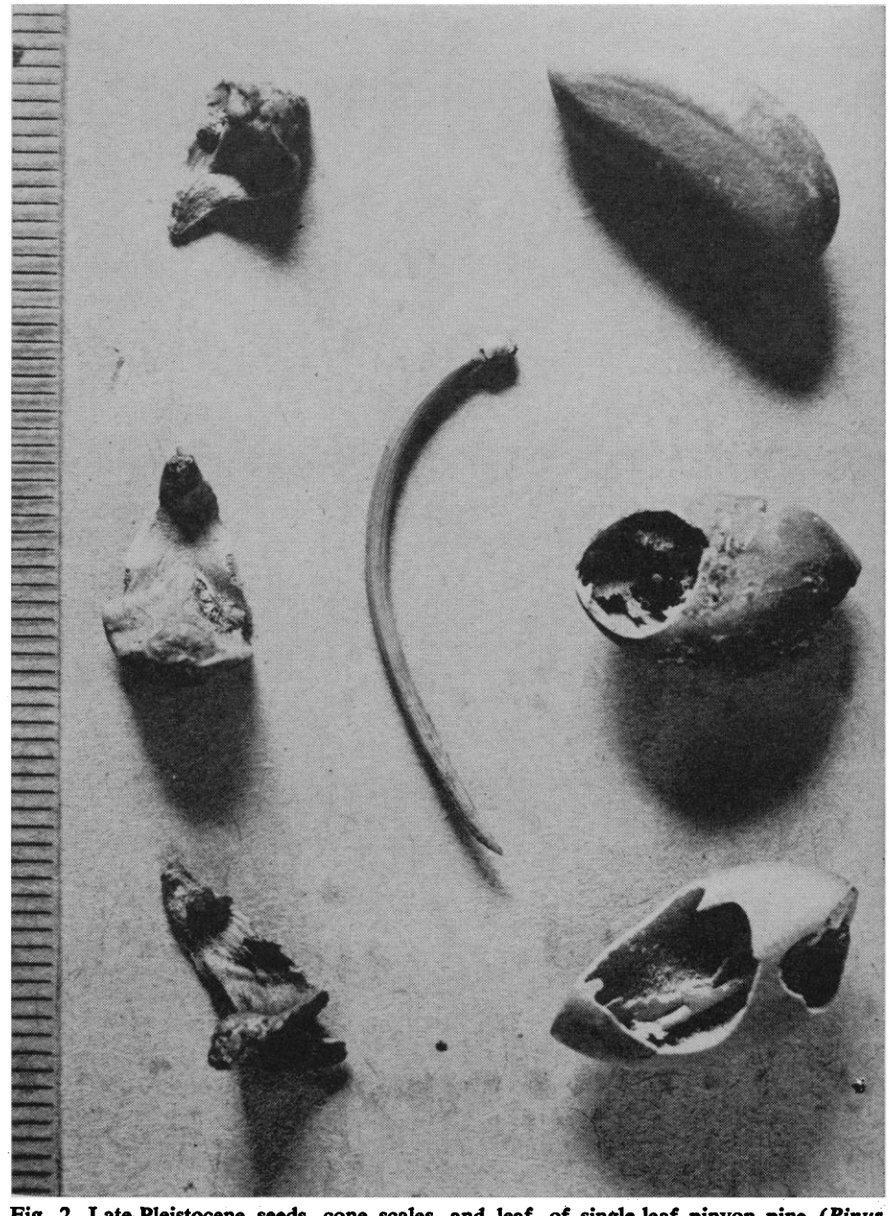

Fig. 2. Late Pleistocene seeds, cone scales, and leaf, of single-leaf pinyon pine (*Pinus monophylla* Torrey & Fremont), selected from a fossiliferous stratum having a radiocarbon age of 9450 ± 90 years in a wood-rat midden from the arid, unwooded Spotted Range of southern Nevada. Scale: millimeters.

