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Number 2

15 September 1990

Holocene Vegetation of the Hornaday Mountains of Northwestern Sonora, Mexico

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ABSTRACT.—The 94 taxa of plants identified from 10 packrat (*Neotoma* sp.) middens from 240 to 260 m elevation in the granitic Hornaday Mountains provide an excellent history of vegetation and climate for the last 10,000 yr B.P. in the Pinacate Region of northwestern Sonora, Mexico. Rocky slopes in this arid area (ca. 120 mm/yr precipitation) in the Lower Colorado River subdivision of the Sonoran Desert have supported desertscrub communities dominated by *Encelia farinosa* (brittlebush), *Larrea divaricata* (creosotebush), and *Carnegiea gigantea* (saguaro) throughout the Holocene. Community composition changed continuously on both long (10,000 yrs) and shorter time scales.

Ephedra nevadensis (Mormon tea), codominant with *Encelia farinosa*, *Larrea divaricata*, and *Carnegiea gigantea* in early Holocene (8910 to 10,000 yr B.P.) samples, and rare *Juniperus* cf. *californica* (California juniper) imply a continuation of the cool summers and primarily winter rainfall of the late Wisconsin glacial. Middle Holocene (4430 to 8660 yr B.P.) samples contained trees and shrubs such as *Acacia greggii* (catclaw acacia), *Cercidium floridum* (blue paloverde), and *Prosopis velutina* (velvet mesquite) that are now restricted to relatively mesic washes, implying summer rainfall greater and freezes more frequent than today. Late Holocene (1720 to 2320 yr B.P.) samples dominated by *Encelia farinosa* and *Olneya tesota* (ironwood) with *C. microphyllum* (foothills paloverde) are similar to present Sonoran Desert vegetation and imply a relatively modern biseasonal rainfall regime with the warmest winters of the Holocene. In the last 1700 years, *O. tesota* disappeared as *Ambrosia deltoidea* (triangleleaf bursage), *Bursera microphylla* (elephant tree), *Jatropha cuneata* (cuneate limberbush), and *L. divaricata* appeared or increased at the sites. The modern vegetation of the Hornaday Mountains is as sparse and the climate is as hot and dry as at any time in the last 10,000 years. The variability in community composition through the Holocene was similar in magnitude to the modern variability among different midden sites and appears to reflect the highly variable climate. Responses of individual species to climatic fluctuations on scales from years to millennia may prevent desertscrub communities from ever reaching equilibrium.

Disjunct populations of *Artemisia ludoviciana* (white sage), *Berberis haematocarpa* (barberry), *Opuntia chlorotica* (silver dollar cactus), *Rhus aromatica* (skunk bush), *Salvia mohavensis* (Mohave sage), and *Stipa speciosa* (desert needlegrass) above 650 to 800 m elevation on the north side of Pinacate Peak are relicts from ice age woodland expansions into the Sonoran Desert. In the late Wisconsin and early Holocene, *Pinus monophylla* (singleleaf pinyon), several species of *Juniperus* (junipers), and *Yucca brevifolia* (Joshua tree) were widespread down to 460 m elevation in the Tinajas Altas Mountains of southwestern Arizona. An 18,700 yr B.P. radiocarbon date on twigs of *Larrea divaricata* documents its regional presence at 330 m in a full-glacial juniper woodland dominated by *J. californica* and *Y. brevifolia*. Creosotebush desertscrub samples with abundant *J. californica* have been found as low as 240 m in the Butler Mountains just to the west. Ice age desertscrub dominated by *Larrea divaricata* without woodland plants was apparently restricted to below 250–300 m in the Lower Colorado River Valley and the Gran Desierto. A lowering of sea level of about 100 m during the Wisconsin exposed additional lowlands around the head of the Gulf of California. Mohave Desert plants such as *Coleogyne ramosissima* (blackbrush), *Salvia mohavensis*, *Y. brevifolia*, and *Y. whipplei* (Whipple yucca) expanded their ranges southward and to lower elevations. Dominants of arid central Baja California communities such as *Fouquieria columnaris* (boojum tree) and *Pachycormus discolor*

(elephant tree) were conspicuously absent from low-elevation Lower Colorado River Valley and Gran Desierto midden assemblages. Arid desertscrub communities have probably been in these Sonoran Desert lowlands throughout the Pleistocene.

Resumen. Las 94 taxa de plantas identificadas en 10 depósitos de *Neotoma* sp. (totl) de 240 a 260 m de altitud en las montañas graníticas de Hornaday proveen una historia excelente de la vegetación y el clima para los últimos 10,000 años en la región del Pinacate en el noroeste de Sonora, México. Las pendientes rocosas en esta área árida (ca. 120 mm/año de precipitación pluvial), en la subdivisión del Río Colorado Bajo del Desierto Sonorense, han sostenido comunidades de matorral xerófilo, siendo las dominantes *Encelia farinosa* (incienso), *Larrea divaricata* (gobernadora) y *Carnegiea gigantea* (saguaro) durante todo el Holoceno. La composición de las comunidades cambio continuamente con una tendencia general desde el glacial tardío al presente y también a escalas de tiempo más cortas.

Ephedra nevadensis (tepopote), codominante con *Encelia farinosa*, *Larrea divaricata*, y *Carnegiea gigantea* en muestras del Holoceno temprano (8910 a 10,000 años antes del presente = A.P.), y el raro *Juniperus* cf. *californica* (enebro) indican una continuación de los veranos frescos y las lluvias principales invernales del glacial de Wisconsin tardío. Las muestras del Holoceno medio (4430 a 8600 años A.P.) contenían árboles y arbustos como *Acacia greggii* (uña de gato), *Cercidium floridum* (paloverde azul), y *Prosopis velutina* (mezquite) los cuales ahora están restringidos a los arroyos relativamente húmedos, indicando precipitaciones veraniegas más elevadas y heladas más frecuentes que en la actualidad. Las muestras del Holoceno tardío (1720 a 2320 años A.P.) en las que dominan *Encelia farinosa* y *Olueva tesota* (palo fierro) con *C. microphyllum* (paloverde) reflejan una vegetación relativamente moderna del Desierto Sonorense e indican un régimen de lluvias biestacional relativamente moderno con las condiciones más subtropicales en el Holoceno. Durante los últimos 1700 años, *O. tesota* desapareció, en tanto que *Ambrosia deltoidea* (chicurilla), *Baobab microphylla* (torote), *Jatropha cuneata* (sangregrado) y *L. divaricata* aparecieron o aumentaron en los sitios. La vegetación es tan escasa en las montañas Hornaday y el clima moderno tan caliente y árido como en cualquier tiempo durante los últimos 10,000 años. La variabilidad de la composición de las comunidades durante el Holoceno era semejante en magnitud a la variabilidad moderna entre los sitios de depósitos de *Neotoma* y parece reflejar el clima altamente variable. Las respuestas de especies individuales a las fluctuaciones climáticas en escalas de años a milenios puedan evitar que las comunidades de matorral xerófilo lleguen a alcanzar el equilibrio.

Las poblaciones disjuntas de *Artemisia ludoviciana* (estafiate), *Berberis haematocarpa* (agruto), *Opuntia chlorotica* (nopal), *Rhus aromatica* (agrillo), *Salvia mohavensis* (salvia de Mojave), y *Stipa speciosa* (flechilla del desierto) en elevaciones mayores de 650–800 m, al lado norte del Cerro Pinacate, son relictos de las expansiones de los bosques del periodo glacial hacia el Desierto Sonorense. En el Wisconsin tardío y el Holoceno temprano, *Pinus monophylla* (piñón), varias especies de *Juniperus*, y *Yucca brevifolia* (árbol de Josue) estaban ampliamente distribuidas, bajando hasta los 460 m de elevación en las montañas Tinajas Altas del sudoeste de Arizona. Una fecha de radiocarbono de 18,700 años A.P., en ramitas de *Larrea divaricata*, documenta su presencia a una altura de 330 m, en bosque glacial de enebro dominado por *J. californica* y *Y. brevifolia*. Se han encontrado muestras de matorral xerófilo de gobernadora con abundante *J. californica* a no más de 240 m en las montañas Butler a poca distancia al oeste. Las comunidades de matorral xerófilo del periodo glacial dominadas por *Larrea divaricata* sin plantas de bosque, aparentemente estaban limitadas a altitudes menores a 250 a 300 m en el Valle del Río Colorado Bajo y el Gran Desierto. El descenso del nivel del mar de aproximadamente 100 m durante el periodo Wisconsin expuso tierras bajas adicionales cerca de la cabecera del Golfo de California. Plantas del Desierto de Mojave, tales como *Coleogyne ramosissima* (arbusto negro), *Salvia mohavensis*, *Y. brevifolia*, y *Y. whipplei* extendieron su área de distribución hacia el sur y a elevaciones menores. Las plantas dominantes de las comunidades áridas de Baja California central, tales como *Fouquieria columnaris* (cirio) y *Pachycornus discolor* (copalquin) estaban conspicuamente ausentes en depósitos de *Neotoma* del Valle de Río Colorado Bajo y el Gran Desierto. Las comunidades áridas de matorral xerófilo probablemente han estado en estas tierras bajas del Desierto Sonorense durante todo el Pleistoceno.

INTRODUCTION

Plant remains preserved in ancient packrat (*Neotoma* sp.) middens allow detailed reconstructions of the local history of vegetation and climate for the last 30,000 years in the North American deserts (Van Devender *et al.*, 1987). Chronological sequences of middens typically begin in the late Wisconsin, when woodlands dominated by pinyons, junipers, and oaks were widespread, and continue through the Holocene as modern desertscrub communities developed. In the Sonoran Desert in Arizona, pinyon–juniper woodlands with *Pinus monophylla* (singleleaf pinyon) at 610–1555 m elevation occurred above xeric woodlands dominated by *Juniperus californica* (California juniper) prior to 11,000 yr B.P. (radiocarbon years before 1950; Van Devender, 1990). During the last glacial, and probably much of the Quaternary, lower areas along the Colorado River in Arizona, California, and adjacent Mexico supported desertscrub dominated by *Larrea divaricata* (creosotebush) without woodland plants.

Packrat middens are hard, dark, shiny organic deposits built by rodents of the genus *Neotoma*. In open areas, packrats construct houses near shrubs or large rocks by using a variety of local plant materials, including thorny branches and cactus stems and pads. Middens are formed near entrances to internal passages where fecal pellets, plant fragments, and general debris are deposited during house cleaning (Finley, 1958). In dens in dry rockshelters where the amount of house material can be reduced or absent, the midden can be cemented with urine and preserved for tens of thousands of years. Packrats gather representative samples of the plants within

about 30–50 m of the shelter (Van Devender, 1990). Radiocarbon dating allows the midden assemblages to be placed in time. Series of radiocarbon-dated midden assemblages from a single cave or several caves in a small local area provide detailed records of the local vegetation history.

In this study, we analyzed plant macrofossils in a series of Holocene packrat middens from the Hornaday Mountains in the arid Pinacate Region, northwestern Sonora.

