FULL-GLACIAL VEGETATION OF DEATH VALLEY, CALIFORNIA: JUNIPER WOODLAND OPENING TO *YUCCA* SEMIDESERT

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ABSTRACT

Full-glacial (13,000–19,000 yr BP) wood rat (*Neotoma*) deposits from Death Valley establish a 1200–1500-m displacement of juniper woodland below modern, mountaintop relicts of *Juniperus osteosperma.* At an elevation of 425 m, however, there was full-glacial (19,550 yr BP) semidesert dominated by chaparral yucca (*Yucca whipplei*) with minor Joshua tree (*Y. brevifolia*). The late Pleistocene climate must have been much less arid and more equable with cooler summers than at present. Modern, hot-desert vegetation appeared at the 425-m site between 11,000 and 10,000 yr BP. The shift from pluvial woodland to hyperarid desert at 775 m was time-transgressive during 13,000–9000 yr BP, as is documented by three dated transitional stages of semidesert from this site.

Death Valley, California, a northern extremity of the Mohave Desert, is now one of the hottest and driest places on earth, but there is evidence that the extreme aridity of the modern climate is less than 11,000 years old. Wood rat (*Neotoma*) middens (Wells 1976) from very low elevations in Death Valley (Fig. 1) provide a detailed macrofossil record (thousands of leaves, twigs, seeds, etc., in many separate deposits) of late Pleistocene and Holocene vegetation over the past 20,000 years, whence the magnitude and nature of climatic change may be inferred. A more generalized indication of vegetational change during this time span is apparent from the pollen records at Tule Springs to the east in Nevada (Mehringer 1967) and at nearby Searles Lake, California (Roosma 1958).

Neotoma macrofossil records from the Amargosa Range, which flanks Death Valley on the east, indicate that late-Pleistocene Juniper Woodland (dominated by *Juniperus osteosperma*) grew in the elevational range 1130–1280 m (Fig. 1a, b), on slopes now occupied by creosote bush scrub. The highest site (a), on the northeast slope of Pyramid Peak at 1280 m, yielded a late-glacial (11,800 yr BP) record of relatively mesophytic juniper woodland with montane gooseberry, mountain mahogany, and shrubby ash (Wells and Berger 1967). A new and significant (though rare) component of this assemblage in the context of the other records reported here (Table 1) is *Yucca whipplei.*

At much lower elevations on the west flank of Death Valley (Fig.

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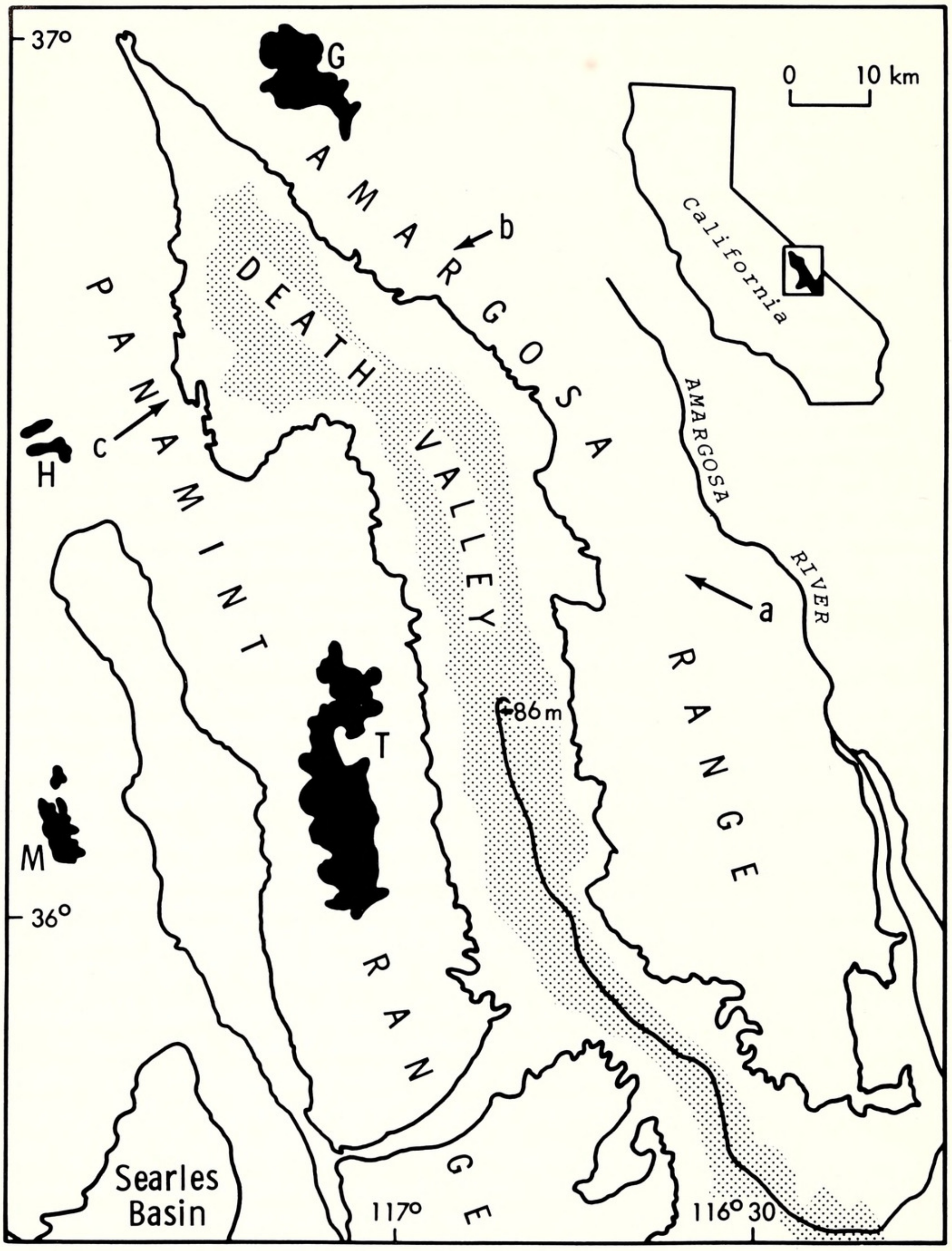