drainage basin is, of course, imposed by the base level of 939 meters at Frenchman Playa, less than 200 meters below the lowest Pleistocene *Neotoma* deposit. However, a much lower range of elevation is available further south in Nevada and adjacent Arizona, where the dung deposits of the ground sloth in Gypsum and Rampart caves provide a record of former vegetation on limestone at 610 and 530 meters, respectively, during the time period spanned by some of the wood-rat middens in the Frenchman Flat area. The macrofossil record at Gypsum Cave was dominated by the Joshua tree and other Agavaceae in association with desert shrubs including creosote bush (*Larrea*), a xerophytic assemblage transitional to the warm-desert vegetation now occupying the site (*4*). This finding contrasts with the lowest midden record at Frenchman Flat, 500 meters higher and about 100 kilometers further north than Gypsum Cave; the evidence from the Flat suggests a transition from juniper woodland to shadscale, a cold-desert vegetation. At about the same time a decidedly warm-desert assemblage was accumulating in sloth dung at Rampart Cave, near the bottom of the lower Grand Canyon in Arizona, as indicated by fossils of creosote bush and other desert shrubs that still grow there.

Hence, in the northeastern Mohave Desert, during the time interval bracketed by radiocarbon ages of about 9000 and 10,000 years, juniper woodlands descended to an elevation of 1100 meters on limestone, some 600 meters below the present average lower limit of woodland on limestone, which lies at an elevation of about 1700 meters in the latitude of Frenchman Flat (*6*). But desert or semidesert shrubs coexisted with the woodland trees throughout much of the span of elevation corresponding to the pluvial lowering of the woodland zone, and the more mesophytic phase of pinyon-juniper woodland (with pinyon pine, mountain maple, and other species requiring more water) was apparently confined to montane habitats at elevations above 1500 meters. Joshua trees, accompanied by desert shrubs, prevailed down to about 600 meters at Gypsum Cave, but only the shrubs of the existing warm-desert vegetation occurred at 530 meters near Rampart Cave.

In the southwestern sector of the Mohave Desert, another wood-rat midden dating from this time period, with a radiocarbon age of about 9140 years, has been uncovered by E. Jaeger and one of us (P.V.W.) near Negro Butte, Lucerne Valley, California, at an elevation of 1070 meters and within the rain shadow of the lofty San Bernardino Mountains. Presence of abundant remains of *J. osteosperma* and absence of pinyon pine, despite a favorable granitic substratum, parallel the *Neotoma* record on limestone at about the same elevation near Frenchman Flat, some 250 kilometers to the northeast. An older *Neotoma* deposit (radiocarbon age, about 11,600 years) at an elevation of 1280 meters in the north-central part of the Mohave Desert, in the arid Funeral Range, California, provides additional macrofossil evidence (again great abundance of leafy twigs and seeds of *J. osteosperma*) of a widespread pluvial occurrence of xerophilous juniper woodlands, lacking pinyon pine, at moderately low elevations in certain sectors of the Mohave Desert. But the southeastern sector of the desert offers a seemingly anomalous record.

Two Pleistocene wood-rat middens have been found at 730 and 850 meters in the arid Turtle Mountains, California, with radiocarbon ages of about 13,900 and 19,500 years, respectively. Both contain abundant macrofossils of single-leaf pinyon pine (*P. monophylla*), as well as the formerly ubiquitous *J. osteosperma*. Woodland conifers, or even relict individuals of woodland shrubs, are now lacking in the low, arid Turtle Mountains (maximum elevation, 1289 meters). The apparent anomaly lies in the presence of pinyon pine at this extremely low elevation (730 meters) and latitude (34°24′N) during a time span when more-xerophytic juniper woodlands, lacking pinyon pine, prevailed at a higher elevation (about 1100 meters) and latitude (36°40′N) near Frenchman Flat, as evidenced by *Neotoma* deposits with radiocarbon ages ranging from 12,700 to 17,400 years (*6*). However, the paradox appears to be resolved by the astonishing fact that lower limits of elevation for existing pinyon-juniper woodlands are, in general, much lower in the southern than in the northern sector of the Mohave Desert and Great Basin. Woodlands of *P. monophylla* and *J. californica* (a close relative of *J. osteosperma*) thrive today at an elevation of 1200 meters in Old Woman Range (maximum elevation, 1620 meters), about 30 kilometers west of the Pleistocene *Neotoma* midden sites in Turtle Mountains. The lower limits of pinyon-juniper woodland in Old Woman Range are in fact more than 500 meters *lower* than the average lower limits of woodland on the much higher (to 3631 meters) and more massive mountain ranges in the region of Frenchman Flat, 200 kilometers to the north.