ENVIRONMENTAL SETTING

The Sonoran Desert is the subtropical arid region centered around the head of the Gulf of California in western Sonora, southwestern Arizona, southeastern California, and much of the Baja California peninsula (Shreve, 1964; Fig. 1). Elevations range from below sea level in the Imperial Valley of California to about 1000 m at the northeastern margin in Arizona. Along the Colorado River they range from 278 m at Needles to sea level in the Gulf of California (Turner and Brown, 1982). Subdivisions of the Sonoran Desert based on vegetation and climate were proposed by Shreve (1964) and refined by Turner and Brown (1982). Most of the Sonoran Desert occasionally experiences freezing temperatures, although rarely for more than a single night. In general, the frequency and intensity of freezes increases to the north, toward the Mohave Desert. Rainfall ranges from a biseasonal regime with strong summer monsoons in Sonora and Arizona to a winter-rainfall regime on the Pacific coast of Baja California. Total precipitation

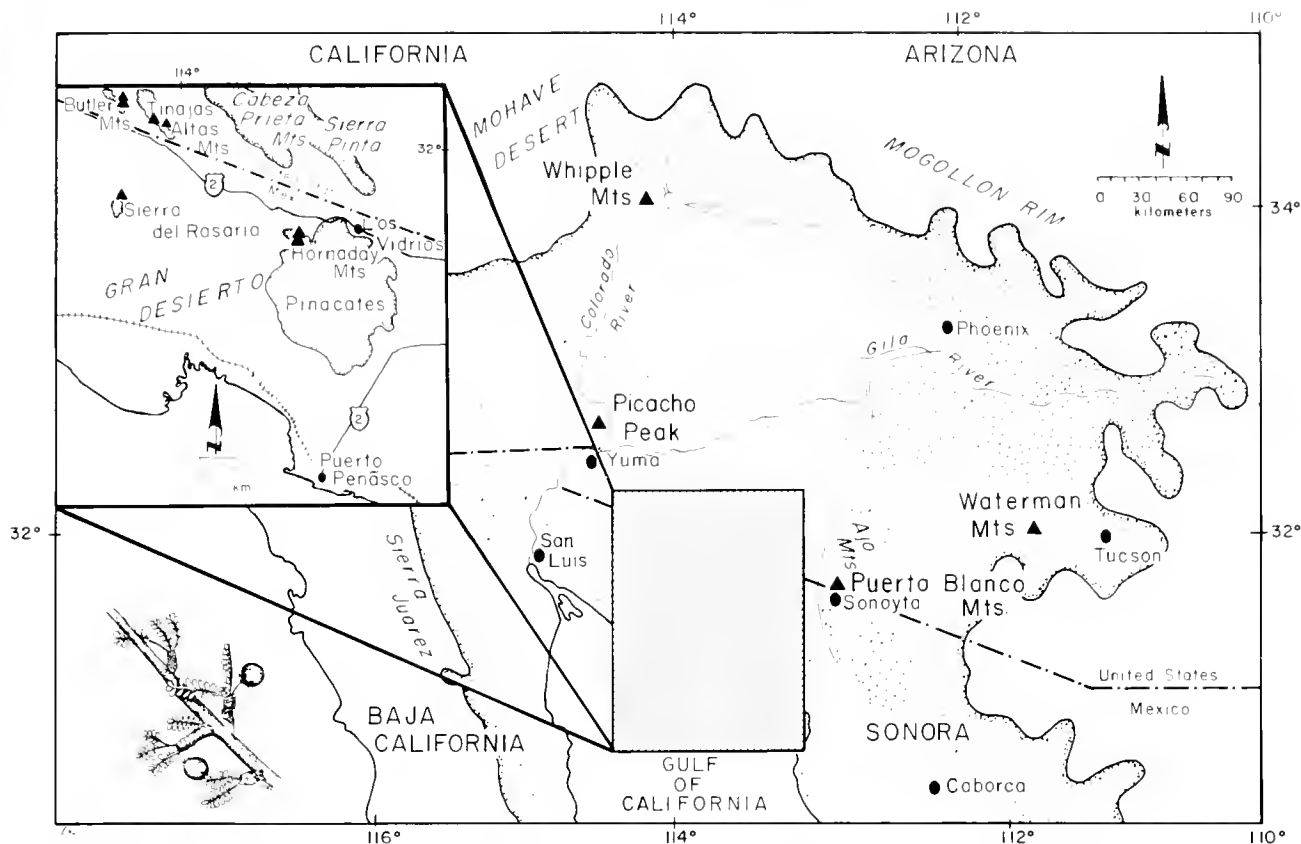


Figure 1. Location of Hornaday Mountains and other areas discussed in text. Limits of Sonoran Desert after Shreve (1964). Arizona Upland subdivision in heavy stipple; Lower Colorado River Valley in light stipple. Branch, *Bursera microphylla* (elephant tree).

decreases with decreasing elevation from the Arizona Upland and Plains of Sonora west to the Lower Colorado River Valley and the Gulf of California. Except in the most arid portions of the Sonoran Desert, trees and arborescent cacti are common and reflect strong affinities with subtropical thornscrub to the south.

The hottest and driest climate in North America is in the Sonoran Desert lowlands of Sonora, Baja California, Arizona, and California in the Lower Colorado River Valley. Precipitation is highly variable and at lower elevations averages less than 100 mm/yr (Ezcurra and Rodrigues, 1986). We estimated precipitation for the Hornaday Mountains at 230 m elevation by using regional regression equations derived from climatic data compiled by the U.S. Geological Survey: 119.5 mm/yr with 31.0% in summer (June-August), 60.6% in summer-fall (June-November), 31.7% in winter (December-February), and 39.4% in winter-spring (December-

May). The estimates for summer and fall may be slightly high because the Hornadays are on the drier western edge of the Pinacate Region (Table 1). The driest portion of the year is from the middle of March through June.

The vegetation in the Lower Colorado River Valley subdivision is mostly an open desertscrub structurally dominated by *Larrea divaricata*, *Ambrosia dumosa* (white bursage), *Encelia farinosa* (brittlebush), and *Hilaria rigida* (big galleta grass). Felger (1980) described the vegetation, flora, and environment of the Gran Desierto (Desierto de Altar), the sandy lowlands of northwestern Sonora. The Hornaday Mountains (Sierrita el Temporal) are a granitic ridge at 210-440 m elevation on the northwestern edge of the Pinacate Volcanic Complex, 56 km north of the Gulf of California (Lynch, 1981). MacDougal Crater (Volcán el Verdugo) in the Pinacates is just to the south. The area is 14 km south of the Tule

TABLE 1. Climatic records for stations in the Pinacate Region of northwestern Sonora, Mexico.^a

Station	Location ^b	Elevation (m)	Mean Temperature (°C)			Mean Precipitation	
			Annual	January	July	Annual (mm)	Warm Season (%) ^c
Sonoyta	73 ESE	303	21.2	11.2	31.9	184.7	62.3
Hornaday Mountains	—	230	—	—	—	119.5	60.6
Puerto Peñasco	76 S	4	20.1	11.4	29.3	73.5	47.6
San Luis del Rio Colorado	120 NNW	27	23.0	12.7	34.1	55.4	42.4

^aData from Hastings and Humphrey (1969).

^bDistance (km) and direction from the Hornaday Mountains.

^cCalculated for July to October for stations and June to November (summer-fall) for the Hornaday Mountains. Hornaday Mountains values were estimated by means of regression equations derived from climatic data compiled by the U.S. Geological Survey.

Desert, which lies between the Cabeza Prieta Mountains and the Sierra Pintada in the Cabeza Prieta National Wildlife Refuge in Yuma County, Arizona. The massive Pinacate volcanic complex, with an area of about 2000 km², is a stark landscape of volcanic craters and lava flows, many of Pleistocene age, bounded by sand dunes (Hornaday, 1908; Ives, 1964, Figs. 1, 2). Pinacate Peak (28 km SSE of the study area) rises from an elevation of 100 m at its southwestern base to 1290 m on top. The Hornaday Mountains and MacDougal Crater were named by the geographer Godfrey Sykes for William T. Hornaday and Daniel T. MacDougal, leaders of a 1907 expedition to explore the Pinacate sponsored by the Carnegie Desert Botanical Laboratory (Hornaday, 1908).

The general environment of the Hornadays is similar to that of the more arid Sierra del Rosario (50 km W; Felger, 1980). The vegetation near the midden rockshelters is a desertscrub dominated by *Bursera microphylla* (elephant tree), *Cercidium microphyllum* (foothill paloverde), *Enecha farinosa*, and *Larrea divaricata* (Table 1). This association was included in the *Larrea divaricata*-*Fouquieria splendens* (cocotillo) communities described in the Pinacate by Ezcurra and Lopez-Portillo (1987). Important shrubs, succulents, and grasses include *Ambrosia deltoidea* (triangleleaf bursage), *A. dumosa*, *Carnegia gigantea* (saguaro), *Fouquieria*

splendens, *Hilaria rigida*, *Hyptis emoryi* (desert lavender), *Jatropha cuneata* (cuneate limberbush), and *Opuntia bigelovii* (teddy bear cholla). Herbaceous perennials and annuals are less diverse in rocky habitats than on nearby bajadas and dunes.

METHODS AND RESULTS

Ten packrat middens were collected from granitic rockshelters at 240–260 m elevation from five areas on the southwest, south, and east slopes of the Hornaday Mountains (31°59'N, 113°36'W; Table 2). Arthropod remains from the samples were reported by Hall *et al.* (1988). We listed all plants occurring within 30–50 m of each rockshelter on rocky slopes, Table 3 lists the flora of the entire study area by growth form and habitat (rocky slopes, bajadas, and stabilized sand dunes). Voucher specimens of 64 species of plants were deposited into the University of Arizona Herbarium. The flora totals 104 species including trees and shrubs (17.3%), subshrubs (15.4%), stem and rosette succulents (8.7%), grasses (10.6%), and herbs (48.1%), especially annuals (36.5%). Sampling periods were restricted to the winter–spring season (19–20 February 1984, 22–24 March 1985); a few additional summer annuals would be expected. Annuals include both the winter and summer seasonal ephemerals



Figure 2. Aerial view toward the southeast of the Hornaday Mountains, MacDougal Crater, and the Pinacate volcanic field and peaks. Photo by Peter L. Kresan.

TABLE 2. Radiocarbon dates on *Neotoma* sp. fecal pellets, sample weights after washing, and site elevation and slope for packrat middens from the Hornaday Mountains, Sonora, Mexico.

Sample	Elevation (m)	Slope	Radiocarbon date (yr B.P.)	Lab. No.	Weight (g)
HO3	240	E	10,000 ± 190	A-4097	120
HO12A	260	S	9370 ± 150	A-4346	153
HO12B	260	S	8910 ± 150	A-4347	134
HO4B	240	S	8660 ± 190	A-4094	72
HO1C	240	SW	6065 ± 90	A-4203	165
HO1B	240	SW	4430 ± 80	A-4202	194
HO2A	240	SW	2320 ± 100	A-4096	159
HO5A	240	SW	1930 ± 110	A-4118	193
HO2B	240	SW	1850 ± 140	A-4119	126
HO5B	240	SW	1720 ± 130	A-4095	134

of Shreve (1964) and plants that germinate in one cool season and survive to the next.

Samples from packrat middens were washed in water, oven-dried, and sorted. Sample weights after washing ranged from 72 to 194 g. Plant macrofossils were identified by reference to specimens in the University of Arizona Herbarium and Desert Laboratory. Internal relative abundances (RA) were assigned to each plant taxon in an assemblage on a scale of 1 to 5. On this scale a single specimen is a 1, the most common taxon is a 5, and other abundances are ranked between. Although the number of plants in ranks 2 to 5 varies according to the total number of identified specimens, the relative abundances of different samples are readily comparable.

Ten radiocarbon dates on fecal pellets of *Neotoma* sp. from the samples yielded ages from 10,000 to 1720 yr B.P. with fairly continuous coverage through the Holocene (Table 3). Careful stratigraphic collection and removal of outer surfaces minimized contamination by younger materials. The chronology presented by Van Devender et al. (1987) is followed in this paper, i.e., late Wisconsin, 22,000–11,000 yr B.P.; early Holocene, 11,000–8900 yr B.P.; middle Holocene, 8900–4000 yr B.P.; late Holocene, 4000 yr B.P. to present.