FIG. 1. Death Valley and surrounding region of eastern California (see inset). Solid line delimiting Death Valley and adjacent basins is the 610-m contour, which estimates the pleniglacial extent of juniper woodland. Stippled area in Death Valley approximates the high stands of Pleistocene Lake Manly (see text). Present-day woodlands and montane zones (black areas) are restricted to elevations above 1950 m on high mountains: G, Grapevine Pk., 2679 m (Grapevine Mts.); H, Hunter Mtn., 2272 m and T, Telescope Pk., 3368 m (Panamint Range); M, Maturango Pk., 2694 m (Argus Range). Locations of Quaternary *Neotoma* macrofossil records: (a,b) Amargosa Range: a, 1280 m (Wells and Berger 1967); b, 1130 m (M. D. Kelly, in Van Devender 1977); (c) Panamint Range, 775 m, 425/414 m, and 260 m (this report).

TABLE 1. PRINCIPAL WOODY PLANT SPECIES OF DATED MACROFOSSIL DEPOSITS FROM DEATH VALLEY, CALIFORNIA. Deposits are listed by elevation and age (^{14}C years BP). Relative abundances of species in deposits are indicated as high (principal constituent: +++); intermediate (++); and low (+). The two highest sites at 1280 m and 1130 m are from the Amargosa Range on the east side of Death Valley; all other sites in foothills of Panamint Range are on the west side (cf. Fig. 1). Direction of slope surrounding rock shelter or cave harboring *Neotoma* middens: north-facing (n.); south- (s.); east- (e.). Laboratory numbers for ^{14}C dates are in order given (left to right): UCLA-755, UCR-347, GX-7807, GX-7806, GX-7804, GX-7805, GX-7811, GX-7810, GX-7812, GX-7809, GX-7808.

	1280 m (n.)	1130 m (?)	775 m (n.)				425 m (s.)			414 m (s.)	260 m (e.)
Trees, shrubs	11,600 ±160	9680 ±300	13,060 ±460	11,210 ±380	9455 ±310	9090 ±300	19,550 ±650	17,130 ±550	10,230 ±320	900 ±130	1990 ±160
Juniperus osteosperma	+++	+++	+++				+				
Ribes montigenum	+										
Fraxinus anomala	+										
Cercocarpus ledifolius	+										
Yucca brevifolia		+					+				
Yucca whipplei	+			++			+++	++			
Atriplex confertifolia			+				+	+			
Chrysothamnus teretifolius				++	+			++			
Purshia glandulosa				++	++						
Haplopappus cuneatus					+	++					
Opuntia basilaris				+	+	++	+	+			
Ambrosia dumosa									+++	++	++
Larrea tridentata										+++	+++