Biogeographic Anomalies

Numerous anomalies, both present and past, concerning the altitudinal and latitudinal distribution of pinyon-juniper woodland in the Mohave Desert and Great Basin region have recently come to light, and their interpretation is of critical importance to an understanding of biogeography in the Southwest (*13*). The "Merriam effect," or inverse relation between mountain mass and elevations of vegetation zones (*14*), seems to be lacking or outweighed by other factors affecting the distribution of vegetation zones in this arid region. For example, the average lower limits of woodland, on mountains greatly differing in massiveness and maximum elevation, are approximately equal in the region of Frenchman Flat in southern Nevada. It is true that in certain deep canyons of the most massive range, namely Pine and Excelsior canyons in Spring Range, pinyon pine descends more than 400 meters below its average lower limits and ponderosa pine occurs fully 1000 meters below its usual lowest level (*15*); but these exceptional distributions clearly correlate with the extraordinary edaphic and microclimatic effects of deep canyons cut in porous sandstone and should not be misconstrued as examples of the "Merriam effect." On the other hand, there does appear to be a general relation between the average minimum elevation of existing woodland and latitude; data for 80 wooded mountain ranges in the Mohave and Colorado deserts and southern Great Basin are plotted in Fig. 3; the usual inverse relation between latitude and the elevation of montane vegetation zones seems to be reversed. A similar downward shift of vegetation zones with decreasing latitude occurs in eastern Arizona and Mexico (*16*), where decreasing distance from the source of moist Gulf air masses, yielding summer rain, may explain the anomaly. The Mohave Desert as a whole receives very little summer rain, although the incidence is significantly greater in the eastern sector (*17*).

However, numerous details of distri-

bution of pinyon-juniper woodland in the Mohave Desert area suggest the existence of major local, as well as regional, orographic effects. For example, in the Avawatz-Granite Range, north of Barstow, woodland is absent from Granite Mountains (maximum elevation, 1680 meters) but present on the summit of Avawatz Mountain at 1890 meters. Nevertheless, Ord Mountains (maximum elevation, 1920 meters), situated south of Barstow, lack woodland entirely, possibly because they lie closer to the maximum intensity of rain shadow cast by the massive Transverse Ranges, particularly the San Bernardino–San Gabriel axis (maximum elevation, 3380 meters). Also, Funeral Range, with a maximum elevation of 2040 meters, now lacks woodland, whereas the less massive Nopah Range has small stands of woodland on the summit at 1940 meters; the high points of both ranges are carbonate rocks of Paleozoic age. Funeral Range lies just to the leeward of the lofty Panamint Range (maximum elevation, 3370 meters) and therefore may be in a more intense rain shadow than Nopah Range, which is 50 kilometers further to the southeast. Similarly, but on a grander scale, the vast rain shadow of the very massive Sierra Nevada (maximum elevation, 4410 meters), coupled with the great distance from air masses bearing summer rain, may cause the general high elevation of the woodland-vegetation zone observed in the northern Mohave Desert and Great Basin (Fig. 3).

Hence the Pleistocene wood-rat middens, at 730 and 850 meters on northward-facing canyon walls cut in porous tuffaceous agglomerate in the low, treeless Turtle Mountains (maximum elevation, 1289 meters), record a relatively large downward shift of the pinyon-juniper woodland zone in the southeastern sector of the Mohave Desert, paralleling the remarkably low minimum elevation of the existing woodland zone (about 1200 meters) on granite in the adjacent Old Woman Range (maximum elevation, 1620 meters) and in the less massive Coxcomb Mountains (maximum elevation, 1340 meters). However, the *Neotoma* deposits in Turtle Mountains, which record a pluvial lowering of the pinyon-juniper zone by 350 to 470 meters, do not necessarily establish a lower limit of woodland in this sector at that time (about 14,000 and 19,500 years ago). The abundance of fossil remains of *P. monophylla* in the middens leads to the inference that more-xerophilous juniper woodlands, lacking pinyon pine, may have extended to still-lower elevations, as was true of the pluvial zonation recorded in the *Neotoma* middens of the northern Mohave Desert.