A total of 94 taxa with 23–38 (av. 30.4) taxa per assemblage was identified from the midden assemblages (Table 4). The midden taxa included trees and shrubs (19.1%), subshrubs (12.8%), stem and rosette succulents (9.6%), grasses (9.6%), and herbs (48.9%), especially annuals (35.1%). A chronological summary of selected perennial species is presented in Figure 3. Distributions of plants were determined through personal observations, notes, and collections, surveys of the University of Arizona Herbarium, which houses Richard S. Felger's extensive regional collection, an atlas of Sonoran Desert plant distributions (Hastings et al., 1972), and regional floras (Bowers, 1980; Felger, 1980, unpublished; Kearney and Peebles, 1964; Munz, 1974; Shreve and Wiggins, 1964; Wiggins, 1980).

VEGETATION HISTORY

Early Holocene

Three early Holocene (8910 to 10,000 yr B.P.) samples record a desertscrub dominated by *Ephedra nevadensis*, *Encelia farinosa*, and *Larrea divaricata* in association with various shrubs. A single twig of *Juniperus* cf. *californica* was in the 9370 yr B.P. sample. The nearest population of *J. californica* is in the Sierra Juarez (265 km W) in northern Baja California (Wiggins, 1980). *Chrysothamnus teretifolius* (rabbit brush), represented by a leaf in the same

sample, is a shrub found in creosotebush and Joshua tree (*Yucca brevifolia*) desertscrub and pinyon–juniper woodland in the Mohave Desert in California (Munz, 1974). The nearest populations are in the Santa Rosa Mountains (380 km WNW), on the western edge of the Sonoran Desert in southeastern California. *Brickellia attractyoides* (brickellbush, *B. arguta* of Munz, 1974) is a Mohave Desert and Lower Colorado River Valley species that is known in Sonora only from steep granitic mountains 99 km east of San Luis on Highway 2 (21 km WNW). *Acacia greggii* (catclaw acacia), *Bebbia juncea* (chuckwalla's delight), *Brickellia coulteri* (brickellbush), *Eriogonum fasciculatum* (California buckwheat), *E. wrightii* (wild buckwheat), *Lycium* sp. (wolfberry), and *Peucephyllum schottii* (pygmy cedar), identified from the samples, no longer occur in the Hornadays but persist in the Pinacate, *Ephedra nevadensis*, *Galium stellatum* (desert bedstraw), *Hofmeisteria plurisetia* (arrowleaf), *Prosopis velutina* (velvet mesquite), and *Viguiera* cf. *deltoidea* (desert goldeneye) presently occur elsewhere in the Hornadays. *Ephedra nevadensis* is occasional above 400 m on the north slope of the ridge. Plants in the samples that still occur at site include *Ambrosia dumosa*, *Bursera microphylla*, *Cercidium microphyllum*, and *Trixis californica*.

Succulents common in the early Holocene middens were *Carnegiea gigantea*, *Ferocactus cylindraceus* (California barrel cactus, *F. acanthodes* of Munz, 1974), and *Opuntia bigelovii*, with lesser amounts of *Agave deserti* (desert agave) and *Mammillaria microcarpa* (fishhook cactus). *Agave deserti* and *F. cylindraceus* no longer occur at the midden sites but are present elsewhere in the range. *Mammillaria microcarpa* and *O. bigelovii* are common today but not as widespread as in the early Holocene. *Carnegiea gigantea* is still present at all midden sites.

Stipa speciosa (desert needlegrass), a widespread C-3 perennial in the Mohave Desert, was in the 8910 and 9370 yr B.P. samples. Relict populations survive in the Tinajas Altas Mountains (60 km NNW) and on Pinacate Peak (28 km SSE). The remainder of the midden grasses, with the exception of the robust *Hilaria rigida*, are short-lived annuals and perennials that have been present in the Sonoran Desert throughout the Holocene (Van Devender et al., 1990).

The early Holocene assemblages contained more short-lived herbs than occur at the sites today. Some species now absent from the Hornadays, including the perennial *Argythamnia neomexicana* (wild mercury), *Mirabilis bigelovii* (wishbone bush), *Lyrocarpa coulteri* (lyrefruit), *Verbena* sp. (vervain), and the annuals *Amsinckia tessellata* (fiddleneck) and *Parietaria hespera* (pellitory), still occur in the nearby Pinacate. Most of the other herbs were observed on bajada or dune habitats in the vicinity of the Hornadays. A number of annuals not observed probably appear in years with adequate rainfall.

Middle Holocene

Three middle Holocene (4330 to 8660 yr B.P.) samples provide records of a desertscrub dominated by *Encelia farinosa* and *Larrea divaricata* with less *Ephedra nevadensis*. By 6065 yr B.P. *Carnegiea gigantea* was a codominant. *Prosopis velutina* increased until it was abundant in the 4430 yr B.P. sample.

Plants no longer in the Hornadays but in the Pinacate include *Acacia greggii*, *Bebbia juncea*, *Eriogonum fasciculatum*, *Peucephyllum schottii*, and *Phoradendron californicum* (desert mistletoe). *Opuntia ramosissima* (diamond cholla) was not seen in the area but is widely scattered in lowland habitats in the Lower Colorado River Valley (Felger, 1980, unpublished). *Cercidium floridum* (blue paloverde), *Ephedra nevadensis*, *Hyptis emoryi*, *Olneya tesota*, and *Prosopis velutina* no longer occur at the sites but remain elsewhere in the range. Trees and shrubs that still occur at

TABLE 3. Distribution and relative abundance of plants in the Hornaday Mountains, Sonora, Mexico.^a

Species ^b	Common Name	Middle Sites ^c										General Distribution					
		HO1&2	HO3	HO4	HO5	HO12	NB	NS	SS	SB	SD						
Trees and Large Shrubs																	
<i>Buxera microphylla</i>	Elephant tree	1	1	4	4	4	X	X	X	X							
<i>Cercidium floridum</i>	Blue palo verde													X	X		
<i>Cercidium floridum</i> × <i>microphyllum</i>	Hybrid palo verde													X	X		
<i>Cercidium microphyllum</i>	Foothills palo verde	1	2	2	2	4	X	X	X					X	X		
<i>Olneya tesota</i>	Ironwood	2					X										
<i>Prosopis velutina</i>	Velvet mesquite				1												
<i>n</i> = 6		3	2	2	3	2	3	2	2	2	2	2	4	4	0		
Shrubs																	
<i>Asclepias subulata</i>	Desert milkweed													X			
<i>Encelia farinosa</i>	Brittlebush	5	1	2	4	5	X	X	X					X	X		
<i>Encelia frutescens</i> *	Green brittlebush						X	X	X								
<i>Ephedra nevadensis</i> *	Mormon tea						X	X	X								
<i>Fouquieria splendens</i>	Ocotillo	1	2		1		X	X	X					X			
<i>Horsfordia newberryi</i> *	Yellow felt plant					4											
<i>Hyptis emoryi</i>	Desert lavender	4	4	2	2	2	X							X	X		
<i>Lanopha cuneata</i>	Cuneate limberbush	4	2	4	4									X	X		
<i>Krameria grayi</i> *	White ratany						X	X	X					X			
<i>Krameria erecta</i> *	Range ratany	4	4	4	3	2	X	X	X					X	X		
<i>Larrea divaricata</i>	Creosotebush						X	X	X					X			
<i>Psoralea emoryi</i> *	Dune indigo bush						X	X	X					X	X		
<i>n</i> = 12		4	5	4	5	4	6	5	6	6	7	7	7	7	2		
Subshrubs																	
<i>Ambrosia deltoidea</i>	Triangleleaf bursage	4	4	1	3		X	X	X					X	X		
<i>Ambrosia dumosa</i>	White bursage						X	X	X					X	X		
<i>Argythamnia brandegeei</i> *	Brandegee wild mercury					1	X	X	X					X	X		
<i>Argythamnia lanceolata</i>	Lanceleaf wild mercury					4	X	X	X					X	X		
<i>Cryptantha rupestris</i> *	Woody nevitas				1									X			
<i>Fagonia laevis</i> *	Fagonia	1			1									X			
<i>Gutierrezia vellutina</i> *	Desert bedstraw						X	X	X								
<i>Helianthus niveus</i> *	Dune sunflower																
<i>Hibiscus denudatus</i>	Rock rose mallow	1	4	2	2	2	X								X		
<i>Holmeisera plariscia</i> *	Arrowleaf						X	X	X								
<i>Machaeranthera pinnatifida</i> *	Goodding goldenbush						X	X	X								
<i>Ponoplyllum gracile</i> *	Odora				1		X	X	X								
<i>Sphaeralcea ambigua</i> *	Desert globe mallow						X	X	X					X	X		
<i>Stillingia linearifolia</i> *	Trixis						X	X	X					X	X		
<i>Trixis californica</i>	Desert goldeneye						X	X	X					X	X		
<i>Viguiera deltoidea</i>							X	X	X					X	X		
<i>n</i> = 16		3	6	4	8	6	9	10	9	9	6	6	6	6	1		
Succulents																	
<i>Agave deserti</i>	Desert agave													X	X		
<i>Carnegiea gigantea</i>	Saguaro	2	1		1	1	X	X	X					X	X		
<i>Ferocactus cylindricus</i>	California barrel cactus													X	X		
<i>Mammillaria microcarpa</i>	Fishhook cactus	1		2	1		X	X	X					X	X		
<i>Mammillaria tenaxistris</i>	Fishhook cactus						X	X	X					X	X		

<i>Opuntia bigelovii</i>	4	2	1	1													X				X
<i>Opuntia echinocarpa</i>																					X
<i>Opuntia fulgida</i>	1										X										
<i>Opuntia kuntzei</i>																					
<i>n</i> = 9	4	2	4	4	1	4	6	5	2	2											
Grasses																					
<i>Aristida adscensionis</i> *	5	5	5	5	5	X	X	X													X
<i>Aristida californica</i> *																					
<i>Aristida purpurea</i>		1		2																	
<i>Bouteloua aristatoides</i>																					N
<i>Bouteloua barbata</i>											X										X
<i>Cenchrus palmieri</i> *																					X
<i>Eriogonum pulchellum</i>					2			X													X
<i>Hilaria rigida</i>		1		1	4																X
<i>Muhlenbergia microsperma</i> *																					
<i>Schizanthus barbatus</i> *																					
<i>Vulpia octoflora</i> *																					X
<i>n</i> = 11	1	3	1	5	2	3	3	3	3	6											3
Herbaceous Perennials																					
<i>Euphorbia polycarpa</i> *																					
<i>Nicotiana trigonophylla</i> *					2						X										X
<i>Nolithaena californica</i> *																					X
<i>Orobanchae cooperi</i> *																					X
<i>Physalis crassifolia</i> *																					
<i>Sarcostemma cymantoides</i> *																					
<i>Tiquilia plicata</i> *																					X
<i>n</i> = 7	0	0	0	0	1	3	3	3	1	2											0
Perennial/Annual Herbs																					
<i>Allionia incarnata</i>	4																				X
<i>Bartleya plenivalvata</i> *																					X
<i>Euphorbia eriantha</i> *																					X
<i>Marina parryi</i> *																					X
<i>Sphaeralcea obtusiloba</i> *																					X
<i>n</i> = 5	1	0	0	0	0	0	0	0	0	3	2										2
Annuals																					
<i>Abronia villosa</i> *																					X
<i>Achyrocline cooperi</i> *																					X
<i>Astragalus usularis</i> *																					X
<i>Boerhaavia</i> sp.																					X
<i>Camissonia californica</i> *																					X
<i>Camissonia claviformis</i> *																					X
<i>Chaenactis carphoclinia</i> *																					X
<i>Chorizanthe corrugata</i> *																					X
<i>Chorizanthe rigida</i> *																					X
<i>Cryptantha angustifolia</i> *																					X
<i>Cryptantha ganderi</i> *																					X
<i>Cryptantha holoptera</i> *																					X
<i>Cryptantha maritima</i> *																					X
<i>Cryptantha micrantha</i> *	4																				X
<i>Cryptantha picrocarpa</i> *																					X