1c) new *Neotoma* records extend the late-glacial (ca. 13,000 yr BP) lower limit of juniper woodland to below 775 m, a level that now supports an extremely sparse, hot-desert scrub of *Larrea* and *Ambrosia dumosa.* Pleniglacial (=full-glacial) deposits from a south-facing site at 425 m contain an unusual abundance of yucca leaves (chiefly *Y. whipplei*; some *Y. brevifolia*), a number of semidesert or cool-desert shrubs, and only occasional twigs of juniper in a large volume of matrix; two of these assemblages yielded dates of 19,550 and 17,130 yr BP (Table 1). The classical Wisconsinan glacial maximum is dated at 18,000 yr BP.

Juniperus osteosperma (cf. Fig. 2a) is now dominant only at elevations above 1950 m in the higher parts of the Panamint Range, some 15–20 km distant from its documented Pleistocene occurrences in the foothills bordering the western floor of Death Valley (Fig. 1). Junipers are no longer extant in the lower and drier Funeral Range (to 2040 m) on the east side of the valley. The late-glacial abundance of juniper (thousands of leafy twigs) at the 775-m, north-facing site, together with the recovery of a few traces of juniper twigs from the pleniglacial, *Yucca*-dominated deposits at 425 m (south-facing), indicates a Pleistocene displacement of 1200–1500 m for juniper. This is one of the most extreme and well-documented Quaternary shifts thus far established for any species or zone in western North America; the exceptional magnitude is especially significant because of the modern aridity of Death Valley.

The geographic extent of the vegetational change near Death Valley is indicated in Fig. 1, where the drastically shrunken mountaintop areas of the modern woodland and higher zones are shown in black; the minimal late-Pleistocene (Wisconsinan) extent of juniper woodland is estimated by the 610-m contour. Thus, most of the mapped area above the valley floor was probably wooded during the last glacial. The extraordinary vegetational displacement documented in Death Valley reflects both the magnitude of relatively recent climatic changes and the unusually large range of elevation locally available for their expression.

A Zone of Chaparral *Yucca* in Death Valley

In contrast to the juniper-dominated woodland assemblages, the semidesert of yuccas indicated by the deposits at 425 m has no modern analog at higher elevations on nearby mountains, so far as is now known. The principal pleniglacial species at the lowest (425-m) site was *Yucca whipplei* (Fig. 2b), a mild-climate rosette-shrub with very distinctive, grooved leaf-surfaces (lacking a smooth cuticular sheath). This *Yucca* is now apparently absent in the Death Valley region, despite the extensive elevational/climatic gradients available on the higher mountain ranges. On the other hand, the