Magnitude of Pluvial Migration of Vegetation

In the present state of knowledge, it would be premature to draw a map purporting to show the maximum pluvial extent of pinyon-juniper woodland vegetation in the Mohave Desert area. It is sufficient to note that, when relatively low arid ranges, such as Turtle Mountains, formerly supported pinyon-juniper woodland, most of the other low arid mountains or drainage divides, not situated in especially intense rain shadows cast by the more massive mountain ranges, were probably also wooded. The fossil evidence speaks for a former continuity of woodland, at least along the higher divides connecting most of the ranges, which implies more or less wooded corridors for the extensive pluvial migrations suggested by the disjunct distributions of existing woodland species (Fig. 1). But there is no macrofossil evidence of pluvial continuity for the more mesophytic coniferous-forest zone of ponderosa pine or white fir now occupying islands of relatively mesic environment on the highest mountains of the region, as in Spring, Sheep, Clark, and Kingston ranges (*18*). Indeed, general discontinuity of the highest zones is suggested by the uneven stocking of the isolated lofty mountains with mesophytic or boreal species of high montane habitats, and by the trend toward endemism (*19*). There is a parallel in

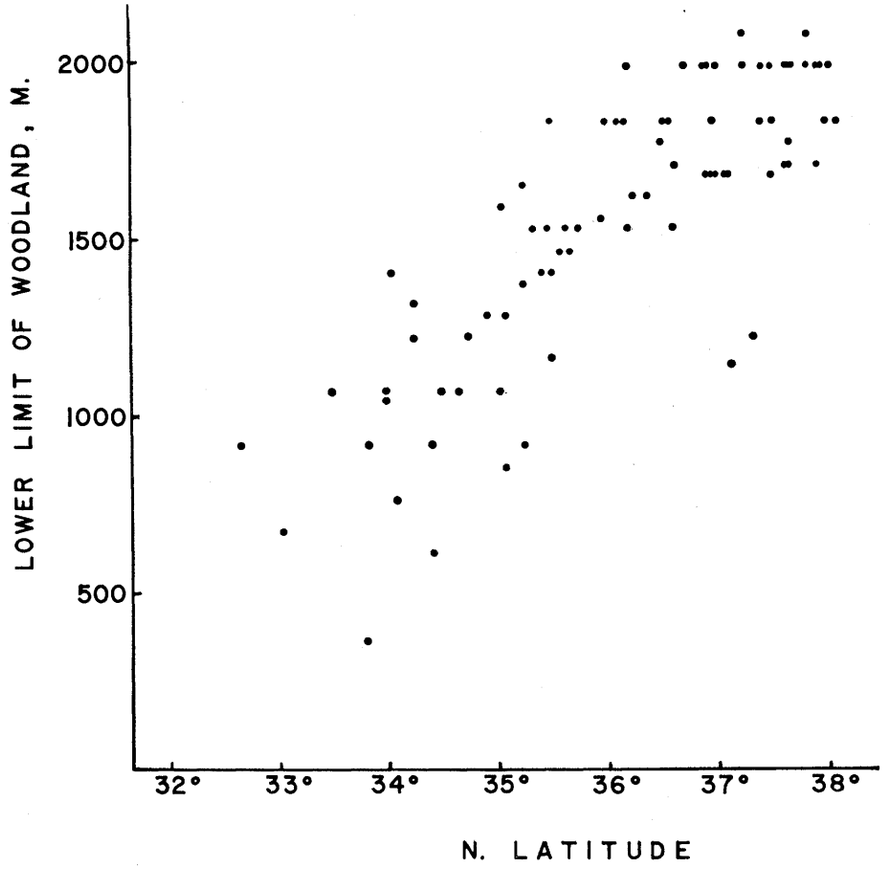

Fig. 3. Lower limits of elevation (in meters) for the existing woodland-vegetation zone in relation to latitude of 80 wooded mountain ranges in the Mohave, Colorado, and southern Great Basin deserts. Prevailing elevations for lower limits of woodland were estimated on open slopes; exceptional downward extensions in canyons and on steep northward-facing slopes were not used. Some of the large variance probably reflects the east-west gradient of decreasing summer precipitation, and local effects of substratum and physiography—especially distance from orographic barriers producing rain shadows. The anomalous latitudinal trend may be related to the declining trend in average elevation, massiveness, or continuity of the principal orographic barriers from north to south along the western margin of the deserts.

the uneven pattern of distribution of montane species on the high peaks of the Chihuahuan Desert region, where a lack of pluvial continuity of range for mesophytic montane species has also been inferred from fossil evidence of xerophilous woodland trees and desert shrubs in the intervening lowlands even during full-glacial Wisconsin time (*20*).