(continued)

TABLE 3 (continued)

Species ^b	Common Name	Midden Sites ^c							General Distribution				
		HO1&2	HO3	HO4	HO5	HO12	NB	NS	SS	SB	SD		
Annuals (continued)													
<i>Dalea mollis</i> *	Silk dalea	2		2	1				X			X	
<i>Datura discolor</i>	Toloache											X	
<i>Diurysa californica</i> *	Spectacle pod											X	
<i>Eriogonum thomasi</i> *	Thomas skeleton weed								X			X	
<i>Eriogonum trichopes</i> *	Yellow trumpet											X	
<i>Geraea canescens</i>	Desert sunflower											X	
<i>Lepidium lasiocarpum</i> *	Peppergrass						X					X	
<i>Linanthus bigelovii</i> *							X					X	
<i>Lotus strigosus</i> *	Deer vetch											X	
<i>Lupinus arizonicus</i> *	Lupine								X			X	
<i>Lupinus sparsiflorus</i> *	Lupine											X	
<i>Lupinus</i> sp.	Lupine						X			X		X	
<i>Malacothrix californica</i> *	Desert dandelion						X					X	
<i>Mentzelia involucrata</i> *	Desert blazing star						X					X	
<i>Monoptilon bellionides</i> *	Desert star	2					X					X	
<i>Nama hispida</i> *	Sand bells											X	
<i>Nemaucalis demudata</i> *	Woolly heads											X	
<i>Oenothera deltoides</i> *	Dune primrose											X	
<i>Palafixia arida</i> *	Spanish needles											X	
<i>Pectocarya heterocarpa</i> *	Hairyleaf combbur											X	
<i>Pentstemon</i>	Rock daisy						X					X	
<i>Plantago insularis</i> *	Indian wheat						X					X	
<i>Stylocine micripoides</i> *	Desert nest straw						X					X	
<i>n</i> = 38		3	0	1	1	0	11	7	2	24	2		
Total = 104		19	18	14	26	16	39	36	28	54	12		

^aBased on surveys by R. M. Turner and T. L. Burgess on 19–20 February 1984 and 22–24 March 1985.

^bAsterisks indicate University of Arizona Herbarium specimens.

^cHO, within 30 m of packrat midden rockshelter at 240–260 m elevation.

^dNB, northern base at 210–240 m; NS, north slope at 300–440 m; SS, south slope at 260–400 m; SB, southern bajada at 220 m; SD, stabilized sand dunes against southern base at 210 m (additional species only). Relative abundance: 1, rare; 2, uncommon; 3, common; 4, very common; 5, abundant; X, present.

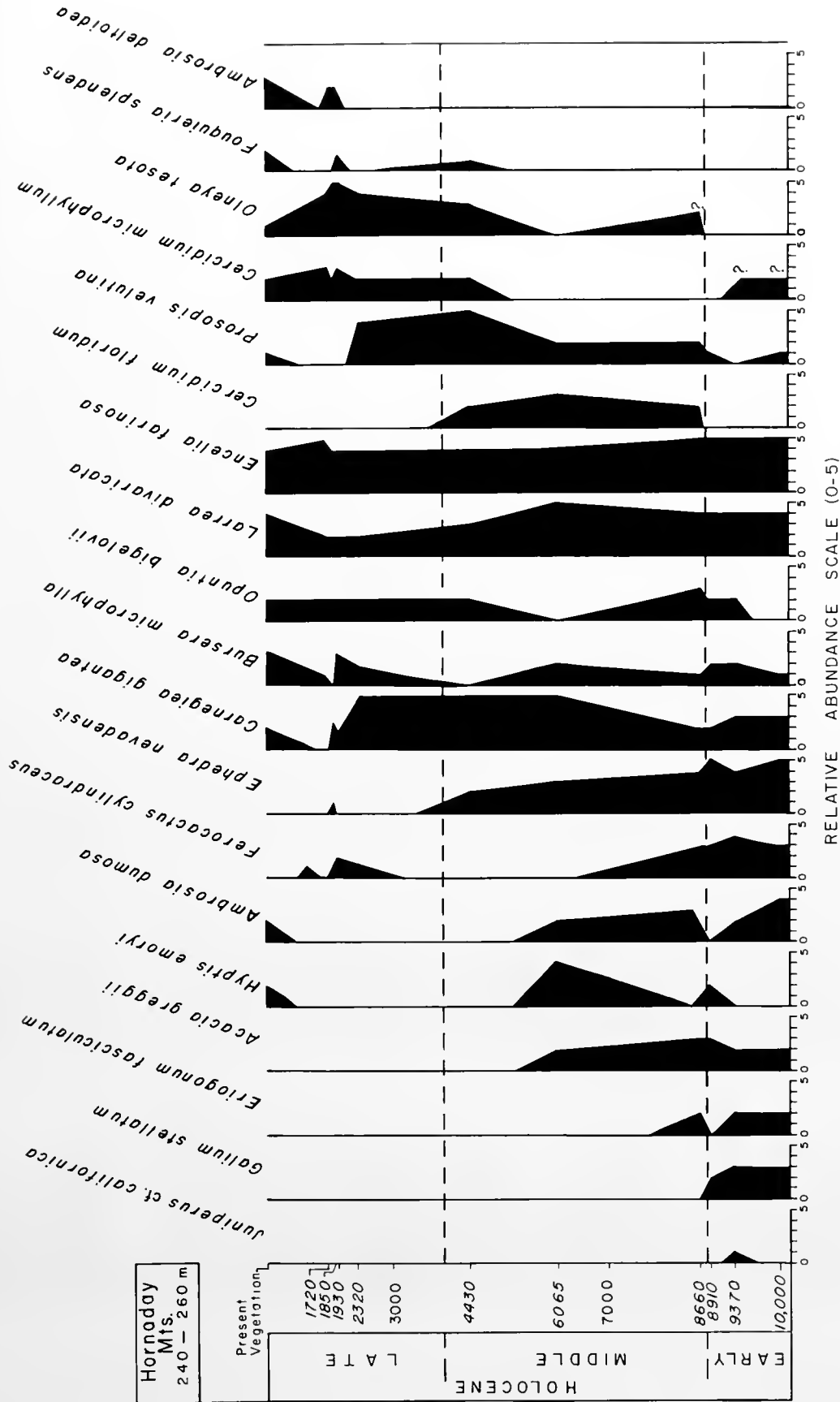


Figure 3. Chronological summary of selected perennial plants identified from packrat middens from the Hornaday Mountains of northwestern Sonora, Mexico. Ages in yr B.P.; radiocarbon ages in italics after Table 3. ?, possible contaminant.

TABLE 4. Relative abundances and distributions of plant macrofossils identified from packrat middens from the Hornaday Mountains, Sonora, Mexico.

Species	Common Name	Material Identified	Age of Sample (thousands of years) ^a											
			10.0	9.4	8.9	8.7	6.1	4.4	2.3	1.9	1.9	1.7		
Trees and Large Shrubs														
<i>Buxera microphylla</i>	Elephant tree	SD, FR, LF	1n	2n	2n	1n	2n	2n	2n	2n	2n	2n	3n	1n
<i>Acacia greggii</i>	Catclaw acacia	FR, LF, TH	2p	2p	3p	3p	2p	2p	2p	2p	2p	2p	3n	1n
<i>Prosopis velutina</i>	Velvet mesquite	SD, LF, TH	1H	1H	1H	2H	3H	5H	4H					
<i>Juniperus cf. californica</i>	California juniper	TW	1e											
<i>Cercidium microphyllum</i>	Foothills paloverde	FR, LF, TW	2n	2n	2n	2H	3H	2n	2n	2n	2n	3n	3n	
<i>Cercidium floridum</i>	Blue paloverde	TW, TH				2H	3H	2H	2H	2H	2H	2H	2H	
<i>Olneya tesota</i>	Ironwood	FR, LF, TH				2H	3H	4H	4H	5H	5H	5H	4H	
<i>n = 7</i>			3	4	4	5	4	4	4	4	4	3	2	3
Shrubs														
<i>Lycium sp.</i>	Wolfberry	SD, LF, TW	2P	2P										
<i>Chrysothamnus teretifolius</i>	Rabbit brush	LF	1e											
<i>Eriogonum fasciculatum</i>	California buckwheat	LF	2P	2P	2P	2P								
<i>Ephedra nevadensis</i>	Mormon tea	SD, BT, TW	5H	4H	5H	4H	3H	2H	2H	2H	2H	2H	1H	
<i>Larrea divaricata</i>	Creosotebush	FR, LF, TW	4n	4n	4n	5n	5n	3n	2n	2n	2n	2n	2n	
<i>Encelia farinosa</i>	Brittlebush	AC, LF, TW	5n	5n	5n	4n	4n	4n	4n	4n	4n	4n	4n	5n
<i>Bobbia juncea</i>	Chuckwalla's delight	AC	2P	2P	2P	2P								
<i>Hyptis emoryi</i>	Desert lavender	SD, FR, LF, TW		2n	2n	4H							2H	
<i>Fouquieria splendens</i>	Ocotillo	TH						1n						
<i>Hymenoclea salsola</i>	Cheesebush	BU							2p					2n
<i>Jatropha cf. cuneata</i>	Cuneate limberbush	SD												
<i>n = 11</i>			5	7	5	5	4	4	4	3	3	3	3	3
Subshrubs and Parasites														
<i>Brickellia atracyloides</i>	Hollyleaf brickellbush	LF	2e											
<i>Hopmeisteria plariseta</i>	Arrowleaf	AC, JV	2H											
<i>Vignera cf. deltoidea</i>	Desert goldeneye	AC		1H										
<i>Brickellia coulteri</i>	Desert brickellbush	AC, JV, TW	2P	2P	2P									
<i>Eriogonum wrightii</i>	Wild buckwheat	LF	2P	2P	3P									
<i>Galium stellatum</i>	Desert bedstraw	LF, TW	3H	3H	2H									
<i>Trixis californica</i>	Trixis	LF, IV	2n	2n	2n	2n								
<i>Ambrosia dumosa</i>	White bursage	BU, LF, TW	4n	2n	3n	2H								
<i>Peucephyllum schottii</i>	Pgymy cedar	AC, LF				2P								
<i>Phoradendron californicum</i>	Desert mistletoe	FR, TW				2P				3P				
<i>Ambrosia deltoidea</i>	Triangleleaf bursage	BU												
<i>Argythamnia cf. lanceolata</i>	Lanceleaf wild mercury	SD												2H
<i>n = 12</i>			7	6	4	2	3	1	0	2	1	1	1	
Succulents														
<i>Ferocactus cylindraceus</i>	California barrel cactus	SD, BT, SP	3H	4H	3H	3H				2H				1H
<i>Mammillaria microcarpa</i>	Fishhook cactus	SD, SP	1H	2H	2H	1n	3n			2H				2n
<i>Opuntia bigelovii</i>	Teddy bear cholla	SD	2H	2H	2H	3n				2n				2n
<i>Carnegiea gigantea</i>	Saguaro	SD, FR, SP	3n	3n	3n	2n	5n	5n	5n	2n				3n
<i>Agave deserti</i>	Desert agave	LF			1H									
<i>Opuntia kunzei</i>	Yuma club cholla	SP					3n							
<i>Opuntia ramossissima</i>	Diamond cholla	ST					2P							
<i>Opuntia fulgida</i>	Chainfruit cholla	SD						3H					2H	
<i>Echinocereus sp.</i>	Hedgehog cactus	SD											1P	
<i>n = 9</i>			2	4	5	4	4	3	3	3	6	2	2	3