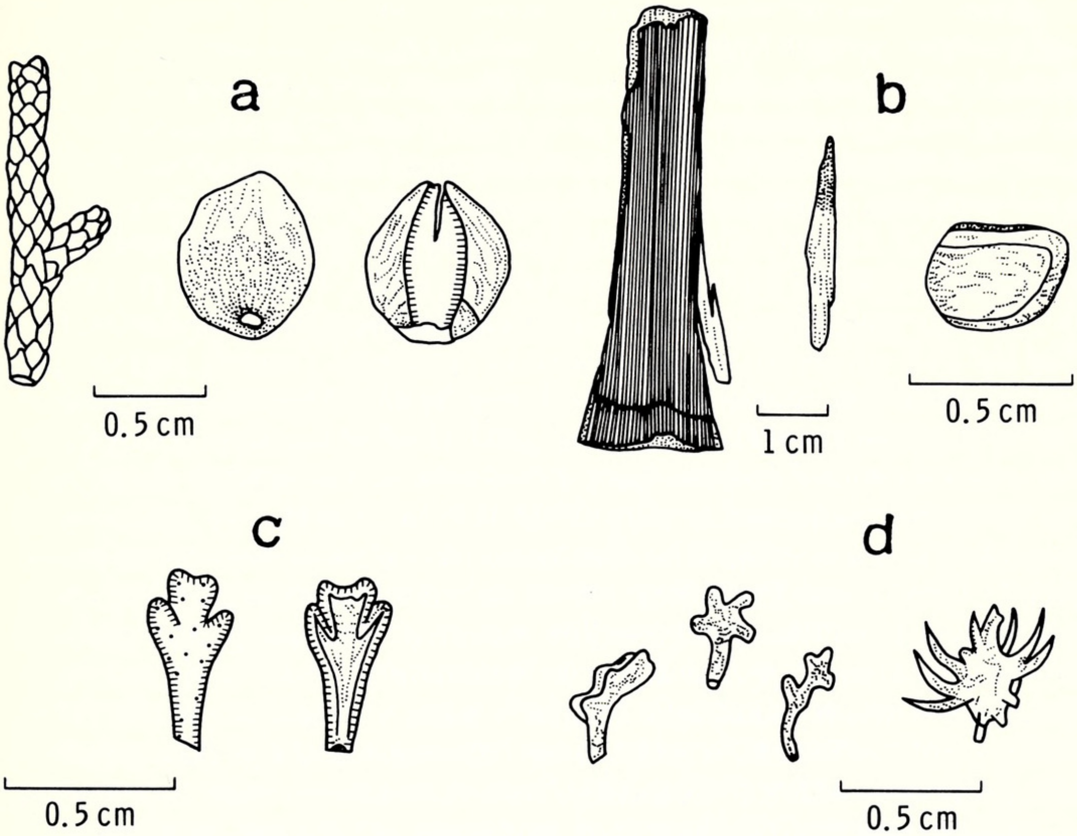

FIG. 2. Drawings of representative specimens among the many thousands of plant macrofossils in late Pleistocene *Neotoma* middens from near the floor of Death Valley: (a) *Juniperus osteosperma*: leafy twig and seeds. (b) *Yucca whipplei*: leaf base and tip, seed. (c) *Purshia glandulosa*: upper and lower surface of leaf. (d) *Ambrosia dumosa*: leaf fragments and fruit.

arborescent *Yucca brevifolia,* a more xerophytic and cold-tolerant species, was also present near the floor of Death Valley at 19,550 yr BP but now occurs only above about 1700 m on the slopes of some of the higher mountains. Of course, Joshua tree woodlands are the most characteristic modern feature of the higher or less arid sectors of the Mohave Desert, of which Death Valley is a northern extremity.

The pleniglacial combination of *Yucca whipplei* and *Y. brevifolia,* however, is decidedly unusual today, occurring on the extreme western margins of the Mohave Desert (e.g., foothills of Tehachapi Mountains) in a zone of transition to Mediterranean climate. Minor components of the pleniglacial *Yucca* community in Death Valley (Table 1) included *Chrysothamnus teretifolius* (a cool-desert species), *Atriplex confertifolia,* and *Opuntia basilaris.* The latter two species are favorite food plants of the desert wood rat, *Neotoma lepida*; therefore their scarcity in the pleniglacial assemblages at the 425-m site was undoubtedly real. The full-glacial *Neotoma* middens clearly indicate a relatively cool semidesert near the bottom of Death Valley, comparable to the "high desert" community of the western Mohave Desert that borders the Transverse Ranges of California.

The *Yucca*-dominated semidesert may have existed only locally, however. There are much more numerous macrofossil records of low-elevation coniferous woodland occurring throughout most of the Mohave Desert, even as late as 8000–10,000 yr BP (Wells and Berger 1967, King 1976, Van Devender 1977, Wells 1983). Under full-glacial conditions, juniper-Joshua tree woodland descended as low as 258 m, even in the northern Sonoran Desert, just to the southeast of the Mohave (Wells 1974, 1983). These low-elevation Mohavean woodlands were accompanied by semidesert shrubs, but there has been no firm pleniglacial evidence of *Larrea* and *Ambrosia,* the modern codominant shrubs of the hyperarid hot desert now prevalent at most of the low-elevation *Neotoma* sites in the Mohave Desert (Wells and Hunziker 1976). In fact, increasingly numerous late-Pleistocene *Neotoma* records establish a monotonous pattern of low-elevation woodland in the Southwest, from southern California to western Texas and adjacent areas of Mexico (Wells 1966, 1969, 1974, 1976, 1979, 1983; Van Devender and Spaulding 1979). The geography of the Chihuahuan Desert (relatively high base levels) permitted species-rich pluvial woodlands of pinyon, juniper and oaks to dominate the lowlands of most, if not all, of this modern desert region (Wells 1966, 1974). Only the more subtropical Sonoran Desert, with elevations descending to sea level at lower latitudes, provided a pleniglacial refugium for the more extreme xerophytes (Wells and Hunziker 1976).