Summary

Seventeen ancient wood-rat middens, ranging in radiocarbon age from 7400 to 19,500 years and to older than 40,000 years, have been uncovered in the northeastern, north-central, southeastern, and southwestern sectors of the Mohave Desert. Excellent preservation of macroscopic plant materials (including stems, buds, leaves, fruits, and seeds) enables identification of many plant species growing within the limited foraging range of the sedentary wood rat.

An approximately synchronous zonal differentiation of vegetation in response to a gradient of elevation on limestone in the northeastern Mohave Desert is apparent from the macrofossil evidence, preserved in wood-rat middens and ground-sloth coprolites, covering a time span bracketed by radiocarbon ages of about 9000 and 10,000 years. Xerophilous juniper woodlands descended to an elevation of 1100 meters, some 600 meters below the present lower limit of woodland (1700 meters) in the latitude of Frenchman Flat. But desert or semidesert shrubs coexisted with the woodland trees throughout much of the span of elevation corresponding to the pluvial lowering of the woodland zone, and the more mesophytic phase of pinyon-juniper woodland was evidently confined to montane habitats at elevations above 1500 meters. Joshua trees, accompanied by desert shrubs, prevailed down to about 600 meters at Gypsum Cave, Nevada, but only the shrubs of the existing warm-desert vegetation occurred at 530 meters near Rampart Cave, Arizona.

Pleistocene middens from the southeastern Mohave Desert record a relatively large downward shift of the pinyon-juniper woodland zone, paralleling the remarkably low minimum elevation of the existing woodland zone in that area. The macrofossil evidence speaks for former continuity of the many disjunct stands of woodland vegetation in the Mohave Desert region, at least along the higher divides connecting most of the ranges. However, there is no macrofossil evidence of pluvial continuity of range for the more mesophytic, montane, coniferous-forest zone of ponderosa pine or white fir now occupying islands of relatively mesic environment on the highest mountains of the region. On the contrary, the uneven stocking of the lofty mountains of the Mohave Desert with mesophytic or boreal species and the trend toward endemism suggest a long history of isolation.

Addendum: We have recently uncovered and dated three more late-Pleistocene *Neotoma* deposits, containing remains of woodland conifers, at elevations now desert in the northeastern Mohave Desert. A midden from Pintwater Cave in southern Nevada, at an elevation of 1280 meters on limestone, contains a relatively xerophytic semidesert assemblage, including remains of shadscale (*Atriplex confertifolia*) and rabbit brush (*Chrysothamnus*) but only a few leafy twigs of *J. osteosperma,* associated with a radiocarbon age of 16,400 ± 250 years (UCLA-1099). Also, pollen analysis of *Neotoma* feces of about the same age suggested semidesert vegetation dominated by *Atriplex,* with a relative percentage of *Juniperus* pollen of only 2.6 in a sample of 1500 grains (*21*). Ecologically the Pintwater Cave site is relatively xeric, since it is high on a steep, westward-facing, limestone scarp, with strong afternoon insolation; it now supports a very scanty warm-desert vegetation, but sparse woodland persists on westward-facing limestone scarps only 500 meters above the cave in the northern part of Pintwater Range (Fig. 1, No. *26*).

Two ancient wood-rat middens at extremely low elevations (530 and 550 meters) in the low, arid North Muddy Mountains of southeastern Nevada, about 50 kilometers northeast of Gypsum Cave (Fig. 1, *P-3*), contain abundant remains of *J. osteosperma* and the semidesert shrubs *Purshia glandulosa* and *Ephedra viridis,* but there are no macroscopic remains of pinyon pine or other relatively less xerophytic woodland species in the fossil material examined. The radiocarbon ages of the 12,900 ± 180 years (UCLA-1218 and 1219). It is important to note that these sites are located in a narrow canyon cut in massive Mesozoic sandstone. On the same type of sandstone raised to much two deposits are 17,750 ± 200 and higher elevations in Spring Range, southern Nevada, existing woodland descends to an elevation of 1180 meters, which is about 500 meters below the average lower limit of woodland on limestone in the same range. Woodland no longer exists in North Muddy Mountains, but the next-lower vegetation zone, dominated by *Coleogyne* (blackbrush), is present there above 1000 meters and permits correlation with the zonation in Spring Range. The lower limit of the *Coleogyne* zone on sandstone is at an elevation of about 1000 meters in both areas. Hence the *Neotoma* fossil record on sandstone in North Muddy Mountains documents a full-pluvial downward shift of xerophilous juniper woodland as much as 650 meters below the existing lower limit of woodland on sandstone, which parallels the 600-meter downward shift of juniper-dominated woodland on limestone that was previously established in the Frenchman Flat area (*6*).