	1	4	3	4	4	4	4	4	3	0	2	3
Graasses												
<i>Vulpia</i> sp.	1H	2H	2P									
<i>Stipa speciosa</i>			2P									
<i>Muhlenbergia microsperma</i>			1H									
<i>Aristida adscensionis</i>		2n	1n	2n								
<i>Hilaria rigida</i>			2n		2H							2n
<i>Muhlenbergia</i> sp.				1H								
<i>Eriogonum pulchellum</i>				2H	3H							2n
<i>Bouteloua barbata</i>				1H	3H	2H	2H				1H	
<i>Bouteloua aristoides</i>				2H	3H	3H	1H				2H	2H
<i>n</i> = 9	1	4	3	4	4	4	4	4	3	0	2	3
Herbaceous Perennials												
<i>Mirabilis bigelovii</i>		2P										
<i>Nicotiana trigonophylla</i>		2n										
<i>Lycocarpus condleri</i>			1P									
<i>Verbena</i> sp.	2P	2P	2P									
<i>Euphorbia cf. polycarpa</i>	2H	2H	3H	3H	4H	3H	3H	3H	2H	2H	2H	2H
<i>Orobanchaceae cooperi</i>											1H	
<i>n</i> = 6	2	4	3	1	1	1	1	1	1	1	2	1
Perennial/Annual Herbs												
<i>Physalis</i> sp.	4H	2H	3H	4H	4H	2H	1H			3H		4H
<i>Sphaeralcea</i> sp.	4H	4H	3H	2H	2H	2H				2H	1H	1H
<i>Nicotiana</i> sp.			2n									
<i>Argemone</i> cf. <i>neomevicana</i>			2P		3P	3P	2P					
<i>Allionia incarnata</i>			2H	2H	3n	3n	3n			5H	3n	5H
<i>Argemone</i> sp.				1H							1H	
<i>Euphorbia pedicellifera</i>								1P				
<i>n</i> = 7	2	2	5	4	4	4	4	4	3	4	3	3
Annuals												
<i>Cryptantha decipiens</i>	2c											
<i>Cryptantha pterocarya</i>	1H											
<i>Eschscholtzia</i> sp.		2w										
<i>Gilia</i> sp.	1w	2w	2w									
<i>Amsinckia tessellata</i>	2P			2P								
<i>Lupinus</i> sp.	2H	3H		2H								
<i>Cryptantha barbiger</i>	2w	2w			1w							1H
<i>Lotus strigosus</i>	1H											
<i>Lepidium lasiocarpum</i>	2H	3H	2H	4H							2H	
<i>Cryptantha maritima</i>	2H	2H	2H		2n				2n		2n	1H
<i>Plantago insularis</i>	2H			1H	2H	2H			2H		2H	
<i>Boerhaavia wrightii</i>	2w			2w	2w	2w	2w		2w	2w	2w	2w
<i>Perilyle emoryi</i>	1H										2H	3H
<i>Placelia</i> sp.		2w			1w						1w	
<i>Astragalus nuttallianus</i>											1w	
<i>Chorizanthe brevicauda</i>												

(continued)

TABLE 4 (continued)

Species	Common Name	Material Identified	Age of Sample (thousands of years) ^a										
			10.0	9.4	8.9	8.7	6.1	4.4	2.3	1.9	1.9	1.7	
Annuals (continued)													
<i>Dalea mollissima</i>	Silk dalea	SD			1e								
<i>Parietaria hirsuta</i>	Pellitory	FR		2w									
<i>Rafinesquia neomexicana</i>	Desert chicory	AC			2e								
<i>Lupinus arizonicus</i>	Lupine	SD, FR		2H	2H	2H							2H
<i>Boerhaavia</i> sp.	Spiderling	FR		1H									2H
<i>Kallstroemia</i> sp.	Summer poppy	SD			1w								3w
<i>Chorizanthe corrugata</i>	Wrinkled spinyherb	FR				1H							
<i>Dicoria canescens</i>	Bugseed	AC				1w							
<i>Mentzelia involucreata</i>	Desert blazing star	SD				2H							
<i>Pectis papposa</i>	Chincheed	AC								2w			
<i>Lupinus concinnus</i>	Elegant lupine	SD				1e					2e		2n
<i>Dalea mollis</i>	Silk dalea	FR				1n				2n	2w		
<i>Amaranthus</i> sp.	Amaranth	SD									1w		
<i>Draba cuneifolia</i>	Whitlow grass	FR										2w	
<i>Chaenactis</i> cf. <i>strevioides</i>	Desert pincushion	AC										3w	
<i>Argythamnia serrata</i>	Sawtooth wild mercury	SD, FR											2H
<i>Camissonia claviformis</i>	Brown-eyed primrose	FR, ST											
n = 33			12	7	7	11	9	9	5	10	8	9	6
Total = 94			34	38	36	36	33	26	26	27	27	24	23

^aMaterial codes: AC, achene; BU, bur; FL, floret; FR, fruit; IF, inflorescence; IV, involucre; LF, leaf or leaflet; SP, spine; ST, stem; TH, thorn; TW, twig.

^bRelative abundances: 1, rare; 2, uncommon; 3, common; 4, very common; 5, abundant. Distribution codes: n, within 30 m of midden rockshelter; H, not near rockshelter but elsewhere in the range; e, extralocal, no longer in the range but in the nearby Pinnacate Mountains; w, could be present in wet year.

the sites include *Ambrosia dumosa*, *Bursera microphylla*, *C. microphyllum*, *Encelia farinosa*, *Fouquieria splendens*, *Larrea divaricata*, and *Trixis californica*.

Succulents common during this period were *Carnegiea gigantea*, *Mammillaria microcarpa*, and *Opuntia bigelovii*. *Ferocactus cylindraceus* was common in the 8660 yr B.P. sample but absent or uncommon in all younger samples and the modern flora. The only fossils of *Opuntia kunzei* (Yuma club cholla) and *O. ramosissima* were in the 6065 yr B.P. sample. *Opuntia fulgida* (chainfruit cholla), the unique spiny arborescent Sonoran Desert succulent that accumulates chains of fruits, was common in the 4430 yr B.P. sample but does not grow at the site today.

The abundances of desert grasses peaked in the middle Holocene, whereas perennial herbs, with the exception of several species adapted to the most arid conditions, declined markedly. Persistent species include *Allionia incarnata* (windmills), *Euphorbia* cf. *polycarpa* (spurge), *Physalis* sp. (probably *P. crassifolia*; ground cherry), and *Sphaeralcea* sp. (probably *S. ambigua*; globe mallow). The annuals were similar to those of the early Holocene with increases in *Boerhaavia wrightii* (spiderling) and the first record for *Kallstroemia* sp. (summer poppy). *Dalea mollissima* (silk dalea) and *Rafinesquia neomexicana* (desert chicory) are winter-spring annuals that are widespread in the deserts of the Southwest but barely enter Sonora in the Gran Desierto. The only locality for *D. mollissima* is 31 km east of San Luis on Highway 2 (140 km WNW). The only localities for *R. neomexicana* are from 45 km west of Los Vidrios on Highway 2 (17 km NW) and at 1100 m in Pinacate Pass. *Lupinus concinnus* is a widespread species in the Southwest that is found in the Gran Desierto only on coastal sand dunes. The nearest collections are from the Bates Mountains in Organ Pipe Cactus National Monument (74 km ENE; Bowers, 1980).

Late Holocene

Four late Holocene (1720 to 2320 yr B.P.) samples record a desertscrub dominated by *Encelia farinosa* and *Olneya tesota*. *Larrea divaricata* declined in abundance from the middle Holocene as *Cercidium microphyllum* modestly increased. Abundances of *Carnegiea gigantea* and *Prosopis velutina* declined after 2320 yr B.P. *Ambrosia deltoidea*, *Argythammia* cf. *lancoolata* (wild mercury), and *Jatropha cuneata* are common desert shrubs that first appeared in the late Holocene.

Argythammia cf. *neomexicana* (wild mercury), *Echinocereus* sp. (hedgehog cactus), *Hymenoclea salsola* (cheesebush), and *Lupinus concinnus* no longer occur in the Hornadays, but except for *L. concinnus*, all occur in the Pinacate today. The seeds of *Echinocereus* sp. probably represent *E. engelmannii*, a species widespread in the Mohave Desert and the Lower Colorado River Valley. *Hymenoclea salsola* is a shrub that in the Sonoran Desert typically grows along the edges of washes rather than on rocky slopes.

Argythammia cf. *lancoolata*, *Fouquieria splendens*, *Olneya tesota*, and *Prosopis velutina* no longer occur at the sites but are present elsewhere in the Hornadays. Trees and shrubs that still occur at the sites include *Ambrosia deltoidea*, *Bursera microphylla*, *Cercidium microphyllum*, *Encelia farinosa*, *Jatropha cuneata*, and *Larrea divaricata*. Except for the decline in *Carnegiea gigantea* and the single record of *Echinocereus* sp., the succulents were similar to those of the middle Holocene.

The grasses in the middens decline markedly in abundance and number of taxa from the middle Holocene. The perennial and annual herbs with a few exceptions were similar to those of the middle Holocene. *Allionia incarnata* increased in importance and was abundant in the 1930 and 1720 yr B.P. samples. *Kallstroemia*

sp. increased in the samples and was common in the 1850 yr B.P. sample. Both *K. californica* and *K. grandiflora* may be found in the Pinacate in years with adequate summer or fall rainfall.

Modern Vegetation

The vegetation near the midden rockshelters is a desertscrub dominated by *Encelia farinosa*, but the composition of the community has shifted markedly in the last 1700 years. Although the abundances of *Carnegiea gigantea*, *Cercidium microphyllum*, and *Fouquieria splendens* did not change significantly, several plants declined or disappeared from the sites. *Olneya tesota*, an important desert tree, is the most notable of these. Others include *Argythammia lanceolata*, *Echinocereus* sp., *Euphorbia polycarpa*, *Ferocactus cylindraceus*, *Opuntia fulgida*, *Physalis crassifolia*, and *Sphaeralcea ambigua*. *Allionia incarnata* declined at most sites.

In contrast, a number of shrubs have increased near the rockshelters, including *Ambrosia deltoidea*, *Bursera microphylla*, *Jatropha cuneata*, and *Larrea divaricata*. Interestingly, *A. dumosa*, *Hypis emoryi*, and *Trixis californica* were present at the sites in the early and middle Holocene, absent in the late Holocene, but have returned to the sites. A number of easily identifiable plants apparently have moved into this habitat only recently: *Argythammia brandegeei* (Brandege wild mercury), *Fagonia laevis*, *Hibiscus demidatus* (desert rose mallow), *Horsfordia newberryi* (yellow felt plant), and *Porophyllum gracile* (odora).

Quantitative Vegetation Trends

Although plant remains in the Hornaday middens document a Sonoran desertscrub dominated for the last 10,000 years by *Encelia farinosa*, *Larrea divaricata*, and *Carnegiea gigantea*, the composition and structure of the community have been remarkably dynamic. Species that no longer occur in the Pinacate region were never common, with only 5.3% in the early Holocene, 5.4% in the middle Holocene, and 2.1% in the late Holocene. After 8910 yr B.P., the only species in the samples but not in the region today were winter-spring annuals. The flora near the midden sites and for the entire range has become progressively more modern (Table 5). Interestingly, all samples record richer, more mesic floras than occur at the sites today. In the last 1720 years, a number of desert shrubs and succulents have declined while others have increased.

We used Sorenson's index of similarity to establish trends in the Holocene vegetation. To calculate this index, twice the number of taxa that two samples share is divided by the sum of the taxa identified from each sample (Mueller-Dombois and Ellenberg, 1974). The index approaches 1.0 as samples become more similar. In biological systems differences in sample sizes usually prevent the index from reaching 1.0. Longer-lived perennials (e.g., trees, shrubs, subshrubs, succulents, and *Hilaria rigida*, a large perennial grass) identified in each midden were compared with the modern flora near each site to assess progressive modernization of the flora. The midden assemblages were also compared with the next oldest and youngest samples to assess variation through time. Plants within 30 to 50 m of the five midden rockshelters were compared to assess variability between sites today.