Thus, the pleniglacial record of *Yucca* semidesert on the lower slopes of Death Valley is the first direct evidence that the ubiquitous Pleistocene woodlands of the arid Southwest did not descend to local base level everywhere during the glacial maximum. Restriction of the extent of any desert vegetation at that time is indicated by several limiting factors: 1) increasing basal elevations in all directions from the uniquely low and rain-shadowed trough of Death Valley; 2) greater lowering of the more mesophytic pinyon pine and evergreen oak (as well as juniper) components of the woodland zone toward the southeast at present (associated with the increasing proportion of summer rain in that direction); a very similar pattern is documented in the pleniglacial macrofossil record (Wells 1979), with juniper descending to local base level in the eastern Mohave, northern Sonoran, and probably all of the Chihuahuan Desert; and 3) occupation of the bottoms of enclosed basins by extensive glacio-pluvial lakes (Hubbs and Miller 1948). A potentially extensive zone of semidesert or desert vegetation on the floor of Death Valley was preempted by Pleistocene Lake Manly (cf. Fig. 1); the highest stand of this lake is not well known, but it may have risen to within 250 m of the lowest *Neotoma* record of *Yucca* semidesert at 425 m above sea level (Hunt and Mabey 1966). Presence of *Atriplex confertifolia* in the full-glacial deposits at 425 m suggests the possibility of zones of *Atriplex* and other halophytes around the fluctuating margins of Lake Manly, comparable to the existing salt-desert vegetation bordering the shrunken remnants of Pleistocene lakes in the cooler, northern Great Basin (cf. Wells 1983).

Time-Transgressive Vegetational Shifts

A major upward shift of the *Yucca* semidesert in Death Valley occurred during 13,000–11,000 yr BP, signifying a large climatic change. A deposit dated to 11,210 yr BP at the 775-m site is composed, not of juniper as at 13,060 yr BP, but of *Yucca whipplei* (previously unrecorded at this site) and of shrubs now characteristic of a cooler zone transitional between woodland and desert (Table 1). Absence of juniper from this still relatively early (11,210 yr BP) record at the 775-m site is doubly significant because this site is a relatively mesic, north-facing wall of a deep canyon, and *Juniperus osteosperma* is a very xerophytic woodland species. This juniper persisted at other localities in the Mohave Desert at comparably low or somewhat higher elevations as late as 10,000 yr BP, or even as late as 8000 yr BP at a few higher sites (Wells and Jorgensen 1964, Wells and Berger 1967, Van Devender 1977, King 1976, Wells 1983).

The explanation for the much earlier upward shrinkage of juniper woodland in Death Valley probably lies in the great vertical relief of the graben and the extreme intensity of rain-shadow induced by the mountain barriers around it. No other valley within the Mohave Desert has so great an elevational span between existing lower limit of juniper woodland (at ca. 1900 m) and local base level (−86 m at Badwater) as now obtains in Death Valley, a span of nearly 2000 m. In most other sectors of the Mohave, the span is considerably less than 1000 m, well within the robust tolerance limits of *Juniperus osteosperma* under the glaciopluvial climate. In Death Valley, the uniquely wide environmental gradient from mountain slope to valley bottom apparently exceeded the tolerance limits of *Juniperus osteosperma* even under the cooler climate of the glacial maximum. Populations of the juniper growing as much as 1200–1500 m below their present lower limits were probably near the end of their tether; and they could have been trimmed back by climatic oscillations too small to affect junipers growing at slightly higher and less marginal levels elsewhere in the Mohave.

An outstanding feature of the 11,210-year-old deposit at the 775-m (north-facing) site in Death Valley is the similarity in composition to the full-glacial (19,550 yr BP) semidesert assemblage at the lowest (and south-facing) site at 425 m (Table 1). Shared dominant species include *Yucca whipplei* and *Chrysothamnus teretifolius*; presence of *Purshia glandulosa* (Fig. 2c) at the 775-m site suggests that woodland was not far above at 11,210 yr BP. The time-transgressive consistency of this *Yucca*-semidesert community seems to be an example of a simple cliseral shift of 350 m along this segment of the elevational gradient. A nearly contemporaneous (11,600 yr BP) record from 500 m higher (at 1280 m) shows *Yucca whipplei* coexisting with juniper woodland (Table 1).

The further shift to modern vegetation at the 775-m site involved at least two other stages (Table 1). About 1500 years later, at 9455 yr BP, *Yucca whipplei* had dropped out locally, but *Purshia glandulosa, Chrysothamnus teretifolius,* and other shrubs of the high desert/woodland transition still persisted. By 9090 BP, however, only two transitional species, *Haplopappus cuneatus* and *Opuntia basilaris,* remained; of the Pleistocene species, only *O. basilaris* survives in the modern creosote bush scrub at the 775-m site today.