References and Notes

1. D. I. Axelrod, *Carnegie Inst. Wash. Publ. 590* (1950), p. 215; *Botan. Rev.* **24**, 431 (1958).
2. J. D. Laudermilk and P. A. Munz, *Carnegie Inst. Wash. Publ. 487* (1938), p. 273.
3. P. S. Martin, B. Sabels, D. Shutler, *Amer. J. Sci.* **259**, 102 (1961); E. A. Olsen and W. S. Broecker, *Radiocarbon* **3**, 141 (1961). The latter publication cites radiocarbon ages of 9900 ± 400 and 11,900 ± 500 years, respectively.
4. J. D. Laudermilk and P. A. Munz, *Carnegie Inst. Wash. Publ. 453* (1934), p. 29. Leaf fragments of *Yucca* constituted fully 80 percent (by volume) of the sloth dung from Gypsum Cave; principal species was *Y. brevifolia* Engelm. (Joshua tree), but *Y. baccata* Torr. and *Y. mohavensis* (*Y. schidigera* Roezl) were also identified. Presence of remains of the desert shrubs *Larrea divaricata* Cav., *Atriplex confertifolia* (T. & F.) Wats., *Ephedra nevadensis* Wats., and *Petalonyx* indicates a decidedly arid environment. Aside from the Joshua tree, only the remains of *Y. baccata, Agave utahensis* Engelm., and *Chrysothamnus* provided any definite evidence of a former lowering of vegetation zones near Gypsum Cave, although a few fiber cells or tracheids of a gymnosperm (genus undetermined) were found in the dung. The great abundance of *Y. brevifolia* and presence of *L. divaricata* imply a type of desert vegetation that occurs today at an elevation of about 800 meters on the slopes of Detrital Valley, Arizona, about 70 kilometers to the southeast of Gypsum Cave (elevation, 610 meters), proving a downward displacement of the existing Joshua-tree vegetation zone of less than 200 meters. Laudermilk and Munz compared their fossil assemblage at Gypsum Cave with the Joshua-tree zone at an elevation of 1500 meters at Clark Mountain, Nevada, about 70 kilometers to the southwest. Later study of the dung deposits in Rampart Cave, Arizona, uncovered three twigs and a seed of *Juniperus* 92 centimeters below the surface and 46 centimeters below a sample dated by radiocarbon as 12,050 ± 400 years old. *Juniperus* now grows about 400 meters above the cave (*3*).
5. J. R. Arnold and W. F. Libby, *Science* **113**, 11 (1951); C. L. Hubbs, G. S. Bien, H. E. Suess, *Radiocarbon* **4**, 204 (1962); **5**, 254 (1963).
6. P. V. Wells and C. D. Jorgensen, *Science* **143**, 1171 (1964).
7. P. V. Wells, *Bull. Ecol. Soc. Amer.* **45**, 76 (1964); **46**, 197 (1965); G. J. Fergusson and