Similarity indices comparing the midden assemblages with the site's current floras generally increase through the Holocene as the flora becomes more modern (Fig. 4). The 10,000 yr B.P. sample was the most different, with a value of near 0.30. Until 6065 yr B.P. the values remained less than 0.5 (0.3–0.48, av. 0.41). From 4430 to 1720 yr B.P. the values increased from 0.53 to 0.70 (av. 0.60), a little lower than the results of modern comparisons between sites. The 2320 yr B.P. sample, with a value of 0.70, was most similar to the modern flora; values for three younger samples were lower. The

TABLE 5. Distribution of plants identified in packrat middens from the Hornaday Mountains, Sonora.^a

Time Period	Number of Samples	Number of Taxa	%n	%n+w	%H	%n+w+H	%P	%e
Early Holocene	3	57	21.1	31.6	38.6	70.2	24.5	5.3
Middle Holocene	3	56	23.6	38.6	40.0	78.6	16.0	5.4
Late Holocene	4	48	29.6	44.2	45.4	89.6	8.3	2.1

^an, found within 30 m of midden rockshelter; w, could be found near the rockshelter in wet years; H, not found near rockshelter but present elsewhere in the range; P, no longer in the range but occurs in the nearby Pinateate Mountains; e, no longer in the Pinateate region.

increase from 0.55 to 1.0 (= modern) indicates substantial change in the vegetation in the last 1720 years.

Similarity indices comparing midden assemblages to the next youngest sample provide an indication of internal changes within the community (Fig. 4). The youngest assemblage was compared to the modern flora at the site. Except for the 6065 to 4430 yr B.P. comparison, the values range between 0.58 and 0.72 (av. 0.64), indicating that species composition of the community changed steadily for most of the last 10,000 years. Increased species turnover between 6065 and 4430 yr B.P. reflects the dynamic nature of the middle Holocene.

Similarity indices comparing the perennial plants near the five midden rockshelters yielded values of 0.43 to 0.91 (av. 0.70). Although the exposure of the sites varied from south to southwest to east, differences in similarity in the flora appeared not to be related to slope. The basic similarities of all sites and the inherent site-to-site variability in the composition of the desertscrub communities reflects the hot, dry climate with highly variable precipitation. Local microhabitat features such as steepness of slope, size of

cliffs, and amount of shade produced by the local bedrock configuration are usually more important than general aspect. The intersite variability in the modern flora is of a magnitude similar to that found between midden assemblages through time.

DISCUSSION

Holocene Floristic History

Early Holocene.—The midden records from the Lower Colorado River Valley help us understand the unusual distributions of plants in northwestern Sonora. Populations of *Artemisia ludoviciana* (white sage), *Berberis haematocarpa* (barberry), *Opuntia chlorotica* (silver dollar cactus), *Rhus aromatica* (skunk bush), *Salvia mohavensis* (Mojave sage), and *Stipa speciosa* occur only above about 650 to 800 m elevation on Pinateate Peak (Felger, unpublished) and are restricted to north-facing slopes or cliffs on the north side of the mountain mass. These populations are relicts of extensive late Wisconsin and early Holocene distributions. Isolated

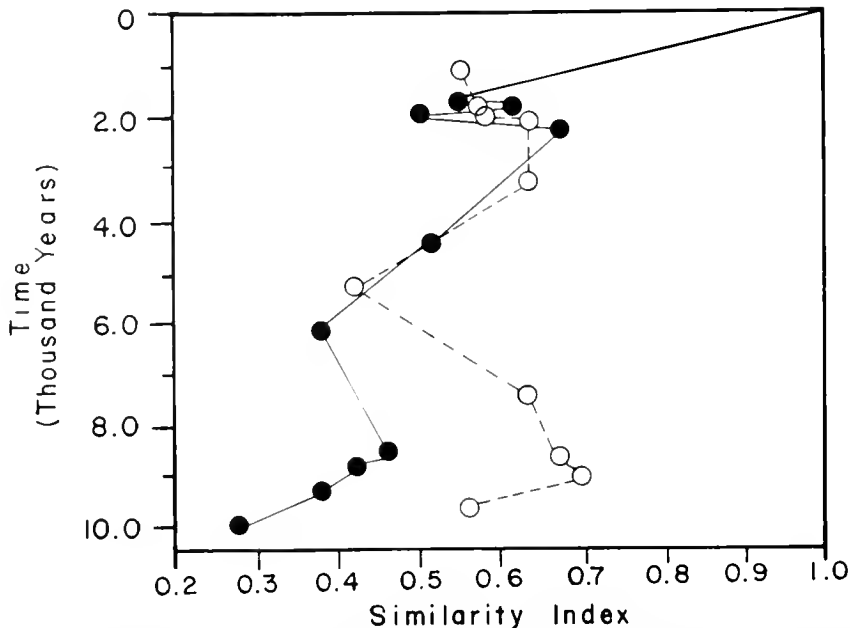


Figure 4. Sorenson's index of similarity comparing long-lived perennial plants from the Hornaday Mountains of northwestern Sonora, Mexico. Comparison of packrat midden assemblages to the modern flora within 30–50 m of the site (solid line, closed circles) reflects modernization of the flora. Comparison of midden assemblages to the next youngest sample (open circles, dashed line) illustrates variability in community composition through time. The youngest assemblage was compared with the modern flora at site. Data points plotted between radiocarbon dates.

populations of *Ambrosia acanthocarpa* (burweed) in sandy areas along Highway 8 between Sonoyta and Puerto Peñasco, of *Nolina bigelovii* (Bigelow beargrass) in the Sierra del Rosario, Sierra los Alacranes, and Cerro Pinto (Felger, 1980), and of *O. basilaris* (beavertail cactus) and *Yucca whipplei* (Whipple yucca) in the Sierra los Alacranes reflect expansions not recorded in the Hornaday samples. *Ephedra nevadensis*, which is scattered in the lower ranges and reaches its southern range limits in Sonora in the Pinacates, was widespread and abundant in the early Holocene.

Ericameria cuneata, *E. laricifolia* (turpentine bushes), *Monardella arizonica*, and *Salvia pinguifolia* (rock sage) were identified from older middens from the Puerto Blanco and Tinajas Altas mountains but were not in the Hornaday samples. The closest populations today are in the Ajo Mountains in Organ Pipe Cactus National Monument (100 km ENE). If their late Wisconsin ranges included the Pinacate they were extirpated in the Holocene. Other species found in Ajo Mountains middens that may have been in Wisconsin woodlands of Pinacate Peak include *Berberis harrisoniana* (Harrison barberry), *Ceanothus greggii* (buckbrush), and *Quercus turbinella* ssp. *ajoensis* (Ajo oak).

The absence of *Opuntia acanthocarpa* (buckhorn cholla) from the Hornaday middens and the Pinacate today is surprising because the species occurs in middens of various ages from other Sonoran Desert sites and is widespread in the Sonoran and Mohave deserts today. Similarly, the absence of *Ambrosia ilicifolia* (hollyleaf bursage), a distinctive shrub endemic to the Lower Colorado River Valley, from the Hornaday middens or modern flora is interesting as this species is abundant in early Holocene samples from the Butler and the Tinajas Altas mountains (60–75 km NNW) and in the modern flora of the Sierra del Rosario (50 km W) and other granitic mountains of northwestern Sonora. Apparently their ranges did not expand as far to the southeast during the early Holocene as did those of some of their modern associates.

The vegetation and climate of the early Holocene in the Hornadays and other areas of the Sonoran Desert were transitional between those of the late Wisconsin and more modern times. Except for a few species, the vegetation was a desert scrub composed of plants that still occur in the region. Important Sonoran species such as *Bursaria microphylla*, *Carnegiea gigantea*, and *Cercidium microphyllum* were present. However, the community reflects an environment more mesic than today's with species now restricted to washes such as *Acacia greggii*, *Bebbia juncea*, and *Prosopis velutina* growing on exposed slopes. Plants that are now rare and apparently limited by aridity were more widespread, e.g., *Agave deserti*, *Brickellia atracyloides*, *B. coulteri*, *Ephedra nevadensis*, *Eriogonum fasciculatum*, *E. wrightii*, *Galium stellatum*, and *Viguiera deltoidea*.

Of the annuals in the early Holocene samples ($n = 17$) 88.2% grow only in the winter–spring rainy season. Annual grasses in the middens included one winter–spring obligate (*Vulpia* sp.) and two species that flower opportunistically (*Aristida adscensionis*, *Muhlenbergia microsperma*). A few fruits of *Boerhaavia wrightii* and *Boerhaavia* sp. in two samples were the only annuals indicating warm-season moisture. The five-sided fruits of *Boerhaavia* sp. could represent *B. erecta* or *B. spicata*, found in the Pinacate. The establishment of *Carnegiea gigantea* seedlings is dependent on occasional periods of adequate summer–fall rainfall (see Steenbergh and Lowe, 1977). These data suggest the relatively mesic conditions in the early Holocene were due to an extension of winter rainfall from the Pacific frontal storms that dominated the late Wisconsin coupled with a modest increase in summer monsoons (Van Devender et al., 1987). The assertions by Spaulding and Graumllich (1986) that woodland plants such as *Juniperus californica* persisted in the early Holocene of the Sonoran Desert as rainfall shifted from winter to a summer monsoonal maximum by

9000 years ago are not supported. The results also strongly differ from the simulations of Kutzbach (1987) based on atmospheric general circulation models for North America. His climatic reconstruction for 9000 yr B.P. for the Southwest included July temperatures 1°C warmer than today's and annual precipitation greater than in both the late Wisconsin and today due to increased summer monsoons.

Middle Holocene.—In contrast, many indicators of enhanced monsoons reported from other Sonoran Desert midden sites (Van Devender, 1987, 1990) were present in the middle Holocene in the Hornadays. Trees and shrubs now restricted to washes grew on exposed rocky slopes. *Acacia greggii*, continuing from the early Holocene, declined and disappeared but was replaced by *Cercidium floridum* and *Prosopis velutina*. Middle Holocene remains of *C. floridum* on slopes have also been found in the Whipple, Butler, Tinajas Altas, and Waterman mountains. *Prosopis velutina*, a tree or shrub widespread in desert-grassland and the portion of the Sonoran Desert enjoying summer rainfall, increased in abundance until it dominated the 4430 yr B.P. samples. *Phoradendron californicum* in the 6065 and 4430 yr B.P. samples is a parasite on desert legumes that is limited by aridity at its lower elevational limit.

Bouteloua aristidoides (needle grama), *B. barbata* (six-weeks grama), and *Erioneuron pulchellum* (fluff grass) first appeared and became common in the middle Holocene. Grass fossils are typically scarce in middens, underrepresenting grasses' abundances (Van Devender et al., 1990). These grasses were probably more common in the community than their fossils (RA = 3) in the 6065 and 4430 yr B.P. samples indicate. Although these opportunistic grasses may also flower after winter–spring rains, plants grow faster, reach larger sizes, and produce more florets after summer or fall rains (Tevis, 1958).