The unfolding in ordered time sequence at this location of three transitional phases of semidesert vegetation, almost entirely distinct from both late-glacial juniper woodland and modern desert scrub, is strong evidence of a slow, secular upward shift of the woodland/desert boundary past this site in the interval 13,000–9000 yr BP. A gradual and protracted warming and desiccation of climate during this late-glacial/Holocene phase of transition is clearly indicated here. Thus, the suggestion (Van Devender 1977) of an abrupt shift from woodland to desert throughout the Southwest at about 8000 yr BP (on the basis of a few coincidental dates at scattered sites) is refuted by the present evidence and by a more detailed review of the whole Mohavean data set (Wells 1983).

The earliest appearance of vegetation similar to the existing, hot-desert scrub in Death Valley was prior to 10,000 yr BP. At the lowest and most xeric (south-facing) 425-m site, which supported *Yucca* semidesert during the full-glacial (17,000–19,500 yr BP), there is a hiatus of seven millennia, followed by a *Neotoma* record of *Ambrosia dumosa,* dated at 10,230 yr BP (Table 1). This deposit is composed entirely of remains of this *Ambrosia* (Fig. 2d), but lacks *Larrea tridentata. Larrea* and *Ambrosia* dominate the existing desert scrub at the 425-m site and throughout Death Valley from below sea level (except on saline deposits) upward to 1500 m or more.

Only the absence of *Larrea* denies characterization of the 10,000-yr BP desert scrub community as really modern; the absence of *Larrea* at 10,230 yr BP, however, may not be of climatic significance at the latitude of Death Valley. This is merely another instance, already indicated by the weight of macrofossil evidence throughout the Southwest (Wells and Hunziker 1976), of the late arrival of *Larrea* over much of its present range in North America. Within the Mohave Desert region, the earliest firmly established *Neotoma* record of *Lar-*

rea tridentata is from the Mohave River valley at 670 m (west-facing), just north of Ord Mountain and east of Daggett; the radiocarbon date of 7400 ± 100 yr BP (UCLA-759) was on a branch and leaves of *Larrea* itself, which dominated the deposit (Wells and Berger 1967). Woodland conifers were lacking in this record, but *Juniperus osteosperma* still dominated as late as 7800 yr BP at higher elevations (1006 m, south-facing site) on the south side of Ord Mountain, as indicated by the *Neotoma* records of King (1976). This juniper is now absent on Ord Mountain, which lacks woodland despite its substantially high elevation (to 1920 m), and *Larrea* ascends the mountain from all sides.

The oldest records of *Larrea* are from the much lower elevations and latitudes of the more subtropical Sonoran Desert. The *Larrea*-dominated *Neotoma* deposits from the low Wellton Hills (at 162 m), in southwestern Yuma County, Arizona, have been dated to at least 10,580 yr BP, but this does not establish the earliest possible occurrence of *Larrea* at elevations approaching sea level (see review in Wells and Hunziker 1976). It should be emphasized that these early, low-elevation records of *Larrea* are about 4° south of the substantially higher Death Valley *Neotoma* sites reported here. A time-transgressive development of the *Larrea* scrub zone in the Sonoran and Mohave Deserts is apparent. In Death Valley, two very late Holocene *Neotoma* middens dated to 900 yr BP (very close to the 425-m site) and 1990 yr BP (at 260 m) serve as a control on the unusual composition of pure *Ambrosia* at 10,230 yr BP. Both of the very recent deposits contain *Larrea* and *Ambrosia* in subequal amounts (Table 1). Thus, there is no indication of *Neotoma* discrimination against *Larrea.* Although the timing of arrival for *Larrea* is yet to be established in Death Valley, it seems clear that it was preceded by its ubiquitous modern associate in the Mohave, *Ambrosia dumosa.*

Late-Glacial/Holocene Climatic Change in Death Valley

With regard to the magnitude and nature of late Quaternary climatic change in Death Valley, the evidence presented here sheds some light on the perennial temperature vs. precipitation controversy (Brakenridge 1978, Wells 1979). A pluvial increase in precipitation is apparent from the present moisture requirements of *Juniperus osteosperma* and its 1200–1500-m displacement as the dominant species of the late-Pleistocene woodlands in Death Valley. This juniper is a relatively xerophytic species, descending at its lower limits to semidesert of *Artemisia tridentata, Atriplex confertifolia,* or *Coleogyne ramosissima*; but rarely does *J. osteosperma* descend into the hot desert of *Larrea* and *Ambrosia. Juniperus osteosperma* forms woodlands (even in the cooler, northern Great Basin) only