W. F. Libby, *Radiocarbon* **4**, 109 (1962); **5**, 1 (1963); **6**, 318 (1964); R. Berger, G. J. Fergusson, W. F. Libby, *ibid.* **7**, 336 (1965); R. Berger and W. F. Libby, *ibid.* **8**, 467 (1966).
8. R. B. Finley, *Univ. Kans. Publ. Museum Nat. Hist.* **10**, 213 (1958); J. M. Lindsdale and L. P. Tevis, Jr., *The Dusky-footed Wood Rat* (Univ. of California Press, Berkeley, 1951), p. 57.
9. P. C. Orr, *Observations* (Western Speleol. Inst., 1957), No. 2, p. 1; R. Berger, W. S. Ting, W. F. Libby, in *Proc. Intern. Conf. Radiocarbon Tritium Dating 6th Pullman, Wash.* (1965), p. 731. This peculiar mineral-like substance was earlier designated "johnsonite" (E. R. Hall, personal communication).
10. P. V. Wells, *Science* **153**, 970 (1966). There appears to be at least one hiatus in this sequence.
11. W. S. Broecker, M. Ewing, B. C. Heezen, *Amer. J. Sci.* **258**, 429 (1960); W. S. Broecker and P. C. Orr, *Geol. Soc. Amer. Bull.* **69**, 1009 (1958). Firm evidence for a subsequent high stand of the pluvial lakes (Lahontan and Bonneville), beginning about 9500 years ago [W. S. Broecker and A. Kaufman, *Geol. Soc. Amer. Bull.* **76**, 537 (1965)], is in agreement with the wood-rat midden record of woodland vegetation (at elevations now desert) at that time.
12. The combination of open stands of juniper (*J. osteosperma*) with a low shrub synusia of shadscale (*Atriplex confertifolia*) and dwarf sagebrush (*Artemisia nova*) occurs today in a transitional zone between the more mesophytic pinyon-juniper woodland–sagebrush (*A. tridentata*) vegetation and the cold desert of treeless shadscale scrub in particularly arid sectors of the Great Basin, as in House Range, Utah.
13. An apparent anomaly, which seems to be particularly significant, is the contrast between interpretations of evidence derived from pollen analysis of sediments, in the light of macrofossil evidence of former vegetation of comparable age from the same region. High relative percentages of pine pollen (species unidentified), recorded in pluvial lake deposits at Tule Springs at an elevation of 700 meters in southern Nevada, are interpreted as implying a downward displacement of vegetation zones by as much as 1220 meters [P. J. Mehringer, *J. Ariz. Acad. Sci.* **3**, 186 (1965)]. On the other hand, the Pleistocene wood rat–midden evidence supports a downward displacement of about 600 meters in the Frenchman Flat area, which is 70 kilometers north of the Tule Springs site. However, the lower *Neotoma* deposits (at an elevation of about 1100 meters) contain abundant remains of juniper (*J. osteosperma*) and several species of desert shrubs, but no pine. The relative downward displacement recorded in Pleistocene wood-rat middens in Turtle Mountains is still less at 470 meters, but this is probably not a maximum figure for that area. As to time of occurrence, the Tule Springs date of 22,600 ± 550 years (UCLA-536, based on carbonate of mollusk shells) is on the further side of the classical Wisconsin glacial maximum (18,000 to 20,000 years ago) from a Frenchman Flat organic-carbon date of 17,450 ± 300 years (UCLA-555), but the Turtle Mountains date of 19,500 ± 380 years (UCLA-1063) is clearly "full glacial." An alternative interpretation of the pollen samples at Tule Springs is that they integrated the pollen rain from a large area of watershed around the site of deposition. Because of the basin-and-range topography, steep gradients of elevation place relatively arid basin floors well within the range of dissemination of pollen of anemophilous conifers of the montane forest and woodland zones. The pollens of *Pinus* and *Abies* are equipped with bladder-like wings which increase the buoyancy in air or water, and *Pinus* produces notoriously large quantities of pollen. If the absolute quantity of pollen produced by vegetation immediately surrounding the depositional site were moderately low—as would be true, for example, of vegetation dominated by entomophilous species—high relative percentages of conifer pollen could have accumulated in the pluvial sediments, with no conifers at the Tule Springs site. The macrofossil evidence reported by us does support at least 600 meters of pluvial downward displacement of the pinyon-juniper woodland zone, and also records a great increase in the area occupied by conifers. Hence, the Tule Springs site, which now lies about 1000 meters below the average lower limits of existing woodland, was probably less than half that vertical distance below a source of conifer pollen during the Wisconsin pluvial. By the same reasoning, the lateral distance to the nearest woodland in Las Vegas Range would have been less than 8 kilometers at that time, compared to about 