Although the annual flora in the middle Holocene samples ($n = 19$) continued to be dominated by winter–spring obligates (78.9%), there were summer rainfall species, including *Boerhaavia wrightii*, *Dicoria canescens* (bugseed), *Kallstroemia* sp., and *Pectis papposa* (chinchweed). Increases in the abundance of *Allionia incarnata* probably signal increases in summer perennial habit rather than as a winter–spring annual. Peak abundances of *Bouteloua aristidoides*, *Carnegiea gigantea*, *Cercidium floridum*, *Erioneuron pulchellum*, *Hyptis emoryi*, and *Larrea divaricata* were in the 6065 yr B.P. sample. Today the distributions of plants in the Pinacate are strongly correlated with rockiness, as discrete communities are found on different substrates, including rocky slopes and sand dunes (Ezcurra and López-Portillo, 1987). The presence of *D. canescens* and other sand-loving species, including *Hilaria rigida*, *Opuntia ramosissima*, and *O. kunzei*, on rocky slopes at 6065 yr B.P. may indicate strong southwesterly winds that blew sand from the lowlands onto the mountain side. Southerly winds transport sands northward from the Bahia del Adair in the Gulf of California (Fig. 1). These indications are in opposition to the conclusions of Lancaster et al. (1987), who suggested that the last major accumulation of sand in the Gran Desierto was in the middle Holocene from high-velocity northerly winds transporting sediments from the Colorado River. These records suggest that the middle Holocene was the time of maximum monsoonal development.

Several other aspects of the middle Holocene record are interesting. The 8660 yr B.P. sample shared a few species not found in the range today (*Bebbia juncea*, *Eriogonum fasciculatum*) as well as high abundances of *Acacia greggii* and *Ephedra nevadensis* with the early Holocene samples. In contrast both the 4430 and 2320 yr B.P. samples had high abundances of *Carnegiea gigantea*, *Olneya tesota*, and *Prosopis velutina*. Although *C. gigantea* was present throughout the Holocene, its abundance peaks in the 6065 to 2320 yr B.P. samples. In the Puerto Blanco Mountains its midden records are very similar, with its appearance by 10,540 yr B.P., continued

presence through the Holocene, and dominance from 7970 to 3440 yr B.P. (Van Devender, 1987). In the Tinajas Altas Mountains, *C. gigantea* was in six samples from 8970 to 1230 yr B.P. but common only at 8970 and 8650 yr B.P. In the Butler Mountains it was present but scarce in samples dated at 11,250, 11,060, 8160, and 3820 yr B.P. and is uncommon today. We suspect the few seeds in older juniper samples are younger contaminants.

Olneya tesota first appeared in the Hornaday midden record at 8660 yr B.P. and increased in importance by 4430 yr B.P. It first appeared at 7560 yr B.P. in the Puerto Blanco Mountains, 7530 yr B.P. in the Butler Mountains, and 8750 yr B.P. in the Wellton Hills. Questionable records of 9900 and 8700 yr B.P. and more reliable records of 4010 and 1230 yr B.P. are from the Tinajas Altas Mountains. *O. tesota* was a dominant in a 3820 yr B.P. sample from the Butler Mountains. In contrast, it was found only in a 110 yr B.P. sample at Picacho Peak and not at all in the Whipple Mountains on the limits of its modern range. Its disappearance from rocky slopes after 1720 yr B.P. in the Hornadays is similar to the Puerto Blanco Mountains record, where it retreated from the slopes between 1910 and 990 yr B.P.

In the Hornadays *Hyptis emoryi* was dominant only in the 6065 yr B.P. sample. It first appeared in the Puerto Blanco and Butler mountains records at 7560 and 7530 yr B.P., respectively. *Peucephyllum schottii* was found only in the 6065 yr B.P. sample. Its rarity in the midden record and absence from the Hornadays today is surprising because it is abundant in nearby MacDougal Crater, the Sierra del Rosario, the Butler and Tinajas Altas mountains, and in the midden record from other areas.

Fouquieria splendens appeared in the 4430 yr B.P. sample but was never common. In the Puerto Blanco Mountains it was uncommon in samples dated at 3440 and 130 yr B.P. In the Tinajas Altas Mountains a few thorns were in samples dated at 5080 and 4010 yr B.P. In the Butler Mountains it was common in a single sample dated at 740 yr B.P. At Picacho Peak it was found only in a 110 yr B.P. and two modern samples (Cole, 1986). In the Whipple Mountains today, *F. splendens* is present with *Olneya tesota* below about 320 m but it apparently did not reach the midden sites at 365–525 m. Because the abundance and geographic, elevational, and ecological ranges of *F. splendens* are so great and because packrats readily eat its bark and stems, the poor record is enigmatic.

Late Holocene.—With declines in *Larrea divaricata* and increases in *Olneya tesota* in the late Holocene, the vegetation of the Hornadays became essentially a wetter version of today's desertscrub. *Prosopis velutina* was a dominant in the 2320 yr B.P. sample before disappearing from the sites. *Carnegiea gigantea* declined after 2320 yr B.P. *Allionia incarnata* continued to be common and outnumbered *Encelia farinosa* and *O. tesota* in the 1930 and 1720 yr B.P. samples. Peak abundances such as these probably indicate heavy fall rainfall from the huge late summer–fall storms from the tropical Pacific (chubasco; Pyke, 1972). The annual flora ($n = 17$) continued to be dominated by winter–spring annuals (82.4%) with few summer species (*Boerhaavia wrightii*, *Boerhaavia* sp., and possibly *Amaranthus* sp.). The hot summers and high evaporation of the Gran Desierto currently favor spring annuals, which comprise 39 species. However, warm-season annuals can occur in huge numbers with enormous biomass after a chubasco. Unpublished floral surveys of the granitic ranges of northwestern Sonora suggest that about 25 species of summer ephemerals appear and flourish when adequate moisture is present. In the Arizona portion of the Sonoran Desert, they mostly flower in summer or fall. The warmer winters of the Gran Desierto and the coast of the Gulf of California induce many species to flower in winter and spring as well. Only a few species, e.g., *Amaranthus palmeri* (pigweed), *B. wrightii*, *Dicoria canescens*, and *Tidestromia lanuginosa* (espanta vaqueras), grow only in summer and fall.

The late arrivals of *Ambrosia deltoidea*, *Argythamnia* cf. *lanceolata*, and *Jatropha cuneata* in the Hornadays are interesting. *Ambrosia deltoidea* is a dominant subshrub in Arizona Upland communities to the east in Arizona and Sonora. *Argythamnia lanceolata* is a widespread subshrub of rocky slopes in the Sonoran Desert. It first appeared in the Puerto Blanco Mountains midden record at 3480 yr B.P.

Jatropha cuneata is a succulent-stemmed, frost-sensitive desert shrub that is widespread on rocky slopes at low elevations in Sonora and Baja California and in Arizona from the Tinajas Altas Mountains to the Puerto Blanco Mountains. It was scarce in the 1720 yr B.P. Hornaday midden but is a dominant at the sites today. In the Puerto Blanco Mountains it was not found in the Holocene middens but is abundant at the Twin Peaks site today. *Jatropha cuneata* was a dominant in a 1230 yr B.P. sample from the Tinajas Altas Mountains.

The shift to a more xeric vegetation after 1720 yr B.P. and the very xeric nature of the modern vegetation at the Hornaday sites resemble the sequence reported for the Puerto Blanco Mountains (Van Devender, 1987). In that study desertscrub assemblages indicated summer rainfall somewhat greater than today's from 3480 to 1910 yr B.P. Samples dated at 990 and 980 yr B.P. reflected an even wetter period. Samples dated at 130 and 30 yr B.P. signaled essentially modern community composition and climate, although the vegetation at the sites today is even more sparse. The Hornaday vegetation was probably more dynamic than our midden results indicate because samples from the inferred mesic period at about 1000 yr B.P. were missing. Photographic rematches from MacDougal Crater record massive die-offs of *Cercidium microphyllum* and *Larrea divaricata* due to prolonged drought from 1936 to 1964 (Turner, 1990). The final "desertification" of these areas took place apparently in this century and was due to regional (or global) climatic changes unrelated to such human activities as grazing and fuelwood cutting.

Historical Biogeography

The midden fossils illuminate the biogeographic affinities in the flora and document dispersals. During the late Wisconsin and early Holocene, the present Sonoran Desert supported species from the Mohave Desert and adjacent California juniper woodland/desertscrub from Arizona and California south to northwestern Sonora and northern Baja California. The early Holocene samples from the Hornadays suggest that the influences from these sources declined along the latitudinal and elevational gradients toward the Gulf of California. A corridor connecting the floras of Baja California and Sonora was apparently well developed for widespread desert species such as *Ephedra nevadensis*, *Eriogonum fasciculatum*, *Larrea divaricata*, and *Viguiera deltoidea*. The paleoclimatic significance of the absence of fossils of *Fouquieria columnaris* (boojum tree), *Pachycormus discolor* (elephant tree), and *V. laciniata* (San Diego goldeneye), apparently indicating a lack of northward movements of dominants of arid Baja California, needs additional study.

Typical dominants such as *Carnegiea gigantea* and *Cercidium microphyllum* retreated from the present Arizona Upland during the glacial and returned during the Holocene as summer rainfall increased. Unfortunately the Hornaday records are not old enough to document the ice age presence of these species or those of *Bursera microphylla* or *Encelia farinosa*. If they were displaced to the southeast by summer drought and cooler winters, it was probably not far. Certainly *Carnegiea gigantea* and *E. farinosa* expanded into Arizona very quickly after 11,000 yr B.P.

The dispersals of other desert species into their modern ranges had different patterns. *Larrea divaricata* was an important member

of late Wisconsin woodland and desertscrub below 330 m. In the Holocene, it dispersed rapidly into the Mohave Desert in California, reaching the Marble Mountains by 7930 yr B.P. (Spaulding, 1990) and the Lucerne Valley by 5880 yr B.P. (King, 1976). In contrast, *L. divaricata*, perhaps the Sonoran Desert tetraploid chromosomal race, did not appear in the Puerto Blanco Mountains until 3400 yr B.P. However, a recent tandem accelerator mass spectrometer (TAMS) radiocarbon date from the Waterman Mountains west of Tucson establishes the presence of *L. divaricata* in the north-eastern Sonoran Desert by 6195 yr B.P.

If the two early Holocene records of *Cercidium microphyllum* are not contaminants, that species was present in the Hornadays 4000 years earlier than its arrival in the Puerto Blanco Mountains (75 km E) by 5240 yr B.P. *Cercidium floridum* and *Olneya tesota* reached Arizona sites soon after they were recorded in middle Holocene samples in the Hornadays. *Bursera microphylla* was present throughout the Holocene in the Hornadays but reached the Tinajas Altas Mountains (55 km N) only by 5820 yr B.P.

In the Puerto Blanco Mountains, the late Holocene is characterized by the arrival of more subtropical Sonoran Desert species, including *Ferocactus emoryi* (Coville barrel cactus, *F. covillei* of Munz, 1974), *Sapium biloculare* (Mexican jumping bean), and *Stenocereus thurberi* (organ pipe cactus). These species occur in the Pinacate but apparently did not reach the Hornadays. Probably the present gradient of aridity between the Arizona Upland and Lower Colorado River Valley subdivisions was established about 4000 years ago. And finally, some species such as *Jatropha cuneata* appear to have reached the Hornadays and the Arizona sites during the last 1300 years. Effective invasions appear to be related to changes in regional climate at various levels of intensity and the dispersal abilities of the individual species. *Jatropha cuneata* with its large seed may have difficulty dispersing northward during warm periods and establishing populations large enough to endure subsequent freezes.