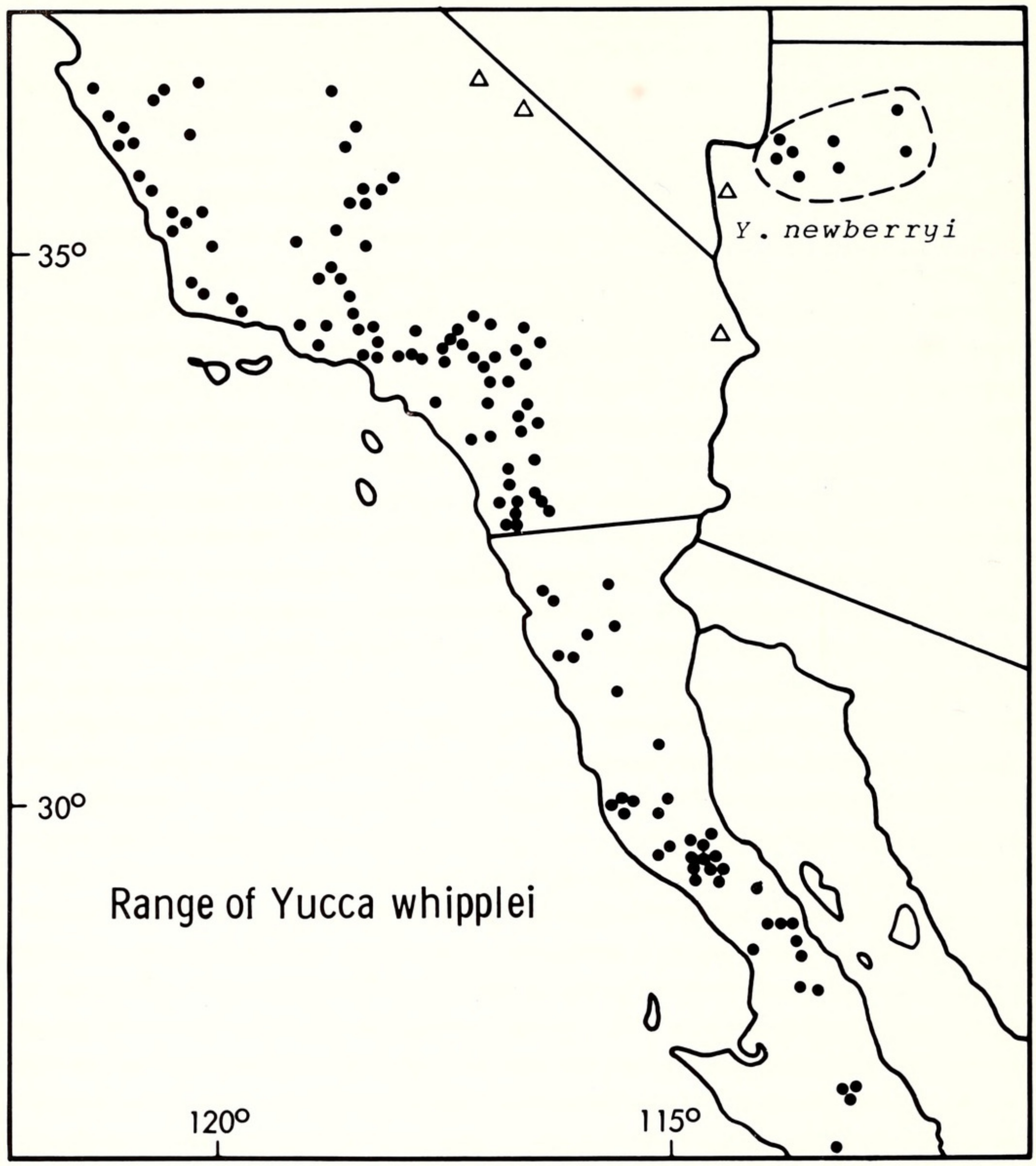

FIG. 3. Distribution of yuccas of the *Yucca whipplei* group (sect. *Hesperoyucca*). Modern records of *Y. whipplei* are in southern California and Baja California; the closely related (if not conspecific) *Y. newberryi* is restricted to northwestern Arizona; documented occurrences indicated by dots (after McKelvey 1938, Hastings et al. 1972). Late Pleistocene macrofossil records of yuccas with the highly distinctive leaf morphology of the *Yucca whipplei* group are indicated by "△"; occurrences at very low elevations indicate continuity of range then.

under mean annual precipitation of 200 mm or more (Beeson 1974). Today, much of Death Valley below 775 m receives 75–100 mm or less of precipitation per year; and there are frequent years with 25 mm or less. The late Pleistocene (13,060 yr BP) record of juniper woodland at 775 m in Death Valley suggests that the precipitation then was about twofold greater than today and probably less variable.