24 kilometers at present; and, of course, the total expanse of coniferous vegetation contributing pollen to the basin was greater during pluvial time. Now, it happens that the exceedingly dominant shrub of the lower woodland and upper desert zones, *Coleogyne ramosissima* (blackbrush), which extends in nearly pure stands about 400 meters below the existing lower limit of woodland, has entomophilous pollination. This xerophytic shrub appears in the fossil record in three late-Wisconsin *Neotoma* deposits in the Frenchman Flat area, and should have extended then at least 600 meters below its present lower limits at about 1300 meters in this latitude; this fact would place the Tule Springs site (at 703 meters) within the zone of dominance by *Coleogyne* during pluvial time. The scanty cohesive pollen of the entomophilous *Coleogyne*, if it entered the pollen record in significant amounts, would be drastically diluted by the abundant pollen rain from coniferous vegetation upslope from Tule Springs. Therefore the pollen preserved in pluvial sediments at the Tule Springs site may provide an integrated record of total pollen production over a large area of watershed, but a record weighted for anemophilous conifers. The likelihood that a weighted integration of pollen from two or more vegetation zones has entered the sedimentary record suggests that calculation of absolute downward displacement of vegetation zones on the basis of *relative* percentages of pollen recorded in pluvial sediments of desert basins is a complex and apparently unsolved problem. Nevertheless, pollen analysis of sediments in desert basins has the advantage of providing a relatively continuous stratigraphic record, which may indeed sensitively portray in a generalized way the expansions and contractions of montane coniferous vegetation in response to changing climate over a wide but undetermined range of elevation.
14. C. H. Lowe, *J. Ariz. Acad. Sci.* **2**, 40 (1961); P. S. Martin, *The Last 10,000 Years* (Univ. of Arizona Press, Tucson, 1963), p. 9. However, F. Shreve [*Ecology* **3**, 271 (1922)] pointed out that in southeastern Arizona the lower limit of the ponderosa-pine zone is fully 550 meters higher on the more massive Pinaleno Range (maximum elevation, 3270 meters) than on the smaller Santa Catalina Range (maximum elevation, 2800 meters), which is similar in bedrock and topography but lower in base level.
15. I. W. Clokey, *Flora of the Charleston Mountains, Clark County, Nevada* (Univ. of California Press, Berkeley, 1951), p. 28.
16. J. T. Rothrock, *Report upon United States Geographical Surveys West of the One Hundredth Meridian* (Washington, D.C., 1878), vol. 6; P. S. Martin, *The Last 10,000 Years* (Univ. of Arizona Press, Tucson, 1963) p. 8.
17. J. Leighly, in *California and the Southwest*, C. M. Zierer, Ed. (Wiley, New York, 1956).
18. The coniferous-forest zone is defined by the dominance of yellow pine (*Pinus ponderosa* Laws.) or, in some instances, white fir (*Abies concolor* Lindl.); at higher elevations on lofty mountains, by dominance of bristle-cone pine (*P. aristata* Engelm.) and limber pine (*P. flexilis* James).
19. I. W. Clokey (*15*, p. 13) reports 31 endemic taxa of vascular plants from the isolated Spring Range, Nevada, which rises nearly 3000 meters above the floor of adjacent desert basins. An example of apparently uneven stocking is the distribution of *A. concolor* (white fir), *P. ponderosa*, *Acer glabrum* (mountain maple), and *Betula occidentalis* (western birch) among the high mountains of the Mohave Desert region. All four are present in Spring Range (maximum elevation, 3631 meters), but only the relatively mesophytic white fir and maple grow in the lower, more arid Clark and Kingston ranges (maximum elevations, 2430 and 2230 meters, respectively), where the hardy *P. ponderosa* is anomalously lacking. However, neither white fir nor ponderosa pine occur in the high Panamint Range (maximum elevation, 3370 meters), although *A. glabrum*, *B. occidentalis*, and other mesophytes of the ponderosa pine–white fir zone are present; and there is even a limited development in the Panamints of the next-higher vegetation zone of bristle-cone and limber pines (as in the more fully stocked Spring Range), a zone that is now totally lacking in the smaller Clark and Kingston ranges.
20. P. V. Wells, *Science* **153**, 970 (1966).
21. R. Berger, W. S. Ting, W. F. Libby, in *Proc. Intern. Conf. Radiocarbon Tritium Dating 6th Pullman, Wash.* (1965).
22. Supported by NSF grants GB-5002 and GP-1893. We thank D. I. Axelrod and W. F. Libby of the University of California, Los Angeles, and P. S. Martin and P. J. Mehringer of the University of Arizona for criticism.