Late-Glacial Deserts

Plant macrofossils in late Wisconsin and early Holocene middens have revealed expansions of woodland communities into the modern warm deserts in much of the southwestern United States (Van Devender et al., 1987). Assemblages of late Wisconsin age without woodland dominants were found at 240–300 m elevation in the Picacho Peak area on the California side of the Colorado River just north of Yuma, Arizona (Cole, 1986). *Larrea divaricata* has been in the area for the last 13,000 years and probably for much of the Pleistocene after its immigration from South America, presumably in a Pleistocene interglacial (Wells and Hunziker, 1976). Four late Wisconsin (13,380 to 11,160 yr B.P.) Picacho Peak samples contained low levels of *Chrysothamnus teretifolius*, *Coleogyne ramosissima* (blackbrush), *Ephedra nevadensis*, *Ferocactus cylindraceus*, *Opuntia acanthocarpa*, *Salvia mohavensis*, *Yucca brevifolia* (Joshua tree), and *Y. whipplei*. In the early Holocene *E. nevadensis* increased in abundance as Mohave Desert species including *Chrysothamnus teretifolius*, *Coleogyne ramosissima*, *S. mohavensis*, *Y. brevifolia*, and *Y. whipplei* declined or disappeared. *Encelia farinosa* and *Peucephyllum schottii* appeared and became codominants by 10,540 yr B.P. Interestingly, *Ambrosia dumosa* and *Olneya tesota* did not appear in the midden record until a few hundred years ago.

Other midden studies in the Lower Colorado River Valley help define the limits of the late-glacial desert (Van Devender et al., 1987; Van Devender, 1990). In the Whipple Mountains of California to the north along the Colorado River, *Juniperus californica* was dominant in late Wisconsin and early Holocene woodlands on rhyolite at 320–525 m. *Pinus monophylla* was present above 510 m

prior to about 11,000 yr B.P. Wells and Hunziker (1976) reported *J. osteosperma* (Utah juniper) at 16,900 yr B.P. from 258 m elevation in the Chemehuevi Mountains, 35 km north of the Whipple Mountains. The simultaneous disappearance of *J. californica* and *Yucca whipplei* from the Whipple Mountains sites about 8900 years and increases in abundances of *Larrea divaricata* and *Peucephyllum schottii* mark the end of the early Holocene. *Ambrosia dumosa* did not become important in the area until 5020 yr B.P. The lowest midden site (320 m) supported a woodland dominated by *J. californica* and *Y. brevifolia* with *L. divaricata* at 11,015 yr B.P. (Van Devender, 1990). Codominants in the assemblage were *Nolina bigelovii*, *Opuntia acanthocarpa*, and *Salvia mohavensis* with lesser amounts of *Atriplex confertifolia* (shadscale), *Eriogonum fasciculatum*, *Ferocactus cylindraceus*, and *Y. baccata* (banana yucca).

The Wellton Hills midden sites are at 160–180 m on granite near the Gila River 35 km east of its junction with the Colorado River, 45 km east-southeast of Picacho Peak, and 85 km north-northwest of the Hornadays. A sample dated at 10,750 yr B.P. was dominated by *Encelia frutescens* (green brittlebush), *Ephedra nevadensis*, *Larrea divaricata*, and *Salvia mohavensis*. Less common species were *Brickellia atractyloides*, *Castela emoryi* (Sonoran crucifixion thorn), *Eriogonum fasciculatum*, *Ferocactus cylindraceus*, and *Gymnosperma glutinosum* (tatalencho). At 8750 yr B.P., *Ephedra nevadensis* and *L. divaricata* continued to dominate as *Acacia greggii*, *Ambrosia dumosa*, *Olneya tesota*, *Peucephyllum schottii*, and *Prosopis velutina* became important. A sample at 8150 yr B.P. was similar, with dominance by *Ephedra nevadensis* and *L. divaricata* and most of the associates. *Acacia greggii*, *Olneya tesota*, and *Prosopis velutina* were absent. *Carnegiea gigantea*, *Encelia farinosa*, *Opuntia acanthocarpa*, and *O. bigelovii* were not found.

The Butler Mountains are a small granitic range west of the Tinajas Altas Mountains on the eastern edge of the Yuma Mesa, the Arizona extension of the Gran Desierto (Fig. 1; 74 km NNW). *Juniperus californica* was a codominant in samples from 240–250 m dated at 11,060 and 10,360 yr B.P. with *Ambrosia dumosa*, *Encelia farinosa*, *Ephedra nevadensis*, *Ericameria laricifolia*, *Eriogonum fasciculatum*, *Koerberlinia spinosa* (allthorn), *Larrea divaricata*, and *Salvia mohavensis*. *Ambrosia ilicifolia*, *Carnegiea gigantea*, *Echinocactus polycephalus* (cotton-top barrel cactus), *Ferocactus cylindraceus*, *Opuntia bigelovii*, *O. ramosissima*, and *Stipa speciosa* were present in small quantities. *Ambrosia ilicifolia* is restricted to desert ranges in the lower Colorado River Valley. Interestingly, *L. divaricata* twigs in a sample differing only in the presence of a few twigs of *J. californica* yielded a date of 11,250 yr B.P. (Van Devender et al., 1985). A sample dated at 8160 yr B.P. was dominated by *Acacia greggii*, *Ambrosia ilicifolia*, *Encelia farinosa*, *Ephedra nevadensis*, *L. divaricata*, and *Peucephyllum schottii* with lesser abundances of *Ambrosia dumosa*, *C. gigantea*, *Echinocactus polycephalus*, *F. cylindraceus*, *Krameria erecta* (including *K. parvifolia*; range ratany), and *Lycium macrodon* (wolfberry). By 7530 yr B.P. *Acacia greggii* and *Prosopis velutina* disappeared, *Ephedra nevadensis* declined markedly, and *Hyptis emoryi* and *Olneya tesota* appeared in the record.

A full-glacial sample from 330 m in the nearby Tinajas Altas Mountains records a woodland dominated by *Juniperus californica*, *Chrysothamnus teretifolius*, *Larrea divaricata*, *Yucca brevifolia*, and *Y. whipplei* with lesser abundances of *Agave deserti*, *Encelia farinosa*, *Ephedra nevadensis*, *Ericameria laricifolia*, *Eriogonum fasciculatum*, *Monardella arizonica*, *Nolina bigelovii*, *Prosopis velutina*, and *Salvia mohavensis*. A TAMS date of 18,700 yr B.P. on twigs from the sample is the oldest record for *L. divaricata*, the widespread dominant in the warm deserts of North America. Higher elevations in the Tinajas Altas supported more mesic woodlands.

The lowest elevational record for *Pinus monophylla* was from 460 m at 11,040 yr B.P. Leaves of *Ambrosia dumosa* from a sample from 580 m elevation yielded an age of 10,600 yr B.P. (Van Devender *et al.*, 1985).

The Puerto Blanco Mountains are on the edge of the Arizona Upland in Organ Pipe Cactus National Monument (75 km E). A 14,120 yr B.P. sample from 565 m on rhyolite was dominated by *Juniperus californica*, *Opuntia whipplei* (Whipple cholla), and *Yucca brevifolia*, with significant amounts of *Agave deserti*, *Chrysothamnus teretifolius*, *Ericameria laricifolia*, and *Salvia mohavensis* (Van Devender, 1987). *Eriogonum wrightii*, *Monardella arizonica*, *Opuntia chlorotica* (silver dollar cactus), and *Yucca whipplei* were present in small quantities. Four early Holocene samples (10,540 to 9070 yr B.P.) record a shift to a Sonoran desertscrub similar to the contemporaneous Hornaday vegetation, i.e., dominance by *Encelia farinosa*, rarity of *J. californica*, and lesser abundances of *Acacia greggii*, *Carnegiea gigantea*, *Ephedra nevadensis*, and *Prosopis velutina*. Interestingly, *Larrea divaricata* did not appear in the Puerto Blanco samples until 3400 yr B.P.

Set in this regional framework, the Hornaday samples provide additional perspective. The single twig of *Juniperus cf. californica* in the 9370 yr B.P. sample dominated by *Encelia farinosa*, *Ephedra nevadensis*, and *Larrea divaricata* indicates that it may have been near its lower elevational limits at 260 m. In light of the magnitude of vegetation change reflected in contemporaneous samples from the Picacho Peak area and the Butler Mountains, the late Wisconsin vegetation of that of the Hornadays was probably a slightly more mesic version of the early Holocene with a little more *J. californica*, *Chrysothamnus teretifolius*, and *Eriogonum fasciculatum*. *Nolina bigelovii*, *Salvia mohavensis*, and *Yucca whipplei* may have reached the area as well. From the top of Pinacate Peak at 1290 m to the Gulf of California, a pinyon-juniper woodland with *Pinus monophylla* probably grew above 610 m, a juniper woodland/chaparral with *J. californica* and associates extended down to perhaps 280 m, and Sonoran desertscrub with additional Mohave desert elements occurred at lower elevations. The paleowoodland on the north slope was probably better developed and supported more mesic and northern plants than did the south slope.

Another factor contributing to the area of the ice age desert was sea level lowering of 120 ± 60 m at the Wisconsin glacial maximum (18,000 yr B.P.) as water from the oceans was incorporated into continental and montane glaciers (Bloom, 1983). A lowering of this magnitude would expose significant areas at the head of the Gulf of California, increasing the area of the Gran Desierto markedly. By 10,000 yr B.P. sea levels on the west coast of the United States had risen to within about 50 m of today's.

Evolution and Community Stability

Axelrod (1979) placed the origin of the Sonoran Desert and the major evolutionary radiation of its unique plants in the latest Miocene, 5 to 8 million years ago, reflecting the culmination of general trends toward aridity that began about 15 million years ago as the Rocky Mountains and Sierra Madre Occidental were uplifted. About 14 million years ago rifting opened the proto-Gulf of California and isolated several large islands from mainland Mexico (Murphy, 1983). By the end of the Miocene the land mass had moved northward to meet California and form the Baja California Peninsula. About 3 to 4 million years ago the Gulf of California extended to the San Geronio Pass area east of Los Angeles, increasing the isolation of Baja California. In response to these events the Baja California Peninsula has been a secondary arena for the evolution of the Sonoran Desert biota. During the 15–20 glacials of the 1.8 million years of the Pleistocene (Imbrie and Imbrie, 1979), temperate woodlands were probably widespread, with the

ranges of most subtropical Sonoran Desert species contracted into southern refugia.

In the 1920s and 1930s, Henry A. Gleason and Forrest Shreve, a pioneering desert ecologist with the Carnegie Desert Botanical Laboratory on Tumamoc Hill, championed the individualistic theory of plant communities (see Bowers, 1988). They felt that each species had its own distribution, physiological tolerances, and evolutionary history, and that communities were dynamic associations of them. The palynologist Margaret D. Davis (1986) has expressed a similar concept from a paleoclimatic perspective, i.e., community composition varies continuously as species respond differently to climatic fluctuations on scales from years to millennia, and rarely if ever reaches equilibrium. The plant macrofossils preserved in packrat middens from the Hornadays and other ranges and studies by later generations of Tumamoc Hill desert ecologists provide elegant support for this concept from the arid core of the Sonoran Desert. Interestingly, today all of the species in the early Holocene samples from the Hornadays can be found in association either within the region today or at the chaparral/desertscrub ecotone on the western edge of the Sonoran Desert in southeastern California or northern Baja California. Late Wisconsin and early Holocene assemblages from higher areas in the Sonoran Desert yielded numerous anomalous associations of species whose ranges no longer overlap (Van Devender, 1990).

ACKNOWLEDGMENTS

Laurence J. Toolin identified the grass fossils. Donald J. Pinkava and Bruce Parfitt examined an unknown cactus stem. Peter L. Kresan provided the photograph for Figure 2. Charles T. Mason and Rebecca K. Van Devender have helped with the thousands of voucher specimens deposited into The University of Arizona Herbarium. The careful reviews and editing of J. Platt Bradbury, Arthur H. Harris, Philip Unitt, and Robert S. Thompson improved the manuscript. Funds were provided by the Southwest Parks and Monuments Association through Organ Pipe Cactus National Monument. Fernando Chiang and Carol Madeheim translated the Resumen. Jean Morgan processed the manuscript. Dana Dornier drafted the figures.

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