The late-Pleistocene climate was undoubtedly cooler than today; but limits to cooling are set by the pleniglacial (19,500 yr BP) dominance of *Yucca whipplei* at the lowest site (425 m) and late-glacial (11,600 yr BP) occurrences of the same yucca as high as 1280 m. At present, *Y. whipplei* appears to be absent in the Death Valley region, despite a large available elevational gradient of over 3000 m on the adjacent Panamint Range (Telescope Peak: 3368 m). It is now widely distributed in chaparral vegetation under the mild, Mediterranean isoclime (winter rain, summer drought) of cis-montane California. But *Y. whipplei* (the polycarpic subsp. *caespitosa*) extends to the extreme western margins of the Mohave Desert, where there is a transition from woodland/chaparral to high desert under a similar climatic rhythm (Fig. 3). It (chiefly as the polycarpic subsp. *eremica*) occurs also in the relatively cool, foggy desert of northern Baja California.

There is one outstanding exception to this restriction of *Y. whipplei* to the Mediterranean isoclime of the Pacific slope: an aberrant, widely disjunct population in the lower, western end of the Grand Canyon, Arizona under a hot-desert climate (Fig. 3). It differs in having reduced placental wings and has been regarded as a distinct species, *Y. newberryi* McKelvey. Furthermore, the Grand Canyon population appears to be entirely monocarpic (McKelvey 1938). The low-elevation *Neotoma* records from Death Valley and the lower Colorado River valley (Wells and Hunziker 1976) document a much wider and more continuous distribution of yuccas of *Y. whipplei* affinity (*Hesperoyucca*) as recently as the last (Wisconsinan) glacial of the Pleistocene (Fig. 3). The climatic characteristics of regions with modern populations of *Yucca whipplei* include very mild winter temperatures and substantial winter rain; and for most populations, summer temperatures are only mildly hot (relative to Death Valley).

Thus, the abundance of *Y. whipplei* under a full-glacial (19,500 yr BP) climate in Death Valley is an indication of cool but relatively mild winters then, coupled with greater precipitation; summers were almost certainly cooler then. A cold, dry pleniglacial climate (Brakenridge 1978) in Death Valley, cold enough to account for juniper woodland 1200–1500 m below its present lower limits, would have been too cold for *Yucca whipplei.* A cool and equable, pleniglacial climate (Wells 1979) with greater precipitation better explains the present evidence. *Yucca whipplei* may have disappeared in the Death Valley region because montane elevations moist enough for its survival are too cold in winter; and the area of mild winter climate near the valley floor now becomes too hot and dry in summer.

At the close of the last (Wisconsinan) glacial, the climate of Death Valley suffered a drastic but gradual decline in equability and precipitation during the interval 11,000–9000 yr BP, giving rise to the extremely hot summers and limited precipitation of the modern desert. The macrofossil evidence indicates that the desertification process began on the floor of Death Valley (already a *Yucca* semidesert during the last glacial) and spread gradually up the slopes of adjacent mountains in the wake of the shrinking juniper and Joshua tree woodlands.

Acknowledgments

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Botanical Systematics Symposium

The Rancho Santa Ana Botanic Garden will sponsor and host a symposium on Trends in Systematic and Evolutionary Botany on 25–26 May 1985, at the Garden in Claremont, California. The purpose of this symposium is to examine current trends and, if possible, suggest and identify promising trends in systematic and evolutionary botany in the coming decade. Invited papers will be presented on pollination biology (H. Baker), chemical systematics (T. Swain), morphology (J. Skvarla), cladistics (M. Donoghue), physiological ecology (P. Rundel), aspects of modern floristics and traditional systematics (G. Prance), and research in botanical gardens (P. H. Raven). Low-cost housing will be available at nearby Pomona College. Attendance will be limited. For further information write: Systematics Symposium, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711.

This will be the first of an annual series of symposia planned at the Rancho Santa Ana Botanic Garden and is intended to provide a forum primarily for botanists in the southwestern United States and adjacent regions of Mexico.